

Functional Reorganization of Primary Somatosensory Cortex in Adult Owl Monkeys After Behaviorally Controlled Tactile Stimulation

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SUMMARY AND CONCLUSIONS

1. Multiple microelectrode maps of the hand representation within and across the borders of cortical area 3b were obtained before, immediately after, or several weeks after a period of behaviorally controlled hand use. Owl monkeys were conditioned in a task that produced cutaneous stimulation of a limited sector of skin on the distal phalanges of one or more fingers.

2. Analysis of microelectrode mapping experiment data revealed that 1) stimulated skin surfaces were represented over expanded cortical areas. 2) Most of the cutaneous receptive fields recorded within these expanded cortical representational zones were unusually small. 3) The internal topography of representation of the stimulated and immediately surrounding skin surfaces differed greatly from that recorded in control experiments. Representational discontinuities emerged in this map region, and "hypercolumn" distances in this map sector were grossly abnormal. 4) Borders between the representations of individual digits and digit segments commonly shifted. 5) The functionally defined rostral border of area 3b shifted farther rostralward, manifesting either an expansion of the cutaneous area 3b fingertip representation into cortical field 3a or an emergence of a cutaneous input zone in the caudal aspect of this normally predominantly deep-receptor representational field. 6) Significant lateralward translocations of the borders between the representations of the hand and face were recorded in all cases. 7) The absolute locations—and in some cases the areas or magnifications—of representations of many skin surfaces not directly involved in the trained behavior also changed significantly. However, the most striking areal, positional, and topographic changes were related to the representations of the behaviorally stimulated skin in every studied monkey.

3. These experiments demonstrate that functional cortical remodeling of the S1 koniocortical field, area 3b, results from behavioral manipulations in normal adult owl monkeys. We hypothesize that these studies manifest operation of the basic adaptive cortical process(es) underlying cortical contributions to perception and learning.

One consequence of these important studies has been the emergence of the general view that beyond a critical period(s) in development, the nervous system becomes a fixed system not amenable to structural or substantial functional changes in response to experience. That view is currently being challenged.

Neocortical representations of the body surface in adult primates reorganize in response to alterations in the patterns of activation of sensory elements within the skin. Several classes of surgical manipulations in the periphery have been used to produce altered patterns of sensory input. One group of recent experiments indicates that when a subset of these sensory elements is silenced by either restricted deafferentation or amputation, there is an extensive reorganization or "remapping" of the remaining active inputs (Kelahan and Doetsch 1984; Merzenich et al. 1983a,b, 1984b; Rasmusson 1982; Wall et al. 1984, 1986). In those studies, neurons everywhere across a large cortical region, including both the former zone of representation of the transected, nonregenerating nerve(s) and an extensive surrounding cortical zone, acquire new, effective excitatory afferent inputs. Several consistent features of this emergent representation of the skin have been observed. First, within these new maps, the internal topographic representations are usually orderly. Microelectrode penetration sequences across the horizontal dimension of the cortex commonly reveal a continuously shifting overlap of cutaneous receptive fields. Second, many of the newly emergent receptive fields do not overlap with receptive fields defined for neurons at those same locations before the peripheral deprivation. That is, some skin surfaces come to be overtly represented at entirely new cortical locations. Third, for some specific skin surfaces, the cortical territory of representation within the reorganized cortical zone is enlarged. Fourth, the relationship between the cortical area of representation and the size of receptive fields recorded for specific skin surfaces is roughly inverse. That is, as the cortical magnification increases for specific skin surfaces, those skin surfaces come to be represented in a finer grain.

A second related class of experiments has explored the consequences of plastic surgical manipulation of skin that greatly alters its spatiotemporal patterns of input (Clark et al. 1986, 1988). Normal behavioral uses of the hand produce substantially independent temporal and spatial patterns of activation of sensory primary afferents innervating adjacent fingers. Interestingly, borders between adjacent

INTRODUCTION

One of the key features of the study of behavior and its underlying neural mechanisms is an understanding of the dynamic properties of the nervous system that normally allow behavior to adapt in response to experience. Biologists and psychologists have long assumed that plasticity must be an inherent, lifelong property of the nervous system. A major research focus until recently has been on the role of early experience in the developing nervous system.

digits in the area 3b cortical representation of the hand in adult owl monkeys are normally very abrupt. As a rule, in this species, receptive fields for closely placed recording sites across digit representation borders are located on either one digit or another—but rarely on both—digits. When two digits are surgically fused to produce a “syndactyly” by a procedure that minimizes peripheral nerve damage, behavioral use of the hand produces now-synchronized patterns of activation within a large group of sensory afferents innervating both of the two fused digits. Apparently as a consequence, the normally abrupt representational border between these two digits is eliminated (Clark et al. 1988). In such monkeys, all neurons in a wide cortical band occupying approximately one-third of the cortical area within area 3b representing the two fused digits came to respond to stimulation of the skin on both digits.

Substantial alterations in the topographies of cortical representations are also observed after the transfer of an innervated patch of skin from one digit to another (Clark et al. 1986). In these “neurovascular island transfer” experiments, there is a novel temporal and spatial coactivation of the island skin with the newly surrounding skin. After such island transfers, novel RF’s are created that encompass both island skin and joined neighboring skin. In addition, new topographic relationships emerge in the cortical representation of the manipulated hand such that the overt representation of some skin surfaces are translocated within area 3b. More recently, island transfers spanning several intermediate digits indicate that reorganizational translocations are possible over 2- to 3-mm distances within cortical area 3b (Merzenich et al. 1988). In both the syndactyly and neurovascular island transfer studies, control experiments indicate that these effects are central in origin and not the result of peripheral nerve sprouting or mechanical coupling artifact.

We have suggested that the alterations of the mapped distributions of effective excitatory sensory inputs after these surgical manipulations provide strong evidence that cortical representational maps in adults are “use dependent” (Clark et al. 1988; Jenkins et al. 1987, 1990; Merzenich et al. 1983a–1984b; 1987; 1988). According to this view, thalamocortical and potentially corticocortical connections provide inputs from broader regions of the skin than is evident in the effective excitatory inputs defined by conventional extracellular electrophysiological recordings (see Merzenich et al. 1988; also see Garraghty and Sur 1987; Hicks and Dykes 1983; Snow et al. 1988; Zarzecki et al. 1982, 1983). Corticocortical connections also have extensive long-range focal collateralization both within and between the architectonic areas of primary somatic sensory cortex (De Felipe et al. 1986).

These and related studies in other sensory and motor cortical areas suggest that the effective excitatory inputs evident in the discharges of cortical neurons represent only a small functionally effective subset of inputs derived from a far larger, largely masked anatomic repertoire. An “input selection” or “input filtering” process presumably underlies receptive-field determination and the functional dynamism observed in cortical maps. The results of the surgical manipulations described above suggest that alterations in the temporal correlation and amounts of activity across

distributed inputs are critical factors in this input selection or input filtering process. By this view, an electrophysiologically derived cortical map of the skin surface can be thought to represent the cumulative effects of the history of behaviorally important spatiotemporal patterns of skin stimulation.

The present experiments were designed to test the reorganizational potential of cortical area 3b in normal adult owl monkeys. We used behavioral conditioning techniques to produce large amounts of tactile stimulation restricted to a limited patch of skin. Such restricted tactile stimulation is presumed to produce high activity levels in a subset of thalamocortical afferents extending across a cortical sector larger than the cortical region overtly representing this patch of skin before stimulation. Furthermore, the applied tactile stimulation would induce nearly synchronous activity across this limited afferent subset. At the same time, other thalamocortical afferents that derive their inputs from regions of the hand not engaged in the behavioral task would have relatively lower levels of activity. Activity-dependent temporal coactivation of afferents has previously been implicated in reorganization in retinotectal maps (e.g., Schmidt and Edwards 1983; Wilshaw and von der Malsburg 1975), has been argued to be the basis for ocular dominance column formation in visual cortex (Chapman et al. 1986; Reiter et al. 1986; Stryker et al. 1982, 1986a,b), and constitutes an integral property of several neural network models of cortical function (e.g., see Edelman et al. 1978, 1981, 1984; Frohn et al. 1987; Grajski 1989; Pearson et al. 1987; Singer 1985, 1987; Takeuchi and Amari 1979; von der Malsburg et al. 1973, 1982). As a consequence of such behaviorally controlled tactile stimulation, the quantities of synchronous or nearly synchronous neural activity in subpopulations of afferents terminating in the same cortical zone could be substantially altered. If the process(es) by which cortical receptive fields and the details of cortical topographic representations operate dynamically throughout life, then this behaviorally controlled differential stimulation should alter cortical-map topography in normal adult owl monkeys. That has been found to be the case.

Preliminary results from a part of this study have been reported previously (Jenkins et al. 1984, 1987; Merzenich et al. 1988).

METHODS

Surgical and recording procedures

These studies were conducted with six feral adult owl monkeys. Although their exact age was unknown, they were judged to be adult by their weights (~ 1 kg) and their full complement of adult dentition (Hershkovitz 1977). All animals were neurologically intact and had no previous experimental use.

In physiological studies, animals were initially anesthetized with halothane (1.5%) in a 75% NO_2 -25% O_2 gas mixture to allow for placement of a venous catheter. They were subsequently anesthetized with pentobarbital sodium (initial dose at 28 mg/kg iv) and maintained at a surgical level of anesthesia with iv supplementation. Heart rate and blood pressure were monitored. Lactated Ringer solution with 5% dextrose was given at the rate of ~ 2 ml/h, adjusted if indicated by cardiovascular system monitoring. Temperature was maintained at 38°C. The cortical mapping procedures employed in these studies have been described in several

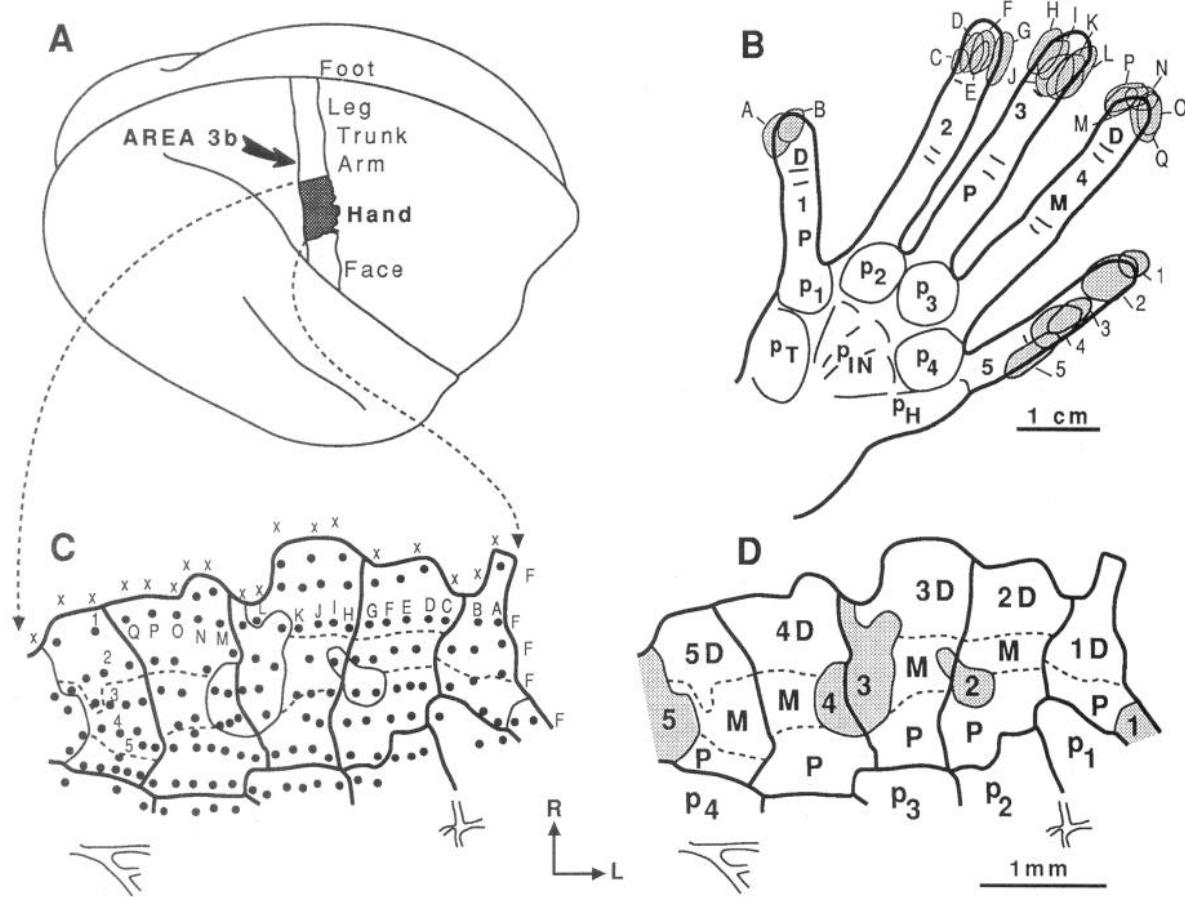


FIG. 1. Location and topographic representation of the hand within area 3b in a normal adult owl monkey. *A*: lateral view of the right neocortex. Approximate location of area 3b is outlined. Large cutaneous representation of the hand is indicated by stippling and is located medial to the representation of the face and lateral to that of the remainder of the body surface representation. *B*: outline of the glabrous hand surface in a normal adult owl monkey, with 2 typical sequences of receptive fields (from sites 1–5 and A–Q in *C*) drawn. Large numbers 1–5 denote the digits (e.g., 1 = thumb; D, M, and P are distal, middle, and proximal phalanges, respectively); p_{1-4} are the palmar pads at the base of the digits; p_H is the hypotenar eminence; p_T is the thenar eminence; and p_{IN} refers to the 3 insular pads. *C*: locations of 174 penetration sites from which the topographic representation of the hand surfaces shown in *D* were reconstructed. Numbers 1–5 and letters A–Q adjacent to penetration sites indicate locations at which the cutaneous receptive fields shown in *B* were obtained. Lines are boundaries between the territories of representation of different hand surfaces shown in *D*. Note that the map has been rotated 90° counterclockwise with respect to *A*. *D*: diagrammatic illustration of the representation of hand surfaces. Stippled zones indicate dorsal (hairy) skin on the digits. Solid lines outline territories of representation of the digits and palmar pads. Broken lines mark the borders between phalangeal representational zones. Distal digit tips are represented along the rostral margin of area 3b. More proximal portions of the digits and palm are represented at successively more caudal locations within area 3b.

earlier reports (Merzenich et al. 1983a,b, 1984b, 1987; Stryker et al. 1987). Briefly, the monkey was placed in a stereotaxic head holder and the hand representation zone in area 3b exposed by a parietal craniotomy and dural resection. A photograph of the brain surface vasculature was taken, and a 35–40 \times print made for siting microelectrode penetrations. The exposed cortex was bathed in a shallow well of sterile liquid silicone (dimethyl polysiloxane) throughout the course of the experiment.

Parylene C-coated tungsten electrodes with impedances of 1–2 M Ω at 1 kHz were used for recording neural responses. Electrode penetrations in each experiment were approximately normal to the cortical surface and were parallel to each other. Each electrode penetration site was marked on the brain photograph. Receptive fields were determined for neurons or small clusters of neurons in the middle cortical layers (\sim 600–1,000 μ m in depth) with the use of fine handheld blue glass probes to produce just-visible indentations of the skin. The tips of these probes were hemispherical in

shape with a diameter of \sim 0.5 mm. All fields were carefully drawn to scale on enlarged hand photographs. In exemplary fields, the field boundaries were also explored with the use of suprathreshold nylon monofilament von Frey hairs (Stoeling pressure aesthesiometer, No. 18011) that apply indenting stimuli at a relatively constant, predetermined force. The most commonly used von Frey hair was 0.2 mm diameter with a 0.5-g bending force and 15.92 g/mm 2 bending pressure.

In experiments in which two (and in 1 monkey, 3) maps were derived in the same animal, all but the final electrophysiological recordings were conducted with the use of strict sterile procedures. In these special preparations, the removed bone flap was refrigerated in sterile Ringer solution; at the end of these recording experiments, the dura was resutured and the bone flap replaced with the use of stainless steel sutures. Antibiotics were administered before and for several days after surgery as a prophylactic. Analgesics were administered through the brief recov-

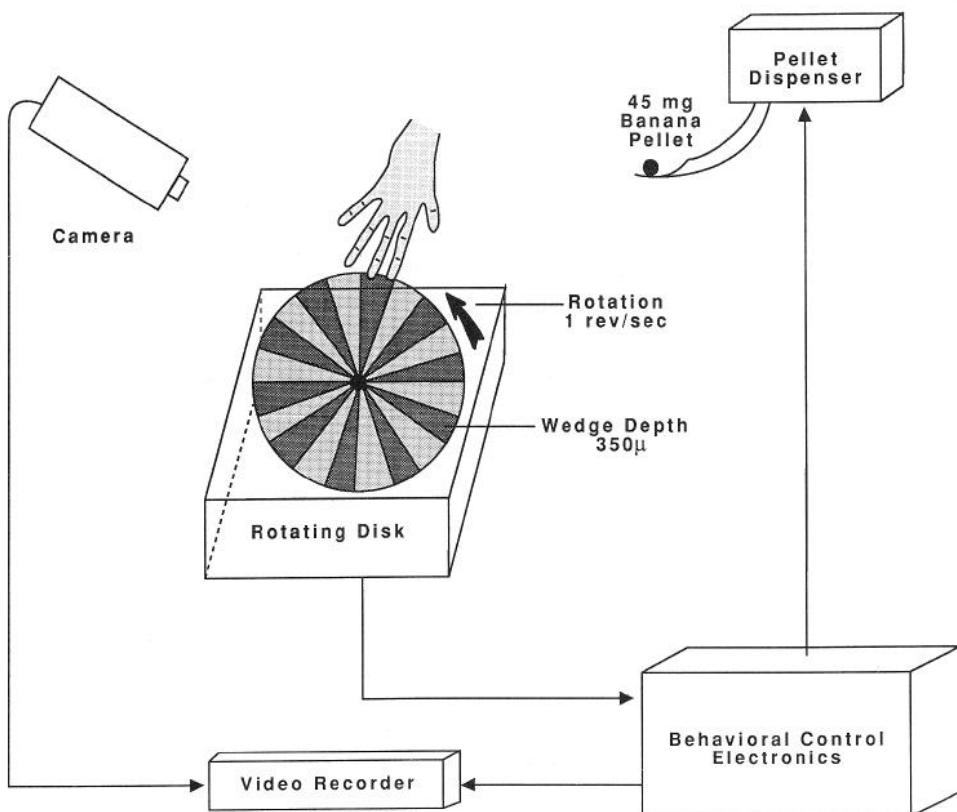


FIG. 2. Behavioral apparatus that required the monkey to maintain contact with a rotating stimulus disk for ~10–15 s per banana pellet reward. Only the distal aspect of the distal segment of ≥1 digits contacted the disk. Ten wedge-shaped grooves 350 μ m deep were machined into the metal disk. Disk, in most experiments, was continuously rotating at 1 rev/s, providing the contacted digital skin with edges moving across the digit at a rate of 20 Hz.

ery period. All procedures were conducted within an approved recovery surgical facility. Recovery was uneventful in every experimental case.

As has been noted in earlier studies (Merzenich et al. 1983a,b), the initial time-limited sterile mapping procedure had no obvious effect on the responsiveness of cortical neurons. No surface damage was seen at the time of the second exposure of the hand representation. Vascular details recorded in the initial procedure provided a clear reference in the second.

Data analysis

The details of construction of hand representation maps have been described elsewhere (Merzenich et al. 1987) and are described in RESULTS. Briefly, hand representation maps were drawn by outlining cortical areas over which receptive fields were centered over given skin surfaces. The delimiting lines in these maps were drawn between penetration sites with receptive fields centered on different labeled skin areas (see Fig. 1). Where receptive fields overlapped onto different skin surfaces, the line position was biased to reflect the extent of that overlap. The degree of error inherent in defining the representational areas was small (see Merzenich et al. 1987 and Stryker et al. 1987 for a discussion of the sources and dimensions of errors in mapping by the use of these procedures). The possible errors in the measurement of representational area associated with the spacing of the microelectrode grid were very small compared with the plasticity observed in this study (see Stryker et al. 1987).

In all cases except OM 2, one map was derived either before initiation of behavioral training or immediately after the behavior, and a second map was derived either immediately after the behavior or several weeks after cessation of the experimental behavioral task. Thus, in five monkeys, maps derived at these different times allow each animal to serve as its own control. All measurements of cortical area and receptive-field size were derived with use of a computerized planimeter.

Behavioral apparatus and procedures

The tactile stimulus delivery device illustrated in Fig. 2 consisted of a 12.8-cm-diam aluminum disk that had been machined to produce an alternating pattern of raised and lowered surfaces. The pattern consisted of 20 pie-shaped wedges that alternated in depth by 350 μ m. This disk was attached to a gear motor that was rotated at the rate of 1 rev/s. The disk and the motor were housed in a small metal enclosure from which a portion of the rotating disk protruded. The disk and motor were mounted in a frame on the animal's home cage that allowed for adjustments in the location of the disk relative to the front of the cage.

Animals were given free access to water and a vitamin C-enriched drink in their home cages. During extended periods of controlled tactile stimulation, food delivery was contingent on appropriate performance on the behavioral task. Initially, 24-h food-deprived monkeys were trained to make contact with the nonrotating aluminum disk. An electronic contact circuit between the disk and the animal's home cage allowed for the detection of finger contact with the disk, and brief contact resulted in the automated (Gerbands D-1) delivery of a 45-mg banana-flavored food pellet (Bio-Serv F0059). The pellets appeared in a small pellet chute (BRS/LVE RPC-001) mounted at the front of the cage on the left-hand side of the centrally located disk apparatus. Retrieval of the pellets occurred by use of one or both hands or, more commonly, by the monkey licking the pellet out of the chute while keeping the hand and arm extended toward the disk apparatus. The nutritional content of the food pellets was comparable with the primate chow fed to other monkeys in our colony. The contact duration necessary for the delivery of a food pellet was gradually increased to 15 s. At this point in training, the position of the disk was progressively moved farther away from the front of the cage until the monkey could only contact the disk surface with the tips of one or two of the longest digits. At this stage, the dc motor was switched on and the disk rotated at the rate of 1 rev/second. Because of the increased difficulty in main-

taining contact with the disk, the contact duration necessary for pellet delivery was reduced to ~ 1 s. The increased difficulty of this task was because of the fact that the animal had to regulate contact pressure to maintain reliable finger contact with the disk; and excessive finger pressure resulted in the digits being carried along the path of disk rotation and eventually breaking disk contact. Monkeys gradually learned to regulate contact pressure, and the minimum contact duration was gradually increased to 15 s once more. Naive monkeys were trained to the final behavioral contingencies over the course of ~ 10 days. The rotating disk was continuously available to the monkey and, therefore, allowed the animals to obtain as many pellets as they cared to work for. These procedures resulted in ~ 600 banana pellets being delivered within a 24-h period.

The total disk contact time and the total number of delivered banana pellets were recorded daily. The monkey's hand contact was also videotaped during periods of disk contact. Analysis of the videotape recordings revealed that all of these monkeys used a single hand exclusively in this behavioral task. After the first few days, for each individual monkey, the motor patterns and skin surfaces stimulated during disk contact appeared the same throughout the course of behaviorally controlled tactile stimulation.

In two cases, a smooth, nonrotating disk was substituted for the wedge-patterned rotating disk over one training period. All other behavioral contingencies were identical for these monkeys.

RESULTS

Before describing the topographic representations of the surfaces of the hands in experimental cases, it is useful to review briefly the normal pattern of representation of the hand in area 3b in adult owl monkeys. Figure 1 illustrates the results of a typical area 3b mapping experiment from a normal (preexperimental behavior) adult owl monkey. A lateral view of the neocortex illustrating the location of area 3b within anterior parietal cortex in this monkey is shown in Fig. 1A. The location of the large cutaneous representation of the hand within this cortical area is indicated by stippling; it is located medial to the zone of representation of the face and lateral to the representation of the remainder of the body surface representation. The typical microelectrode map of the zone of representation of the fingers in cortical area 3b derived in this adult owl monkey is illustrated at the bottom of Fig. 1. At the left (C), parallel microelectrode penetration sites within the hand representation of area 3b are indicated by filled dots; penetrations across the rostral border of the cutaneous representation, in which neurons are driven only by higher threshold tactile stimulation and joint manipulation, are marked by Xs. In penetrations marked by Fs, receptive fields were exclusively on the skin surfaces of the face. Two typical sequences of glabrous receptive fields defined for neurons in the middle cortical layers at a series of cortical sites are shown in Fig. 1B. They illustrate the normal, orderly shifting-overlap topography of receptive-field sequences defined within closely spaced rows of penetrations across area 3b. Note that in lateral-to-medial penetration sequences (A-Q in Fig. 1, B and C), there was an orderly progression of cutaneous receptive-field locations across the radial-to-ulnar (1st digit-to-4th digit) surfaces of the hand digits. In rostral-to-caudal sequences, receptive fields shift in an orderly sequence from distal to proximal along the digits (in this example, down digit 5). Glabrous digit tips are repre-

sented along the extreme rostral border of area 3b in this monkey; the remainder of the digits are represented more caudally.

The borders defined between the cortical representation of adjacent digits were always sharp. With few exceptions, receptive fields defined for neurons flanking these representational discontinuities had receptive fields exclusively on the skin of one of the two adjacent digits. A similarly sharp functional boundary was defined between the representation of the radialmost surfaces of the hand and the face and between the cutaneous and higher threshold representations within cortical areas 3b and 3a, respectively. Again, all along these borders, receptive fields exclusively represented skin of either the hand or the face or were driven selectively by light tactile or by high threshold "deep" inputs, respectively. A topographic representation of these data is shown in Fig. 1D. Boundaries between areas 3b and 3a are drawn midway between penetrations in which cutaneous receptive fields were defined and penetrations at which only higher threshold, noncutaneous stimuli evoked neural activity. These high-threshold sites were defined by manual manipulation (to provide an adequate stimulus for joint or muscle afferents) or by vigorous tapping. At a small number of penetration sites rostral to the cutaneous area 3b representation, not even very vigorously applied stimuli evoked neural activity. These fields were interspersed with the deep response fields of functionally defined field 3a and hence were included within it in the following drawings.

In contrast to functional discontinuities observed between adjacent digits, receptive fields continuously shifted down the long axes of digits and across most of the representation of the palm. In the topographic drawing in Fig. 1D, boundaries between zones of representation of digit segments or palmar surfaces mark the lines over which equal parts of receptive fields fell on the two adjacent skin surfaces.

The observed cortical representation of the hand dorsum is indicated by stippling in the reconstructed map of the hand illustrated in Fig. 1D. These small islands of dorsum representation were embedded in the larger representation of glabrous digital skin surfaces. The representation of dorsal digits in this hand map was fragmented and incomplete, as is often the case (see Merzenich et al. 1987).

The hand representations within area 3b defined in all normal mapping experiments in this, as in earlier studies (Kaas et al. 1984; Merzenich et al. 1978, 1983a,b, 1987), share several common features. 1) There was a single, complete representation of the glabrous hand surface in area 3b. 2) The most distal aspects of the digits (the skin under the projecting fingernails) were represented along or near the functionally defined 3b-3a (cutaneous-deep) border. 3) The more proximal digit skin surfaces were represented in topographic sequence in progressively more caudal portions of area 3b. 4) The radial aspect of the hand (e.g., *digit 1*) was represented in the lateral part of the hand representation adjacent to the representation of the face. 5) The more ulnar aspects of the hand were represented in topographic order in progressively more medial parts of area 3b. 6) The cortical area devoted to the representation of each distal phalanx was always greater than the cortical

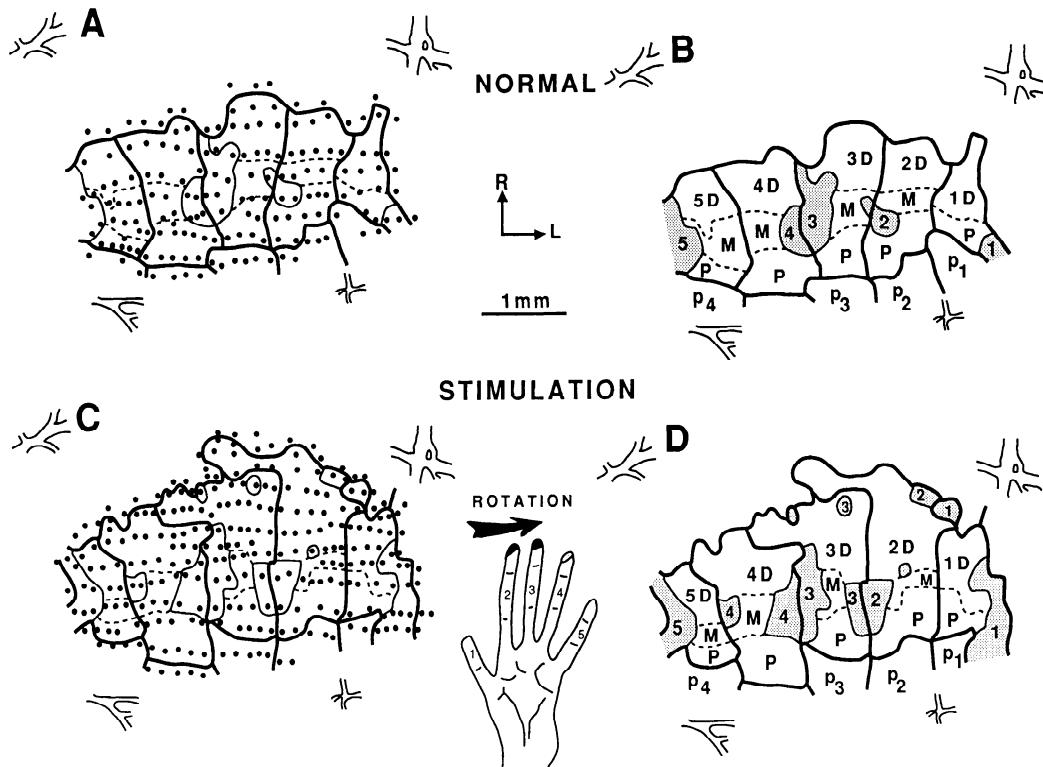


FIG. 3. *A*: penetration grid in and across the borders of the hand representation within area 3b in a normal adult owl monkey. *B*: reconstruction of the hand representation in area 3b for *OM 1* before differential stimulation. Map labels as in Fig. 1. *C*: penetration grid for a mapping experiment conducted 109 days after daily differential stimulation on the rotating disk, totaling ~ 1.5 h/day. *D*: poststimulation reconstruction of the hand representation. Skin surfaces differentially stimulated during the disk contact behavior are indicated in black on the hand inset at the bottom center. Skin surfaces on the tips of digits 2 and 3 and occasionally the tip of digit 4 were stimulated in the behavior in this monkey. Cortical representation of the stimulated skin surfaces expanded greatly in all such experiments (compare the distal aspects of digits 2, 3, and 4 in *B* and *D*).

area of representation of either the middle or proximal phalanx. 7) The internal topographic order was maintained throughout the field, with very few receptive fields out of topographic sequence. 8) The dorsal surfaces of *digit 1* were represented in the most lateral aspect of these maps and the dorsum of *digit 5* along the medial aspect of the glabrous representation. 9) These and other dorsal skin surfaces were represented in a number of small, fragmented, discontinuous patches embedded in a much larger glabrous digital skin representation. 10) The functionally defined borders within the cortical representation between adjacent digits were always sharp.

Reorganization of cortical representations after differential stimulation of restricted skin surfaces

The principal results recorded in this experimental series were that 1) differentially stimulated skin surfaces had expanded cortical representations; 2) the observed cutaneous receptive fields within these expanded cortical representational zones were often unusually small; 3) the details of topographic representation of digit tips and subjacent skin on the proximal aspect of the distal phalanx and on the middle phalanx of differentially stimulated digits were unusual, with abnormal receptive-field overlap distances and with breaks in topography; 4) there were unequivocal shifts in the representational borders between individual digits

and digit segments; 5) there were shifts in the functionally defined rostral 3b-3a (cutaneous-deep) border, reflecting an apparent expansion of the cutaneous hand representation; 6) there were shifts in the borders between the representations of the hand and face, or between the representations of *digit 5* dorsum and glabrous skin, consistent with an overall expansion of the territory of cortex occupied by the representation of the digits; and 7) there were substantial differences in representation of skin surfaces not directly involved in the behavior.

ENLARGEMENT OF THE CORTICAL REPRESENTATION OF STIMULATED SKIN. The results of two detailed microelectrode mapping experiments conducted before and immediately after differential tactile stimulation for *OM 1* are shown in Fig. 3. The locations of the 176 electrode penetration sites within and across the borders of the hand representation for this normal adult owl monkey before differential stimulation are shown in Fig. 3*A*. The overlying solid and dashed lines define the various borders between the zones of representation of specific skin surfaces. A reconstruction of the hand representation within area 3b from this normal adult owl monkey is shown in Fig. 3*B*. Note that the areal extents of cortical representation of the distal phalanges (labeled 1–5d) are of similar size. The cortical area representing the individual distal phalanges ranged from 0.28 to 0.48 mm² (also see Table 1).

TABLE 1. *Cortical areas and receptive field sizes*

Cortical Area, mm ²					Receptive Field, mm ²				
Digit 1	Digit 2	Digit 3	Digit 4	Digit 5	Digit 1	Digit 2	Digit 3	Digit 4	Digit 5
<i>OM 1</i>									
<i>No disk experience; map 1</i>									
0.28	0.32	0.48	0.42	0.29	8.478 ± 3.598	7.345 ± 2.16	11.531 ± 4.234	8.658 ± 2.416	6.171 ± 2.519
<i>After 109 days of rotating disk; map 2</i>									
0.36	0.92	0.64	0.53	0.23	6.894 ± 2.515	4.676 ± 2.181	4.995 ± 3.09	9.379 ± 6.107	6.654 ± 2.976
<i>Map 2 as a percentage of map 1</i>					<i>p</i>				
129	288	133	126	79	0.2626	0.0041	0.0001	0.7099	0.8609
<i>OM 3</i>									
<i>After 52 days of rotating disk; map 1</i>									
0.56	0.69	1.24	0.67	0.40	19.595 ± 6.267	16.012 ± 8.908	8.981 ± 4.585	7.545 ± 4.031	14.562 ± 5.787
<i>80 days after terminating rotating disk; map 2</i>									
0.62	0.67	0.71	0.66	0.44	13.665 ± 4.056	12.509 ± 7.989	11.217 ± 4.451	13.165 ± 4.786	11.659 ± 5.176
<i>Map 1 as a percentage of map 2</i>					<i>p</i>				
90	103	175	102	91	0.0016	0.1028	0.0526	0.0001	0.2198
<i>OM 4</i>									
<i>After 103 days of rotating disk; map 1</i>									
0.46	0.60	1.03	0.66	0.36	7.961 ± 5.323	8.381 ± 4.166	6.866 ± 5.744	10.345 ± 5.107	10.058 ± 2.841
<i>31 days after terminating rotating disk; map 2</i>									
0.48	0.58	0.38	0.51	0.33	10.085 ± 5.321	7.68 ± 4.71	8.781 ± 2.96	11.527 ± 7.776	5.849 ± 2.626
<i>Map 1 as a percentage of map 2</i>					<i>p</i>				
96	103	271	129	109	0.2677	0.588	0.2394	0.5478	0.0049
<i>OM 5</i>									
<i>No disk experience; map 1</i>									
0.44	0.41	0.43	0.43	n.a.	7.578 ± 3.129	6.941 ± 2.231	8.369 ± 3.318	8.573 ± 2.956	
<i>After 74 days of static flat disk; map 2</i>									
0.28	0.39	0.49	0.29	n.a.	6.404 ± 1.538	7.942 ± 3.37	6.953 ± 4.676	11.008 ± 8.084	
<i>Map 2 as a percentage of map 1</i>					<i>p Map 1 vs. map 2</i>				
64	95	114	67	n.a.	0.2747	0.2418	0.2541	0.3251	
<i>After 278 days of rotating disk; map 3</i>									
n.a.	n.a.	0.77	0.47	n.a.	n.a.	6.949 ± 2.703	6.2 ± 3.079	5.912 ± 2.405	n.a.
<i>Map 3 as a percentage of map 1</i>					<i>p Map 1 vs. map 3</i>				
n.a.	n.a.	179	109	n.a.	n.a.	0.9918	0.0165	0.0046	n.a.

TABLE 1. (Continued)

Cortical Area, mm ²					Receptive Field, mm ²				
Digit 1	Digit 2	Digit 3	Digit 4	Digit 5	Digit 1	Digit 2	Digit 3	Digit 4	Digit 5
<i>OM 6</i>									
<i>After 580 days of rotating disk; map 1</i>									
0.53	0.90	1.22	0.41	0.32	8.318 ± 3.843	5.352 ± 3.54	3.806 ± 1.545	7.869 ± 4.628	11.552 ± 3.447
<i>63 days after terminating rotating disk; map 2</i>									
0.43	0.60	0.54	0.78	0.24	10.254 ± 5.73	11.675 ± 6.559	13.954 ± 5.924	11.971 ± 4.369	8.763 ± 2.37
Map 1 as a percentage of map 2					<i>p</i>				
123	150	226	53	133	0.3086	0.0001	0.0001	0.0135	0.0656

Values for receptive field are means ± SD. n.a., not applicable. Analysis of variance procedures were used to calculate *p* values.

The skin surfaces stimulated during 109 days of daily differential stimulation on the rotating disk lasting ~1.5 h/day are indicated in black on the hand *inset* (*bottom center*). Analysis of the videotapes obtained during disk contact indicates that the distal radial glabrous aspect of the distal phalanx of *digit 2* was always stimulated by the rotating disk. The distal glabrous aspect of the distal phalanx of *digit 3* was stimulated >50% of the time. The stippled skin surface on the distal phalanx of *digit 4* was stimulated <20% of the time. No other skin surfaces were directly stimulated during disk contact.

The penetration grid consisting of 264 recording sites for the mapping experiment conducted immediately after 109 days of daily differential stimulation on the rotating disk lasting ~1.5 h/day is shown in Fig. 3C. A reconstruction of the hand representation from this normal adult owl monkey after differential stimulation, principally of the distal aspect of *digit 2*, is shown in Fig. 3D. Note that the representations of the distal phalanges are no longer of similar size. The areal extents of cortical representation of the distal phalanges (labeled 1–5d) in this poststimulation map ranged from 0.23 to 0.92 mm². The largest absolute change in cortical representational area occurred for the most heavily stimulated (and 1st-stimulated) phalanx. Within area 3b, before tactile stimulation, the glabrous distal phalanx of *digit 2* was exclusively represented within a 0.32-mm² cortical zone; and, immediately after 109 days of tactile stimulation, it was represented within a 0.92-mm² cortical zone. This represents nearly a threefold increase in the cortical area representing the glabrous surface of this phalanx. Less striking changes in cortical representational area were seen for the other differentially stimulated skin surfaces. There was ~33% increase in the representational area of the distal phalanx of *digit 3*, and ~25% increase in the representational area of the distal phalanx of *digit 4*.

Reconstructions of area 3b hand representations for cases *OM 3*, *4*, *5*, and *6* are shown in Figs. 4 and 5. For cases *OM 3*, *4*, and *6*, the first electrophysiological mapping experiments were conducted immediately after a period of behaviorally controlled disk stimulation. The hand *inset* for each case indicates the approximate skin surface stimu-

lated by disk contact. For cases *OM 3*, *4*, and *6*, a second mapping experiment was conducted after several weeks during which time there was no access to disk stimulation. *OM 5* was mapped before initiation of the behavioral task (Figure 5, *top left*) and again after several weeks of behaviorally controlled stimulation with a rotating disk (Figure 5, *bottom left*). In each case, the representational zone of the stimulated skin surfaces was greater immediately after controlled stimulation with the rotating disk as compared with the control maps. For each case, there was a distal phalanx on one digit that was always stimulated during disk contact. For those phalanges, the area of representation was 1.76–2.71 times larger than the area of representation observed in the control mapping experiments (see Table 1 for a summary).

An additional experiment was conducted in *OM 5* and *OM 2*. In these two cases, a nonrotating flat disk was substituted for the usual disk. All behavioral procedures were identical to those employed with the grooved rotating disk. Unlike the task with the rotating disk, no regulation of contact force was necessary for successful completion of a rewarded sequence, nor was there repetitive tactile stimulation during disk contact. Comparisons between the normal map and the map obtained immediately after several weeks of experience indicate little change in the areas of representation for the skin surfaces that contacted the static disk (for *OM 5* see Fig. 5 *top and middle left*). For *OM 5*, *digit 2* and *3* distal phalanges were 0.95 and 1.13 times normal, respectively. For *OM 2*, a mapping experiment was conducted only after disk training, because this animal did not recover from surgery, which was complicated by an undiagnosed chronic glomerulonephritis of unknown etiology. The results from this single mapping experiment did not suggest any unusual representational topography or differential enlargement of the behaviorally engaged skin surfaces.

CORTICAL MAGNIFICATION AS AN INDEX OF REPRESENTATIONAL CHANGE. One method of comparing the relative sizes of cortical representations is by calculating a “cortical magnification” factor. Cortical magnification is defined as

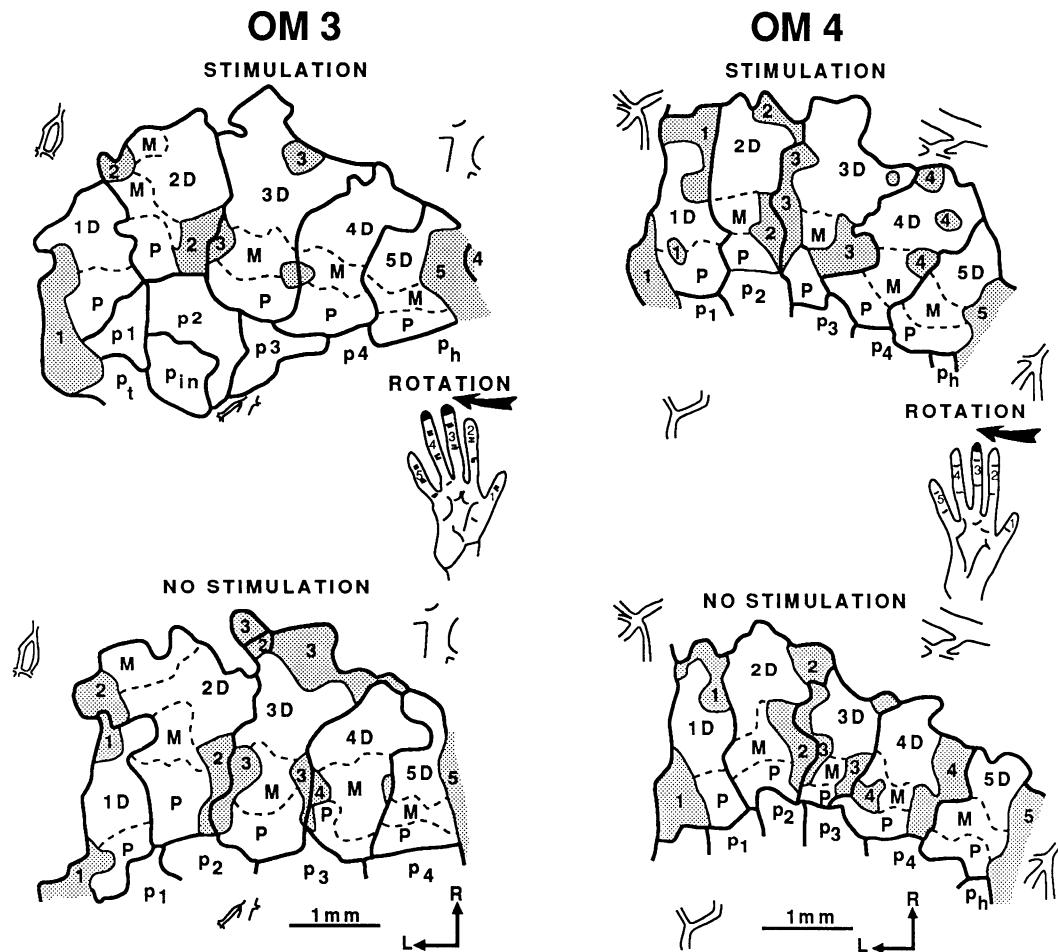


FIG. 4. Reconstructions of the hand representation for *OM 3* and *OM 4* immediately after differential stimulation with a rotating disk (*top*) and after 80 and 31 subsequent days without differential stimulation, respectively (*bottom*). Locations of the skin surfaces stimulated during disk contact are indicated in black on the hand figurines. Note that the cortical representations of the stimulated distal phalanges of *digit 3* in *OM 3* occupied a larger cortical area immediately after disk stimulation (*top left*) as compared with the map obtained 80 days later (*bottom left*). Similarly, the cortical representation of the stimulated distal phalanx of *digit 3* in *OM 4* occupied a larger cortical area immediately after disk stimulation (*top right*) as compared to the map obtained 31 days later (*bottom right*).

the cortical area of representation divided by the skin surface area. That is, cortical magnification is the proportional quantity defined as cortical area per unit hand-surface area. For the present purpose, we have calculated the cortical magnification factor of each phalanx by the use of the cortical areas of representation defined in normal- and differential-stimulation mapping experiments. Areal estimates of various skin surfaces were obtained from reconstructions based on multiple-perspective photographs of the hand (also see Sur et al. 1980). These cortical magnification factors for *OM 1* are depicted in Fig. 6, *top*, and for *OM 6* in Fig. 6, *bottom*. A linear transformation of cortical magnification factors (i.e., $\times 10^3$) was performed to facilitate ordinate labeling. The open symbols depict the cortical magnification factors for the glabrous phalanges on the basis of the cortical areas of representation defined in the "normal" mapping experiment (*OM 1*) or after a period of no stimulation (*OM 6*). The closed symbols depict the cortical magnification factors obtained on the basis of the poststimulation mapping experiments. Note that, for *OM 1* (Fig. 6, *top*), there has been a substantial increase in the

cortical magnification factor for the distal phalanx of *digit 2*; progressively smaller increases were found for the distal phalanges of *digits 3* and *4*. Similar results were seen in *OM 6* (Fig. 6, *bottom*) and in all other cases immediately after behaviorally controlled stimulation with the rotating disk. Note also that, in these mapping experiments, little change in cortical magnification was observed for the representations of any other phalanges.

CHANGES IN RECEPTIVE-FIELD SIZES. In addition to the observed expanded cortical representation of the differentially stimulated skin, the cutaneous receptive fields within these cortical zones of representation were often unusually small. All of the defined glabrous cutaneous receptive fields located on the distal digit phalanges from two mapping experiments for *OM 1* are illustrated in Fig. 7. In the normal mapping experiment, the size of distal phalangeal receptive fields (Fig. 7, *top*) were not significantly different across digits [$F(4, 38) = 1.875, P = 0.1349$]. The mean receptive-field area on individual phalanges ranged from 7.3 to 11.5 mm^2 .

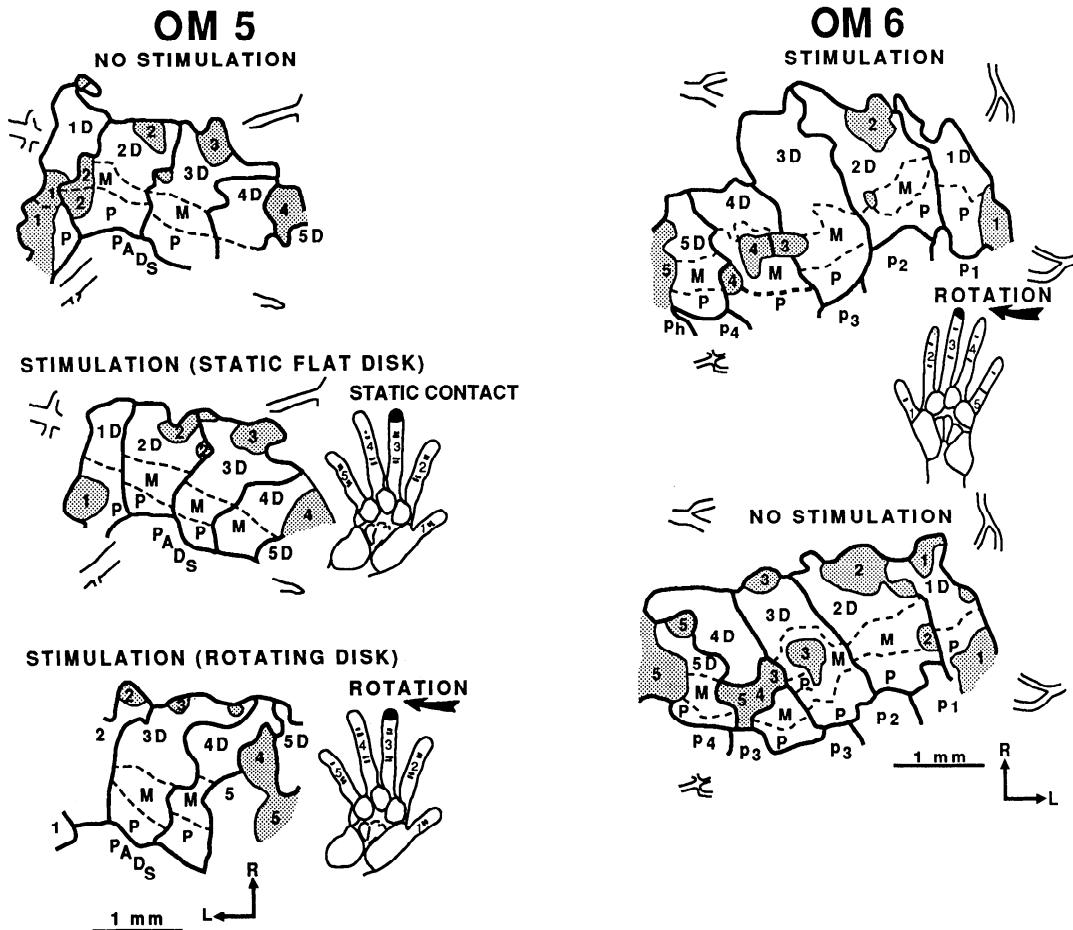


FIG. 5. Reconstruction of the hand representation within area 3b for *OM 5* is illustrated on the left before behavioral training (top), immediately after behaviorally controlled stimulation with the use of a static flat disk (center), and immediately after differential stimulation with a rotating disk (bottom). Hand representation within area 3b for *OM 6* is illustrated on the right immediately after differential stimulation with a rotating disk (top) and 63 days later (bottom). For each of the stimulation experiments, the location of the skin surfaces consistently stimulated during disk contact are indicated in black and by stippling for occasional disk contact on the hand figurines. Note that, for both cases, the cortical representation of the stimulated distal phalanx of *digit 3* occupied a larger cortical area immediately after disk stimulation as compared with the representation defined either before stimulation (*OM 5*) or that obtained 63 days later (*OM 6*). Note also that, after stimulation provided by the static flat disk, little obvious task-related alteration in the cortical representation of the hand was recorded.

Significant differences were observed in receptive-field sizes across the digits in the second mapping experiment [$F(4, 101) = 6.918, P < 0.0001$]. In the poststimulation mapping experiment, the distal phalangeal receptive fields were significantly smaller [$F(1, 104) = 22.95, P < 0.0001$] on the most heavily stimulated skin surfaces (*digits 2 and 3*; Fig. 7, *middle*). The mean receptive-field area on individual phalanges in this poststimulation mapping experiment ranged from 4.7 to 9.9 mm². Figure 7, *bottom*, is a histogram of the mean receptive-field area in square millimeters (bars indicate 1 SD). Receptive fields on the distal phalanges of *digits 2 and 3* were significantly smaller in the poststimulation map compared with the normal map for these two skin surfaces [*digit 2*, $F(1, 35) = 9.42, P < 0.005$; *digit 3*, $F(1, 44) = 32.54, P < 0.0001$]. In another case (*OM 5*) in which a normal and a poststimulation map were obtained, similar significant changes in receptive-field sizes were recorded. Receptive-field sizes on the other distal phalanges were not significantly different between the normal

and poststimulation mapping experiments in these two owl monkeys.

In other owl monkeys in which the poststimulation map was obtained first and a subsequent map was obtained several weeks after a period of no disk stimulation, similar changes in receptive-field sizes were seen, except for case *OM 4*. All glabrous receptive fields located on the distal phalanges obtained from the two mapping experiments for *OM 6* are depicted in Fig. 8. Immediately after disk stimulation (Fig. 8, *top*), significant differences were observed in receptive-field size across the distal phalanges [$F(4, 103) = 16.278, P < 0.0001$]. The distal phalangeal receptive fields were significantly smaller [$F(1, 106) = 33.578, P < 0.0001$] on the stimulated skin surfaces (*digits 2, 3, and 4*). The mean receptive-field area on individual distal phalanges in this poststimulation mapping experiment ranged from 3.8 to 11.6 mm². In the mapping experiment after a period of no disk stimulation (Fig. 8, *middle*), the sizes of distal phalangeal receptive fields were not significantly different

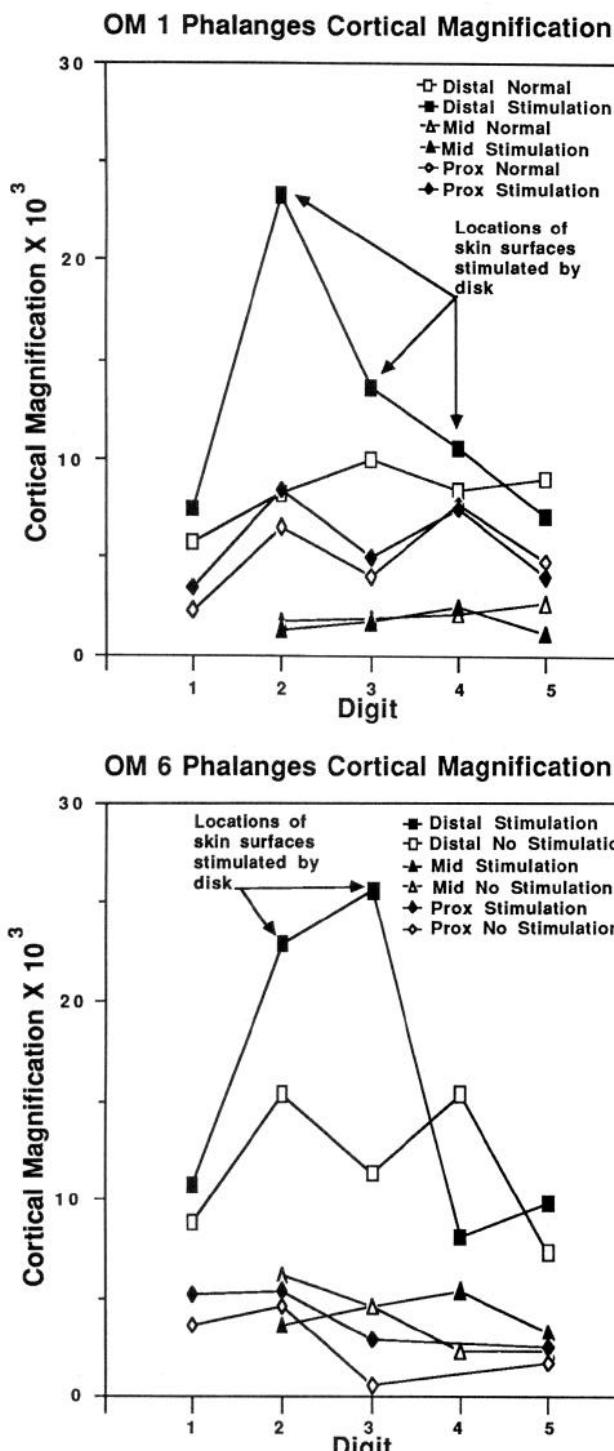


FIG. 6. Cortical magnification (cortical area of representation/skin surface area) $\times 1,000$ of the glabrous representation of all 5 digits for normal and poststimulation middle, distal, and proximal phalanges for OM 1 (top) and OM 6 (bottom). Note that the magnification of the representation of each phalangeal surface is relatively constant across the 5 fingers in both monkeys at these 2 stages of life, except for the striking increase in the magnification of representation of the stimulated phalanges. Arrows indicate the locations of skin surfaces stimulated by disk contact.

OM 1 RF SIZE ON DISTAL PHALANGES

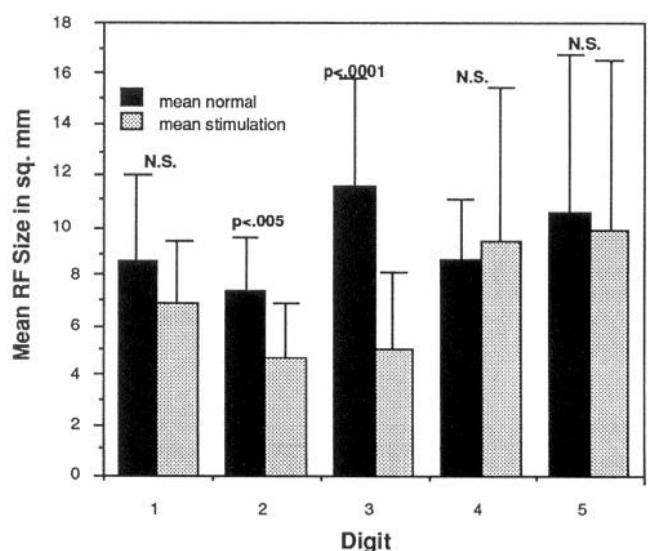
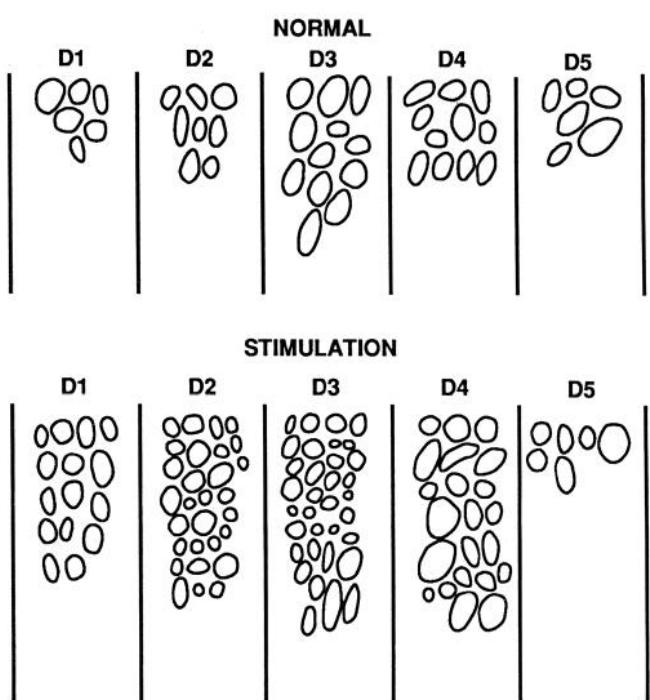


FIG. 7. Receptive fields from the distal phalanges of a normal monkey (OM 1) are outlined at the top (Normal). Receptive fields from the post-stimulation map are shown in the middle (Stimulation). Receptive fields from both experiments are drawn to the same scale. These data are summarized at the bottom, where the bars indicate mean receptive-field size in square millimeters in the normal map (black) and after differential stimulation (gray). Error bars indicate standard deviations. Receptive fields representing skin surfaces heavily engaged (distal phalanges on digits 2 and 3) in these differential stimulation behaviors in area 3b are significantly smaller [digit 2, $F(1, 35) = 9.416, P < 0.005$; digit 3, $F(1, 44) = 32.54, P < 0.001$] than those recorded in the same representational zones before the behavior.

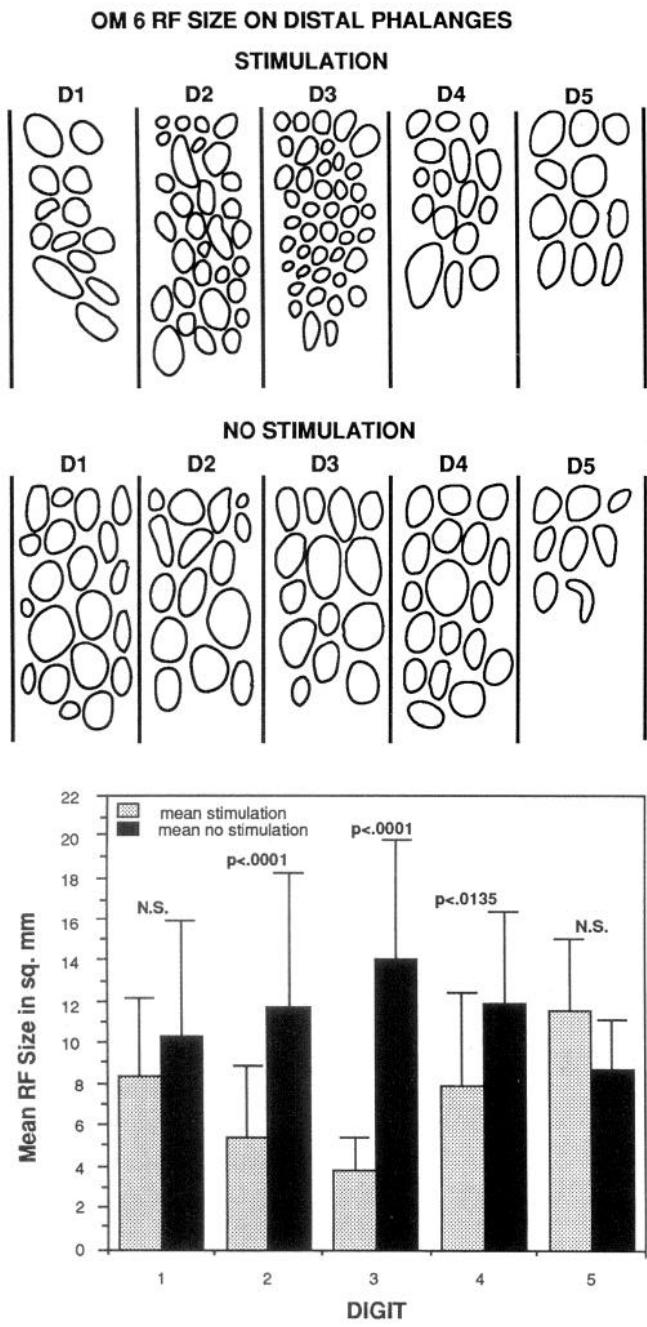


FIG. 8. Receptive fields from the distal phalanges of *OM 6* from the poststimulation map are outlined at the top (Stimulation). Receptive fields from a 2nd map, obtained after 63 days without disk stimulation, are outlined in the middle (No Stimulation). Receptive fields from both experiments are drawn to the same scale. These data are summarized at the bottom, where the bars indicate mean receptive-field size in square millimeters in the no-stimulation condition (black) and after differential stimulation (gray). Error bars indicate the standard deviation. Receptive fields in area 3b located on skin surfaces engaged in disk contact are significantly smaller [digit 2, $F(1, 42) = 17.413, P < 0.0001$; digit 3, $F(1, 52) = 101.113, P < 0.0001$; digit 4, $F(1, 31) = 6.861, P < 0.0136$] than those recorded after a period of no differential stimulation.

across digits [$F(4, 69) = 1.528, P = 0.2038$]. The mean receptive-field area on individual distal phalanges ranged from 8.8 to 13.9 mm². Figure 8, bottom, shows a histogram of the mean receptive-field area in square millimeters for

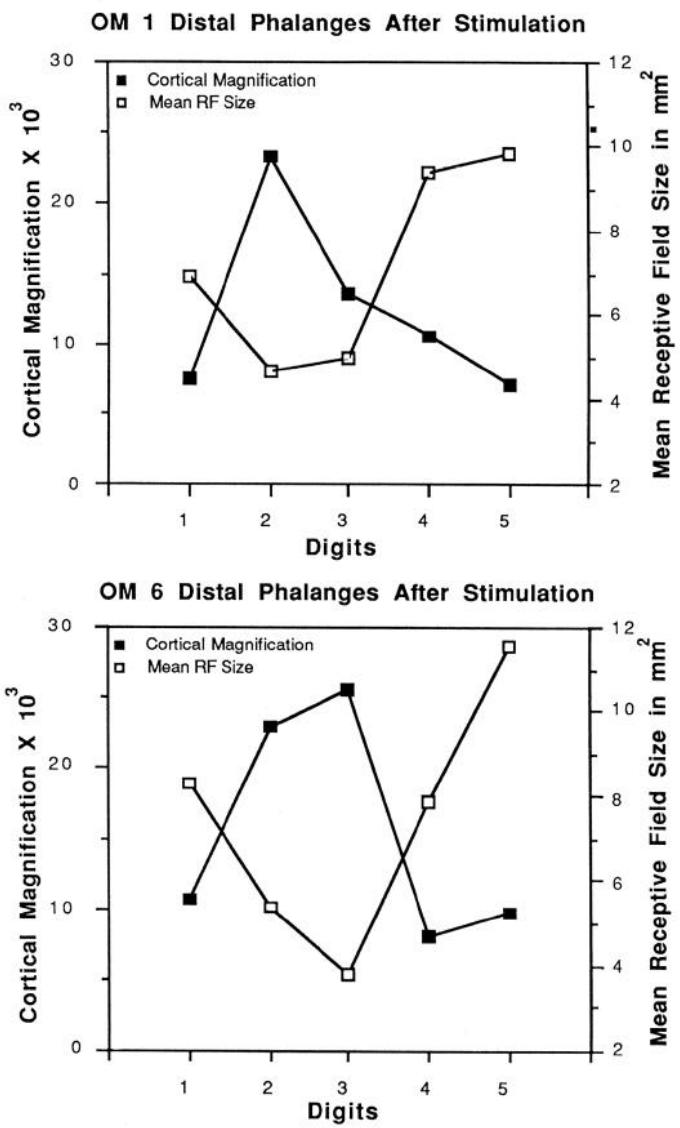


FIG. 9. Cortical magnification (black squares) for distal phalanges obtained after differential stimulation is plotted for *OM 1* (top) and *OM 6* (bottom; ordinate is on the left axis). Note that cortical magnification has been linearly transformed by a factor of 1,000. Mean receptive-field size in square millimeters plotted for these same skin surfaces obtained after differential stimulation is also plotted (ordinate on the right axis). It can be seen that in both exemplary cases these 2 functions are roughly inversely related. That is, as cortical representations of these struck surfaces expanded, they came to be represented in finer grain.

these two mapping experiments (bars indicate 1 SD). Receptive fields on the distal phalanges of digits 2, 3, and 4 were significantly smaller in the poststimulation map compared with the no-stimulation map [digit 2, $F(1, 42) = 17.413, P < 0.0001$; digit 3, $F(1, 52) = 101.113, P < 0.0001$; digit 4, $F(1, 31) = 6.861, P = 0.0135$]. In one case (*OM 4*), no significant differences in receptive-field sizes for the stimulated phalanges were seen when the poststimulation data was compared with the no-stimulation data. Perhaps this can be accounted for by the fact that the shortest interval between mapping experiments (31 days) occurred in this case. These data suggest that the cortical area of representation and receptive field size are not strictly coupled. Recall that substantial enlargements in cortical

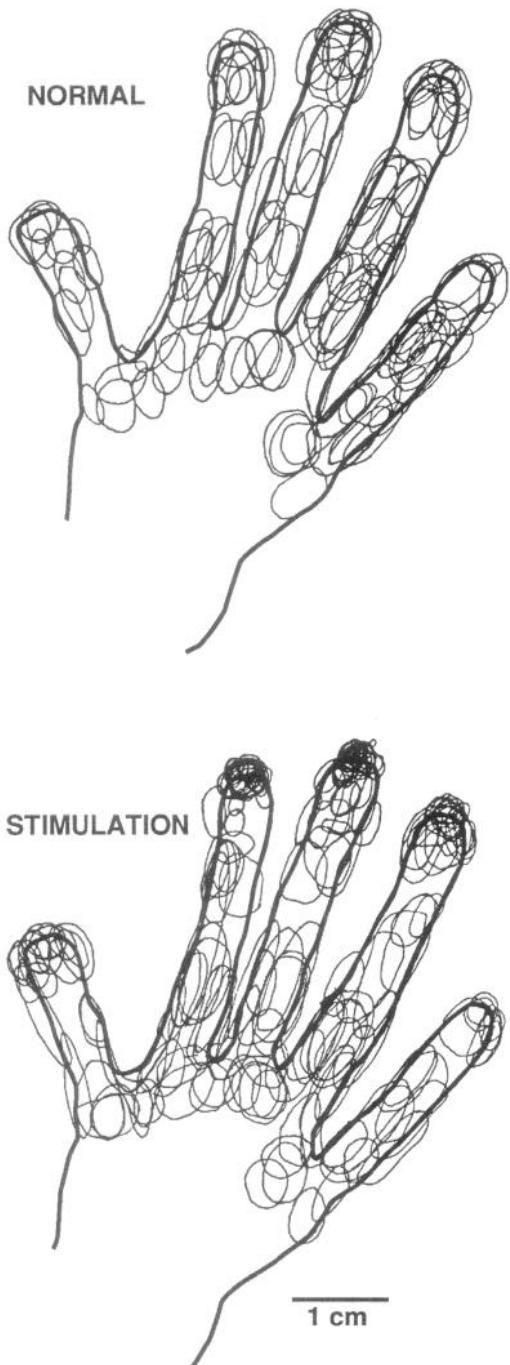


FIG. 10. All glabrous receptive fields identified for recording sites within area 3b for *OM 1* before differential stimulation (Normal, top) and after differential stimulation (Stimulation, bottom). Note the large number of receptive fields identified for skin locations (distal phalanges of digits 2, 3, and 4) stimulated during the trained behavior.

area of representation of the stimulated skin surfaces were observed for *OM 4* (see Fig. 4).

RELATIONSHIPS BETWEEN CORTICAL MAGNIFICATION AND RECEPTIVE-FIELD SIZE. It has previously been suggested that there is an inverse relationship between cortical magnification and receptive-field size within areas 3b and 1 (Sur et al. 1980). A rough inverse relationship between cortical magnification and receptive-field size on the distal

phalanges was observed in the poststimulation mapping experiment for *OM 1*. In Fig. 9 (top), the black squares indicate the cortical magnification (scale on the left ordinate), and the open squares indicate the mean receptive-field size (scale on the right ordinate) for each of the five distal phalanges. The distal phalanx (*digit 2*) with the largest cortical magnification (0.02337) had the smallest mean receptive-field size (4.676 mm^2). The distal phalanx (*digit 5*) with the smallest cortical magnification (0.00706) had the largest mean receptive-field size (9.852 mm^2). A similar relationship between cortical magnification and mean receptive-field size was also seen in *OM 5*. Recall that in this monkey, like *OM 1*, the poststimulation mapping experiment was preceded by a normal mapping experiment a number of weeks earlier.

The relationship between cortical magnification and mean receptive-field size in a second case (*OM 6*), in which the first mapping experiment was initiated after disk stimulation, is shown in Fig. 9 (bottom). Once again, it is clear that cortical magnification and mean receptive-field size are roughly inversely related. The distal phalanx on *digit 3* was always stimulated during disk contact. This distal phalanx had the largest cortical magnification (0.02562) and the smallest mean receptive-field size (3.806 mm^2). In two

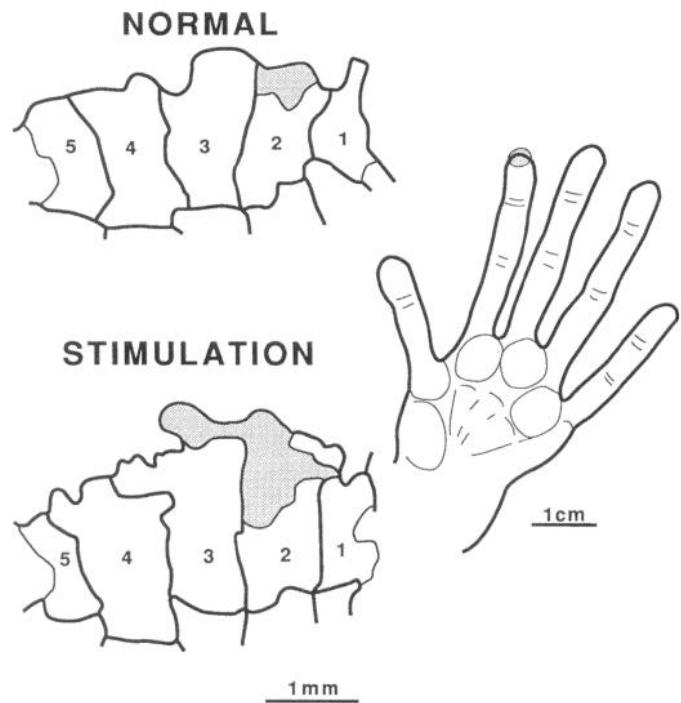


FIG. 11. Outlines of the area 3b cortical territories representing the surfaces of the digits for *OM 1* before differential stimulation (Normal, top) and after differential stimulation (Stimulation, bottom). Most of the differentially stimulated skin surface on *digit 2* is indicated by stippling in the hand drawing at the right. Zones of representation of the struck skin surface on the distal phalanx of *digit 2* are stippled in both drawings, i.e., in this zone, all defined receptive fields overlapped onto this heavily stimulated surface. Note that after a period of differential digit tip stimulation in this monkey—as in other monkeys studied with this paradigm—there was a substantial enlargement of its territory of representation. In this monkey, most of the gain in territory was from across the area 3b-3a border as defined functionally before the initiation of this digital stimulation behavior.

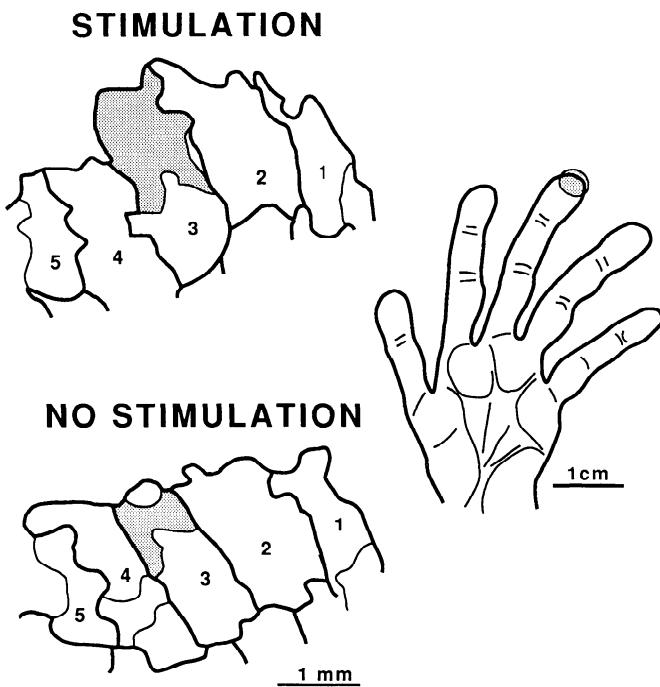


FIG. 12. Outlines of the area 3b cortical territories representing the surfaces of the digits for *OM 6* after differential stimulation (Stimulation, top) and long after differential stimulation (No Stimulation, bottom). Note that, after a period of differential digit tip stimulation in this monkey, there was a substantial enlargement of its territory of representation.

other cases (*OM 3* and *OM 4*) where the first map was obtained after disk stimulation, the largest cortical magnification and small mean receptive-field sizes were also seen for the stimulated skin surfaces. However, this relationship was not as striking as in other cases, and some exceptions were evident. Thus, for example, in *OM 3* where the distal phalanx of *digit 3* (it was always stimulated during disk contact) exhibited the largest cortical magnification, a slightly smaller mean receptive-field size was seen for the distal phalanx of *digit 4*, which was usually stimulated during disk contact.

STIMULATION SITE SPECIFICITY FOR OBSERVED CHANGES. Thus far, we have considered the effects of stimulation of individual distal phalanges on receptive-field sizes and cortical magnifications. The stimulated skin surface on *digit 2* in *OM 1* directly engages no more than ~20% of the surface of the phalanx. The question arises: is there a preferential enlargement of these limited stimulated skin surfaces within the cortical representational zone of the distal phalanx? The locations of all of the glabrous cutaneous receptive fields defined in the two mapping experiments are shown in Fig. 10. The receptive fields defined before differential stimulation were relatively uniformly distributed across each of the distal phalanges (Fig. 10, top). However, in the map obtained after differential stimulation, most of the receptive fields defined for the behaviorally engaged distal phalanges were centered over the stimulated skin surfaces (Fig. 10, bottom). This result is most apparent for *digit 2*, the most differentially stimulated digit, where 87% of the defined receptive fields included differentially stimulated skin. We have considered the possibility that this re-

sult might reflect a sampling bias in the location of the recording sites used to define the distal phalanges. However, in both mapping experiments, the locations of recording sites within the representational zone of each distal phalanx were evenly distributed spatially. Furthermore, the number of penetrations when corrected for distal phalanx representational area indicate that each distal phalanx in a given mapping experiment was defined by penetrations of similar density. For example, if we divide the cortical area of representation of each phalanx by the number of penetrations located within that zone, we have an index of mapping density. For the poststimulation mapping experiment, this resulted in 0.024, 0.030, 0.022, 0.024, and 0.033 mm²/penetration for digits 1–5, respectively (0.026 ± 0.0046, mean ± SD). Thus the large number of receptive fields on digits 2, 3, and 4, which included skin surfaces stimulated in the behavioral task, is not simply the result of a spatial sampling bias. A similar, nearly uniform mapping density also applied for all other poststimulation cases.

These results suggest that not only has there been an expansion of the distal phalanges of the behaviorally engaged digits but also that this representational enlargement occurred specifically for the stimulated skin. The enlargement of the cortical area representing the stimulated skin surface of the distal phalanx of *digit 2* in *OM 1* and *digit 3* in *OM 6* is shown in Figs. 11 and 12, respectively. In the hand insets (Figs. 11 and 12, right) the consistently stimulated skin surfaces are approximated by the stippled region on the distal aspect of *digits 2* or *3*. A reconstruction of the cortical representation of the hand in area 3b obtained before (top) and after (bottom) differential stimulation is shown in Fig. 11. For *OM 6*, the stimulation map was obtained first (top), and a second map (bottom) was obtained after a period without disk access. The cortical zones over which these differentially stimulated skin surfaces were represented at these two epochs in the monkeys' lives are indicated by stippling in both drawings. Within these stippled zones, all defined receptive fields included at least a portion of this heavily stimulated skin surface. The cortical area of representation of these skin surfaces has increased by nearly 500%. These data, as well as those from other studied cases, indicated that the expansion of cortical representation is occurring specifically for the stimulated skin surfaces.

ALTERATIONS IN THE DETAILS OF CORTICAL-MAP TOPOGRAPHY. As a result of this expanded cortical representation, striking changes should be apparent in the internal topography of the cortical zones representing the stimulated phalanges. Recall that, in 3b maps of the hand representation in normal adult owl monkeys, there is an orderly shift from distal to proximal in the location of receptive fields for rostral-to-caudal sequences of electrode penetration sites (e.g., Fig. 1, B and C, 1–5). (For an extensive treatment of this feature of the internal topography of area 3b representations, see Merzenich et al. 1987.) Two caudal-to-rostral sequences of penetration sites and associated receptive fields for the poststimulation mapping experiment in *OM 1* are shown in Fig. 12. The caudal-to-rostral sequence of penetration sites labeled 1–6 (Fig. 13A) on the palm and *digit 5* had receptive fields that illustrate a nor-

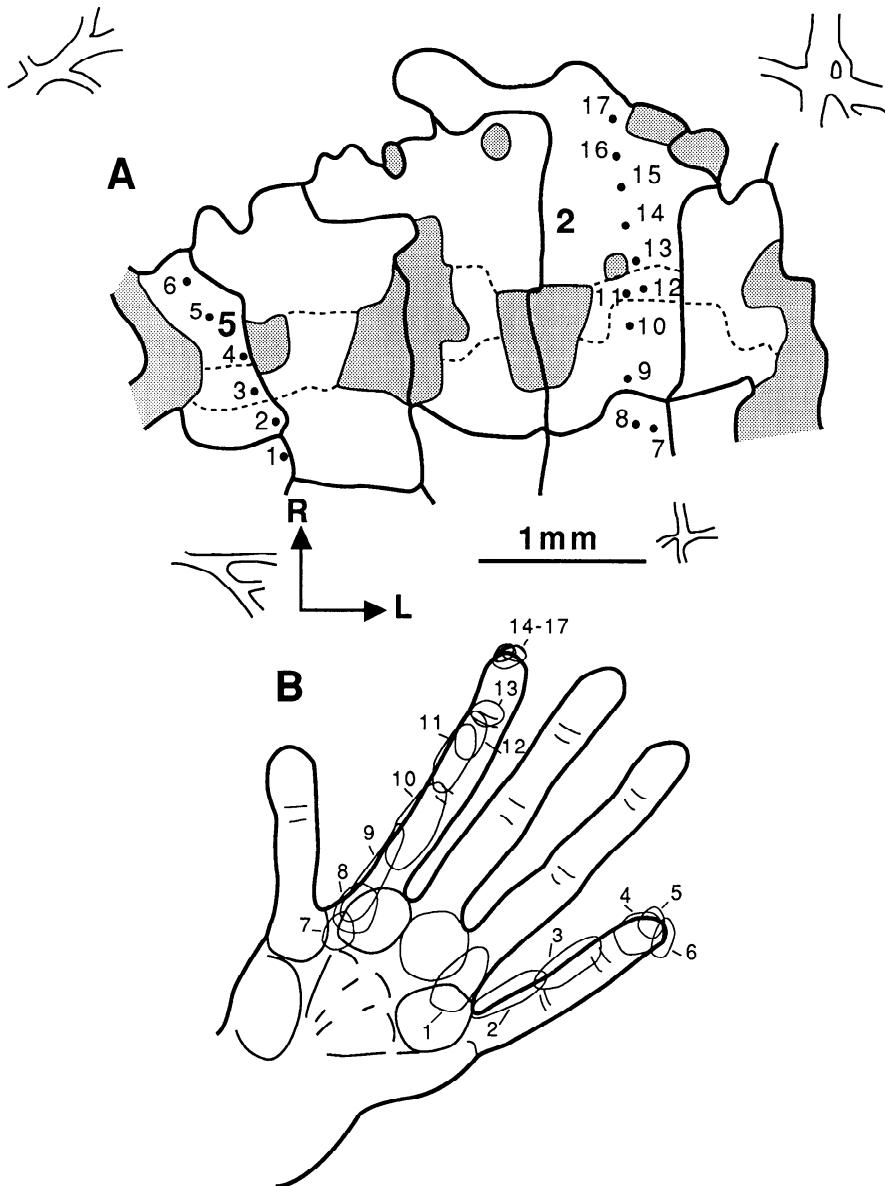


FIG. 13. Caudal-to-rostral sequences of recording sites within area 3b (*top*) and corresponding receptive fields (*bottom*) defined after behaviorally controlled differential stimulation for *OM 1*. Caudal-to-rostral sequence of penetration sites labeled 1–6 had receptive fields that illustrate a normal gradual shift from proximal to distal in receptive-field locations. Electrode penetration sites and their associated receptive fields in the sequence labeled 7–17 indicate a striking change in the internal topography of the representation of *digit 2*. A normal gradual shift in receptive-field locations from the palm to the proximal aspect of the distal phalanx was observed for sites 7–13. Note that there was an abrupt jump in the location of the next receptive field in sequence (14) despite only a small shift (125 μm) in the location of the recording site. Note also that, for additional movements in the locations of subsequent recording sites (15–17), the locations of those receptive fields closely overlapped with one another.

mal gradual shift from proximal to distal in receptive-field locations (Fig. 13*B*). This example also illustrates that small discontinuities in receptive-field sequences (see RFs 3 and 4) were occasionally observed in regions not directly stimulated by the disk or in sequences from normal maps. In contrast, inspection of the electrode penetration sites and their associated receptive fields in the sequence labeled 7–17 (Fig. 13, *A* and *B*) indicates a striking change in the internal topography of the representation of *digit 2*. The sequence of penetration sites 7–13 shows a normal gradual shift in receptive-field locations from the palm to the proximal aspect of the distal phalanx of *digit 2*. However, the next penetration site in this sequence (14) had a receptive field located on the extreme distal and radial aspect of the distal phalanx of *digit 2*. That is, despite the fact that these two adjacent penetration sites are separated by only $\sim 125 \mu\text{m}$, their receptive fields are decidedly nonoverlapping. The other penetration sites in this sequence (15–17) had receptive fields that were also located over the skin stimulated during disk contact on the extreme distal aspect of the

distal phalanx of *digit 2*. Rostral-to-caudal sequences all across the distal phalanx representation of *digit 2* and, to a lesser extent, across *digits 3* and *4* exhibited a discontinuity between the representation of the stimulated and other nearby skin surfaces. For each of these digits, these non-overlapping representational boundaries marked the boundary of representation of the skin surfaces stimulated directly during disk contact.

The existence of a break in the topographic sequence of representation of the stimulated skin surfaces was a feature common to all poststimulation mapping experiments. Another example of this unusual map feature is illustrated in Fig. 14 for *OM 6*. A caudal-to-rostral sequence of penetration sites labeled 1–8 (Fig. 14*A*) on the palm and *digit 1* had receptive fields that illustrate a normal gradual shift from proximal to distal in receptive-field locations (Fig. 14*B*). This normal gradual shift was usually seen in each case for digits not stimulated by disk contact. In the penetration sequence labeled 9–19 (Fig. 14, *A* and *B*), it can be seen that, once again, there is an abrupt shift in the orderly

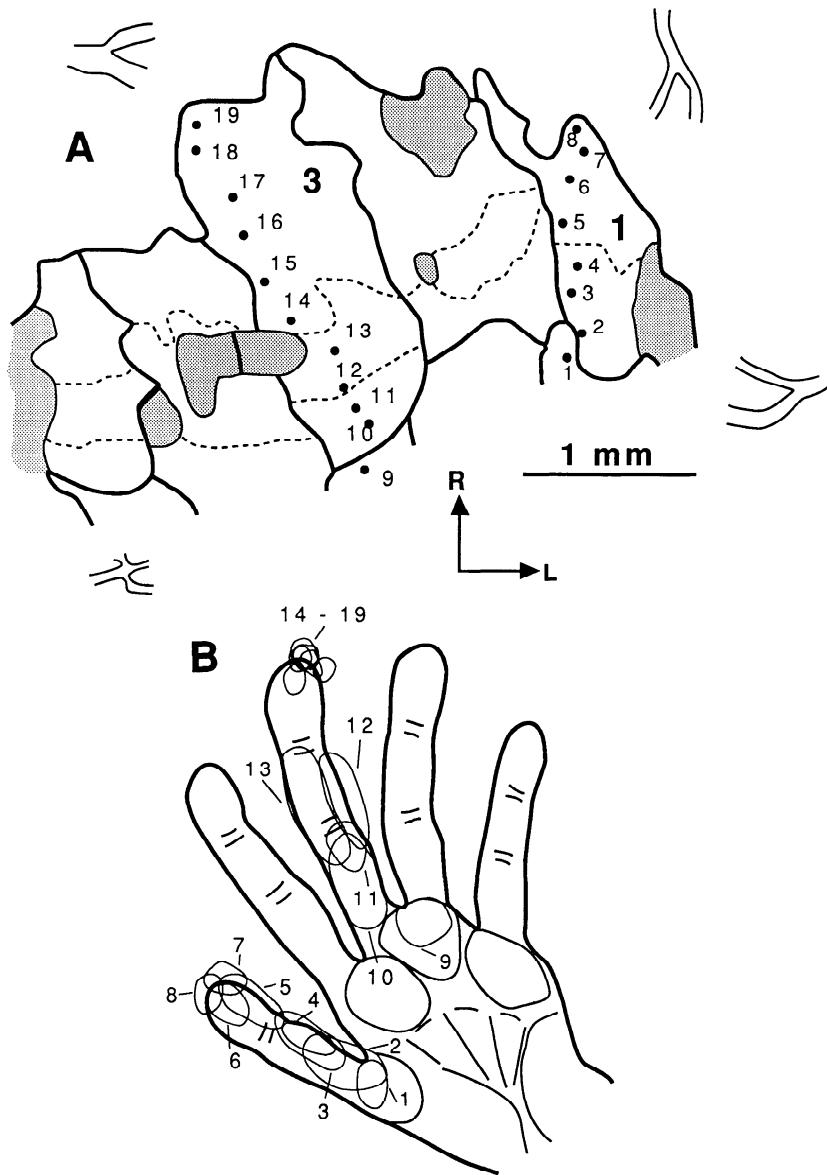


FIG. 14. Caudal-to-rostral sequences of recording sites within area 3b (*top*) and corresponding receptive fields (*bottom*) defined after behaviorally controlled differential stimulation for *OM* 6. Caudal-to-rostral sequence of penetration sites labeled 1–8 had receptive fields that illustrate a typical gradual shift from proximal to distal in receptive-field locations. Penetration sequence from 9–19 again illustrates the typical, unusual topography of representation of the stimulated digit. A normal gradual shift in receptive-field locations from the palm to the distal aspect of the middle phalanx of *D*3 was seen for sites 9–13. At site 14, there was an abrupt shift in the location of the receptive field to the distal aspect of the distal phalanx of *D*3. For electrode penetrations sites located over the next 1,000+ μ m in this sequence (sites 15–19), there was little change in the location of the receptive field.

progression of receptive-field locations at the border of the representation of the stimulated phalanx. In this sequence, which covers $\sim 1,250 \mu\text{m}$ across the cortical surface, again little change in receptive-field locations was observed. Once again, the cortical zone exhibiting a discontinuity in digital surface representation was seen along the borders of representation of the skin surfaces directly engaged in the behaviorally controlled stimulation. As previously mentioned, occasional smaller discontinuities in receptive-field sequences were observed on unstimulated digits or in control maps. However, these discontinuities were not associated with cortical zones of nonshifting, largely overlapping receptive fields or with systematically smaller receptive-field sizes.

ADJACENT CORTICAL REPRESENTATIONAL ZONES ALTERED BY STIMULATION. One consequence of the expansion of the cortical zones representing skin surfaces stimulated in the behavioral task is a change in topographic relationships with surrounding somatic representations. These changes

are illustrated in Fig. 15 for representative skin surfaces (i.e., the distal phalanx of the digit most heavily involved in the task). The illustrations presented for *OM* 1, 3, 4, and 6 are derived from data obtained after differential stimulation with the use of the rotating disk procedures. For comparison, the illustration presented for *OM* 5 was derived from data obtained after stimulation with the use of the flat static disk procedure. Each of the cases differentially stimulated by the use of the rotating disk share the following common features with regard to the changes in topographic relationships: 1) there was a centrally located cortical zone within area 3b that was common to the two representations; 2) within area 3b, there was a loss of cortical territory to either adjacent digits or the middle phalanx; 3) within area 3b, there was a gain in cortical territory from either adjacent digits, the middle phalanx, or dorsum representation; and 4) there was a gain in functionally defined area 3b that was obtained at the expense of functionally defined area 3a.

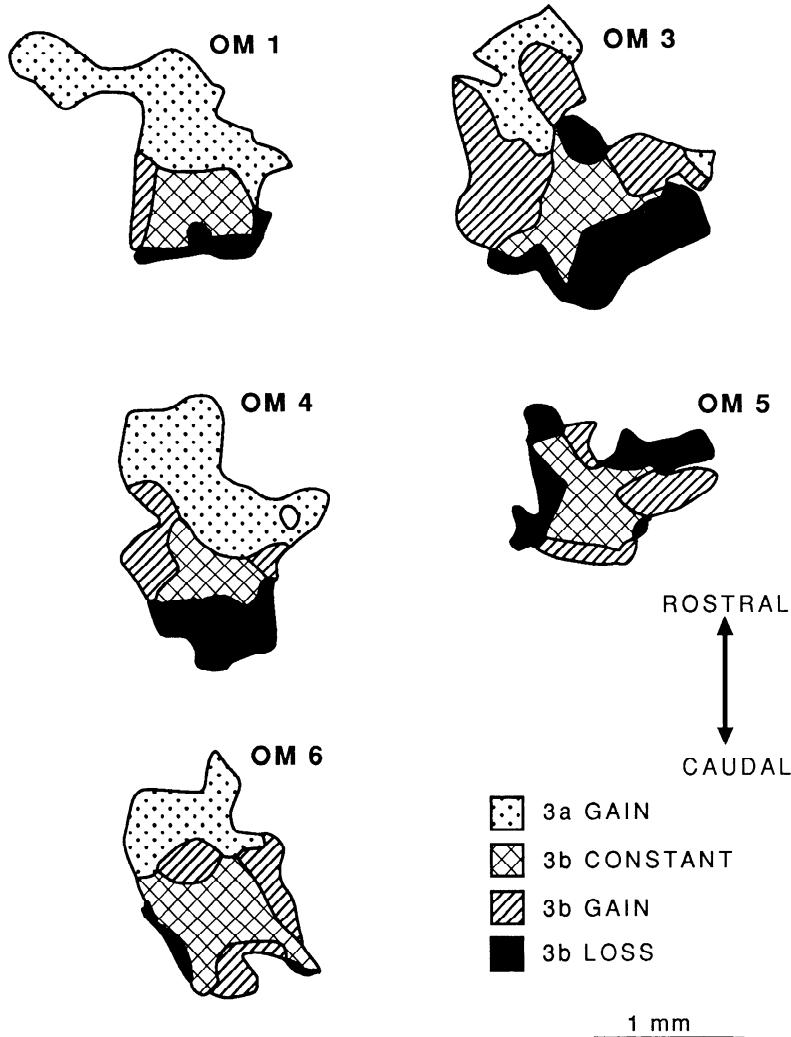


FIG. 15. Changes in the cortical zones of representation of stimulated glabrous distal phalanges. For *OM 1*, the illustrated changes are from a normal map and a subsequent poststimulation map. For *OM 3, 4*, and *6*, the illustrated changes are from a poststimulation map as compared with a subsequent map after a period of several weeks without access to the behavioral apparatus. For *OM 5*, the illustrated changes are from a normal map and a subsequent map obtained after a period of controlled stimulation with the use of a static flat disk. Stippled zone indicates a cortical gain from functionally defined area 3a. Cross-hatched region indicates a constant cortical zone within these 2 maps that represent these phalanges. Diagonal lines indicate a cortical gain from other skin surfaces within functionally defined area 3b. Black zone indicates a loss in cortical representation from functionally defined area 3b for the stimulated phalanx. Note that, for all cases, there were positive changes in the cortical zone of representation of the stimulated phalanx that included gains in territory from functionally defined area 3a (except *OM 5*) and 3b, as well as some more limited area 3b loss. Note that, for all cases except *OM 5*, the net result was an increase in the area of cortex within functionally defined 3b representing the stimulated phalanx. For *OM 5*, there was no gain in cortical territory from the adjacent functionally defined area 3a. There was little net effect on the size of the representational zone as a consequence of the observed changes in cortical zones of representation of the distal phalanx for *OM 5*.

The net effect of these alterations in topographic relationships was a gain in area of the cortical zone representing differentially stimulated skin surfaces. The topographic changes observed after exposure to the static flat disk (Fig. 15, *OM 5*) were similar to those seen in the other cases, except that there was no gain in territory from functionally defined area 3a. The net effect of these alterations in topographic relationships on the area of cortex representing the skin surface that contacted the static disk was insignificant.

It is important to point out that the aforementioned changes in representational topography necessarily indicate that there is an alteration of topographic relationships for other skin surfaces on the hand. Three examples of these changes for a distal phalanx not directly engaged in disk contact are shown in Fig. 16. In each of these examples, as well as many others, we observed changes that were qualitatively similar to those seen for stimulated skin surfaces. That is, between the two representations, there was usually 1) a central common zone, 2) a loss within area 3b, 3) a gain within area 3b, and sometimes 4) a gain or loss in territory from functionally defined cortical field 3a. However, unlike stimulated skin surfaces, the net effect on the cortical area of representation was usually negligible.

CHANGES ACROSS THE AREA 3a-3b BORDER. As previously stated, in every poststimulation experiment, there were unequivocal changes in location of the functionally defined 3a-3b border. This somewhat surprising result is summarized in Fig. 17. There, for each of the five illustrated examples, the dashed line represents the functionally defined 3a-3b border along the rostral margin of 3b obtained either before disk stimulation (*OM 1* and *5*) or after a several-week period without disk stimulation (*OM 3, 4*, and *6*). The solid line represents the functionally defined 3a-3b border obtained immediately after disk stimulation training. Recall that lines defining the borders between various skin surfaces or functionally defined cortical areas are drawn by interpolating between adjacent recording sites. Therefore it is reasonable that some small variation in the exact location of these borders may occur as a result of differences in the exact locations of sampled recording sites between any two mapping experiments. However, most of the changes along the rostral 3a-3b border cannot be explained by such an artifact in methodology. For example, the stippled regions in Fig. 17 represent the cortical regions over which the recording sites from the two mapping experiments directly overlapped spatially and for which no

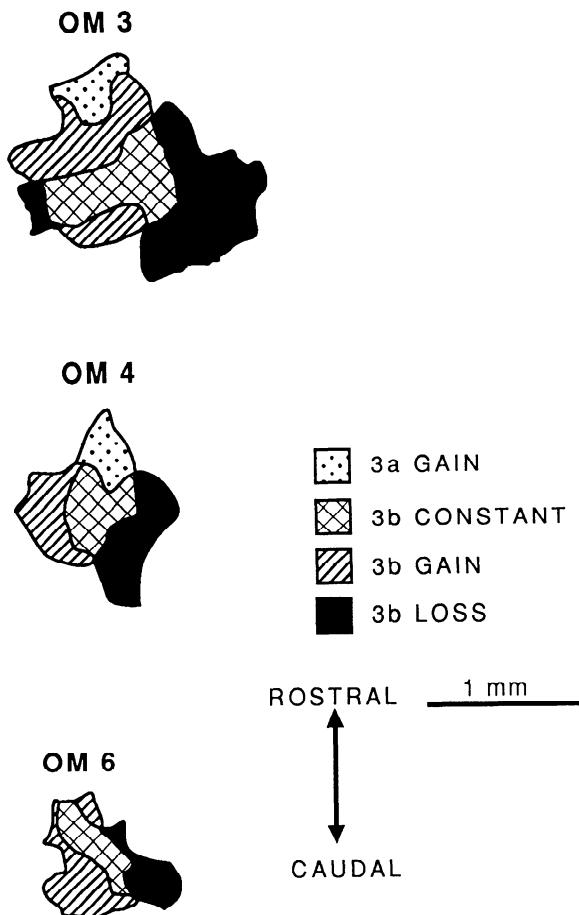


FIG. 16. Changes in the cortical zones of representation of nonstimulated glabrous distal phalanges. For *OM 3* (digit 2), *OM 4* (digit 5), and *OM 6* (digit 5), the illustrated changes are from a poststimulation map as compared with a subsequent map after a period of several weeks without access to the behavioral apparatus. Various patterned fills are as indicated in Fig. 14. Note that, in spite of the fact that there were changes in the absolute locations of the cortical zones of representation of distal phalanges not specifically engaged in the behavioral task, there was little net effect on the sizes of their cortical representation.

interpolation was used. That is, they represent a conservative estimate of the cortical region over which neurons exhibited changes from 3a to 3b response properties or vice versa. Note that, for *OM 1*, *3*, *4*, and *6*, there is a substantial region over which the functionally defined border has shifted, resulting in an expansion of the defined area 3b representation. Of particular interest is the fact that the largest caudal-to-rostral expansion occurred in the region immediately adjacent to the stimulated skin surfaces. The most striking example of this can be seen in the bottom of Fig. 17 for *OM 6*. There, the cutaneous/deep border has been translocated rostrally adjacent to the stimulated distal phalanges and translocated caudally adjacent to the distal phalanges not directly stimulated during disk contact. Note also that for *OM 5*, in which the disk was not rotating and had a smooth surface, little change was observed in the location of the functionally defined 3a-3b border.

CHANGES ACROSS THE HAND/FACE BORDER. Changes in the functionally defined hand/face border were also observed. Figure 18 presents a summary of these results.

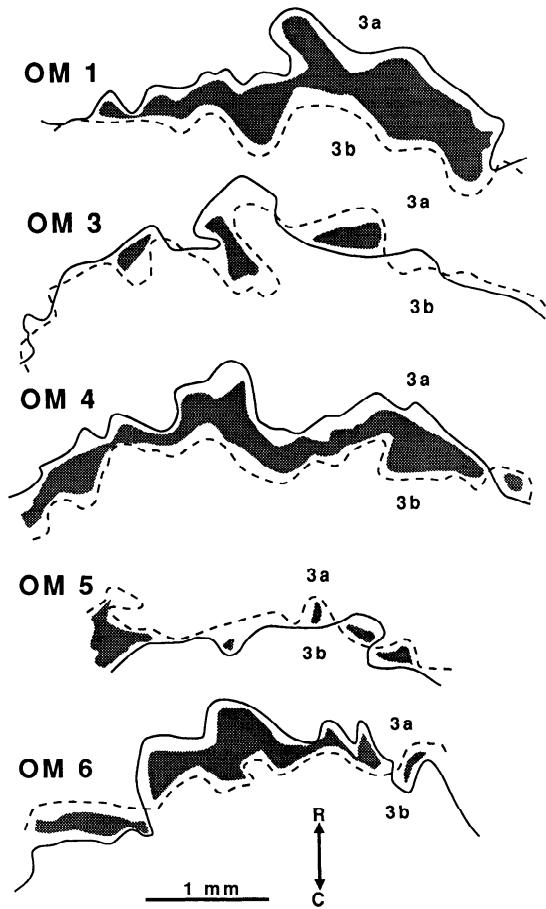


FIG. 17. In each of the 5 illustrated examples, dashed line represents the functionally defined 3a-3b border along the rostral margin of 3b obtained either before disk stimulation (*OM 1* and *5*) or after a several-week period without disk stimulation (*OM 3*, *4*, and *6*). Solid line represents the functionally defined 3a-3b border obtained immediately after disk stimulation training. Recall that lines defining the borders between various skin surfaces or functionally defined cortical areas are drawn by interpolating between adjacent recording sites. Stippled areas represent the cortical regions over which the recording sites from the 2 mapping experiments directly overlapped and for which no interpolation applies. That is, these recorded representational borders minimally and unequivocally shifted by the extents indicated by the stippled area.

Again, the dashed line represents the functionally defined hand-face border along the lateral margin of the hand representation within area 3b obtained either before disk stimulation (*OM 1* and *5*) or after a several-week period without disk stimulation (*OM 3*, *4*, and *6*). The solid line represents the functionally defined hand-face border obtained immediately after disk stimulation training. The stippled area represents the cortical regions over which the recording sites from the two mapping experiments overlapped spatially. Three of the cases exposed to the rotating-disk stimulation (*OM 1*, *3*, and *4*) show clear evidence of a lateral translocation of the hand-face border. The largest translocation was seen in *OM 3*, where there was as much as a 600- μ m lateral displacement of the hand-face border with the use of the more conservative measure. No significant change in the hand-face border was observed for *OM 6*. Interestingly, *OM 5*, which had been stimulated with the static flat disk, also exhibited a shift in the hand-face

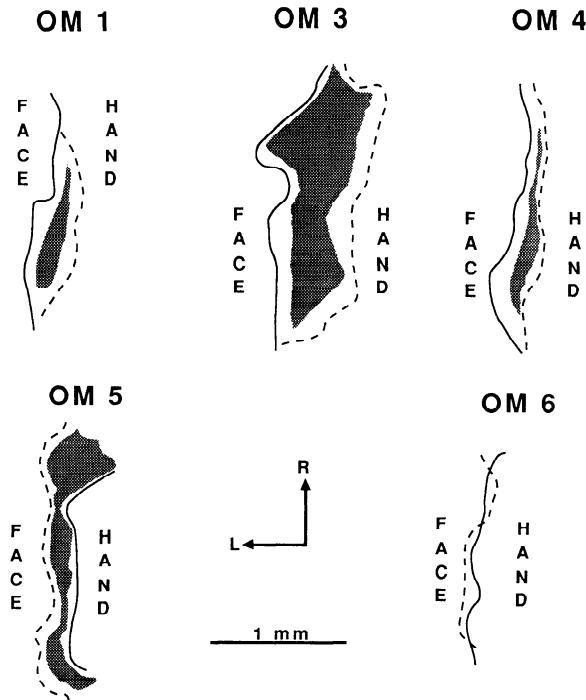


FIG. 18. In each of the 5 illustrated examples, dashed line represents the functionally defined hand-face border along the lateral margin of the hand representation within area 3b obtained either before disk stimulation (*OM 1* and *5*) or after a several-week period without disk stimulation (*OM 3*, *4*, and *6*). Solid line represents the functionally defined hand-face border obtained immediately after disk stimulation training. Stippled area represents the cortical regions over which the recording sites from the 2 mapping experiments overlapped directly. For *OM 1*, *3*, *4*, and *6*, stimulation was with the rotating disk. For *OM 5*, stimulation was accomplished with a static flat disk.

border. However, unlike other cases, the hand-face border in this case was translocated medially by as much as 200 μm , again with the use of a conservative estimate.

DISCUSSION

The disproportionately large representation of the heavily stimulated skin surface resulted in substantial translocations of the sites of representation of surrounding skin surfaces. Significant shifts in the cortical locations of the functional area 3b-*arca* 3a border and in the location of the hand-face border were recorded. Across the mapped sector of area 3b, the topographic order of defined receptive fields was altered. Surprisingly, except for the representation of the nonstimulated surfaces of the distal phalanx of the same digit, the enlargement of the cortical representation of behaviorally engaged hand surfaces did not result in a substantial underrepresentation of surrounding skin surfaces. That was apparently a consequence of the long-distance "borrowing" of representational territory, which was a striking feature of these experimental cases.

Interestingly, in two special cases in which the behavioral task required minimal attention because the stimulandum was not moving, no significant representational enlargement of the behaviorally engaged skin surfaces was recorded. It is not possible to determine, at this point, if this lack of representational plasticity in these two special cases

was because of the static nature of the stimulandum and/or because of the relatively low level of attention requisite for the monkey to successfully perform this simpler task—or to some other differences in the features of the stimulus provided by disk contact.

Some implications

INPUT-SELECTING PROCESSES CONSTITUTE FUNDAMENTAL OPERATIONS OF THE NORMAL ADULT NEOCORTEX. These studies demonstrate that the receptive fields of cortical neurons can be altered and the representational topographies of cortical fields modified by use throughout life. We have earlier summarized a large body of evidence that suggests that 1) this representational plasticity involves alterations in the effectiveness of in-place afferent inputs (see Clark et al. 1988; Jenkins et al. 1987, 1989; Merzenich et al. 1985, 1987, 1988). 2) The coincidence of afferent inputs plays a powerful role in reshaping cortical receptive fields and representational topographies (Clark et al. 1988; Merzenich et al. 1988; Yun et al. 1987). 3) Input effectivenesses are likely modulated as a function of behavioral state (see Merzenich et al. 1988), and 4) Use-driven alteration of cortical representations accounts for most of the great normal variability in the details of cortical representations recorded in adult monkeys (Merzenich et al. 1987).

These present results are consistent with these earlier findings and hypotheses. First, representational translocations recorded in these experiments are recorded over cortical distances of up to 600–700 μm , i.e., within the limits of the spreads of divergent-convergent anatomic inputs (Garraghty and Sur 1987; Snow et al. 1988) and within "distance limits" defined in earlier reported experiments conducted in this cortical area in owl monkeys (Merzenich et al. 1983a,b, 1985). Although their possible contributions are difficult to rule out completely, no sprouting or movement of afferent input arbors would be required to explain representational translocations on this scale.

Second, this behaviorally controlled stimulation resulted in increased amounts of nearly coincident stimulation of small digital skin patches. Most of the small receptive fields in the expanded zones of representation of these small skin surfaces were limited to these small, nearly simultaneously excited skin zones. These results are therefore consistent with a growing body of evidence suggesting that the quantities of temporally coincident or nearly coincident inputs play a major role in shaping cortical receptive fields and representational topographies (see Clark et al. 1988; Merzenich et al. 1988).

Third, dramatic changes were recorded in monkeys performing a behavioral task—maintaining light contact with a ridged, moving disk—that required their close "attention." By contrast, little or no task-related changes in the hand representational zone was recorded in monkeys performing a simpler task—maintaining contact with a static surface—that required little attention on their part. These data are consistent with the view, generated largely by functional studies of other cortical areas (Diamond and Weinberger 1986; Spitzer et al. 1988; Weinberger and Diamond 1988; Woody et al. 1972; but see Yun et al. 1987), that the effectivenesses of afferent inputs for generating

representational change are modulated as a function of behavioral state.

At the same time, differences in the quantities of sensory input may also contribute to observed differences between static and rotating disk cases. Although initial contact with either disk would excite virtually all cutaneous mechanoreceptors, static pressure on a flat surface excites only SA mechanoreceptors in monkeys. These receptors are innervated by only 25% of the large-diameter myelinated cutaneous afferents in the median nerve (Darian-Smith and Kenins 1980). By contrast, maintained contact on a moving disk with ridged surface features periodically (at 20 Hz) excites all cutaneous mechanoreceptors. Furthermore, both RA and SA mechanoreceptors fire at significantly higher rates when moving edges cross their fields than when smooth surfaces contact their fields because they are most sensitive to "curvature gradients" (Johnson and Lamb 1981; LaMotte and Srinivasan 1987a,b; Srinivasan and LaMotte 1987). The relative contributions of firing rates and population size of cutaneous afferents versus attentional factors to the observed map differences are not separable in these experiments.

Fourth, these simple behaviors contributed to an idiosyncratic remodeling of the area 3b representation of the hand, different in each of these monkeys, different from all others studied, and related specifically to one of a number of behaviorally important hand uses. Presumably any behaviorally important hand use requiring subtle sensory feedback or discrimination would have impacts on the details of this (and many other) cortical representation(s). These studies provide further evidence that the strikingly individual representational details of hand representations in different adult monkeys (Merzenich et al. 1985, 1987) have been shaped by each monkey's unique experiential history.

CHANGES ALONG THE AREA 3a-AREA 3b BORDER. There was a significant extension of the cutaneous representation of the behaviorally stimulated digital surfaces into presumptive area 3a in four behavioral cases (*OM 1, 3, 4, and 6*; Fig. 17). The deep input representation in functionally defined area 3a extended significantly into area 3b in three studied monkeys (*OM 3, 5, and 6*; Fig. 17). These changes in the functionally defined 3b-3a border are especially interesting in *OM 6*, in which the cutaneous representation of the behaviorally engaged digit tips expanded >500 μm into functionally defined area 3a, while at the same time the deep representation adjacent to the cutaneous representation of nonengaged digits appeared to move up to several hundred micrometers into functionally defined area 3b.

We have explored the area 3b-3a border in >60 normal adult owl monkeys. In the great majority, progressing rostrally, receptive fields at the extreme digit tips, under cover of the fingernails or in the fingernail beds, were followed by recording sites in which no cutaneous responses could be recorded. The hand area of this latter zone, presumptive area 3a, has been mapped in entirety in several adult monkeys. It is ~2 mm wide rostrocaudally. Neurons within it often respond vigorously to tapping unrestrained fingers. However, when joint movement is disallowed, very few or no sites respond to light tactile stimulation in this zone.

This is consistent with the observation that muscle spindle and other deep receptor inputs predominate in this cortical area (Hore et al. 1976; Jones and Porter 1980; Lucier et al. 1975; Phillips et al. 1971).

At the same time, in some normal cases, cutaneous receptive fields have been recorded in area 3a. Pacinian input responses are occasionally recorded along the 3b-3a border—although we cannot usually assign them unequivocally to either field 3b or 3a. Relatively large cutaneous fields innervating the dorsal surfaces of the digits or extending over one or more fingertips have also been recorded rostral to the small-field digit tip representation in some monkeys. Although these receptive fields are cutaneous by our definition (i.e., they respond to light indenting of the skin when the digit joints are stabilized), they usually resemble high-threshold tapping response fields in the sense that their defined receptive fields commonly extend over the surfaces of more than one digit. The finding of occasional large-field cutaneous responses in cortical area 3a is consistent with the finding that 3a receives anatomic inputs ultimately arising from purely cutaneous nerves (Heath et al. 1976; Oscarsson et al. 1966).

Given these observations, is the functional border of areas 3a and 3b truly plastic? Electrophysiological data are consistent with the functional 3b representation expanding into area 3a. There is nothing in the small receptive-field responses or representational topography to distinguish clearly the most rostral response sites from the more caudal ones. The skin on the extreme fingertip under the fingernail is represented in the rostral aspect of this zone. By these criteria, the 3b-stimulated skin representation has enlarged to occupy now a significant sector that was formerly functionally 3a. A presumption might be that this plasticity would require a significant anatomic overlap of input arbors and output destinations of neurons in a relatively broad 3a-3b transitional zone.

On the other hand, nearly the same results could have been obtained if a caudal sector of 3a was converted from a large-field, multiple-digit deep representational zone to a small-field, single-digit cutaneous representational zone. It is difficult to eliminate this second possibility. Indeed, the emergence of a large cutaneous overrepresentation of a stimulated fingertip in a cortical field that provides critical sensory inputs to motor cortex might have important implications for control of a behavior in which the animal has to regulate very closely skin position in relation to a moving surface. Whether this is the case or not, the topography and selected effective cortical inputs have been dramatically altered in two functionally defined cortical fields. In either event, all sign of normally large deep multiple-digit receptive fields has been lost over this zone. This presumably requires topographic adjustment elsewhere in field 3a.

If an emergence of a functional 3a zone with small cutaneous receptive fields is occurring in these monkeys, then the net changes in representation occurring in functional area 3b are more modest than those recorded in Table 1. However, the unmistakable changes in topography and the distorted representation of the limited, struck digit tip surfaces would still apply to area 3b alone. Moreover, in one monkey (*OM 3*), net positive changes are almost entirely

attributable to enlargement of the digit tip representation into functional area 3b alone.

In recent experiments not reported herein, we have directed training to proximal digit segments, in part to eliminate this possible confusion along the 3b-3a border. In those studies, training has resulted in a severalfold increase in the representation of the behaviorally engaged skin within area 3b, as well as alterations in the response properties over large sectors of area 3a (Recanzone et al. 1989).

OTHER CHANGES IN REPRESENTATION. Other representational changes were observed in these experiments. Some unstimulated digital surfaces on either the distal, middle, or proximal phalanges exhibited unpredictable gains or losses in cortical representation immediately after stimulation when compared with control maps. For example, the distal phalanx of *digit 1* in case *OM 1* had a 29% increase (see Table 1), whereas *digits 1* and *5* in case *OM 3* had a 10% smaller cortical representation. In these instances, the absolute cortical territorial gains or losses were not great (e.g., 0.08 mm² for *digit 1* in *OM 1*). Moreover, significant gains in cortical territory were not always observed for some skin surfaces stimulated by disk contact. For example, the cortical representation of the distal phalanx of *digit 4* in *OM 3* only increased by 6%, whereas changes in the territories of representation of other engaged digital surfaces in this case were great. Similarly, the representation of the distal phalanx of *digit 4* in *OM 6* was actually smaller immediately after disk stimulation. A much smaller skin region on this digit was only occasionally stimulated in the behavior. On the other hand, representations of other more frequently stimulated digits in the same case increased greatly.

Several factors may have contributed to these results. First, there are aspects of behavior that resulted in differential stimulation of various skin surfaces of the hand that were not controlled in these experiments. For example, even though all of the monkeys commonly retrieved banana pellets with their tongue, they were occasionally also observed retrieving pellets with their hands. In addition, no attempt was made to control other hand use before, during, or after behavioral training on the disk. Undoubtedly, these monkeys had idiosyncratic patterns of hand use for food retrieval, locomotion, grooming, and other behaviors that, given the present data, would be expressed in control or experimental maps. Furthermore, these behavioral patterns of hand use may well have been perturbed by behavioral training. Second, although it is not possible to determine the effects of selective attentional factors in these studies, it is interesting to note that, when multiple digits were engaged in contacting the rotating disk, the first-struck digit always exhibited the largest change in cortical representation. Finally, some of the variation in cortical representational territory is because of measurement error. These measurement errors, given a fixed statistical criterion, are affected by both the number of sites used to estimate the area of representation and the absolute size of the cortical area to be estimated. The end result, given the relatively constant spatial sampling of these studies, is that smaller cortical regions of representation are subject to greater measurement errors (Merzenich et al. 1987). Small

changes in representation, especially for smaller outlined map sectors, are sometimes not statistically significant.

AN HYPOTHESIS: USE-DRIVEN ALTERATIONS IN NEOCORTICAL REPRESENTATIONS MANIFEST CORTICAL CONTRIBUTIONS TO USE-DRIVEN IMPROVEMENTS IN PERCEPTUAL JUDGMENTS AND ACQUISITION OF SKILL. The view that the adult nervous system, in particular the neocortex, exhibits physiological plasticity in response to historical patterns of sensory input is a premise on which most of the nineteenth-century physiologists and psychologists based their notions of the modifiability of behavior through experience. William James (1890) summarized this view by stating that practiced behaviors must ". . . leave their traces in the paths which they take. [They] . . . deepen old paths or . . . make new ones. . . . [The] . . . whole plasticity of the brain sums itself up in two words when we call it 'an organ' in which currents pouring in from the sense organs make with extreme facility paths which do not easily disappear."

Early psychophysicists clearly recognized that experience on a particular sensory discrimination resulted in marked improvement in the discriminability of all kinds of sensory stimuli (for a review, see Anderson 1981; Gibson 1953). For the early psychologists "this fact was so familiar that few . . . have even recognized it as needing an explanation" (James 1890). It was also recognized historically that this improvement in perceptual judgments with practice or experience was an important feature of human cognition that was largely an "inexplicable fact." Contemporary psychophysicists have largely ignored this problem and have commonly considered measurements of discrimination capacity along a single physical dimension to reflect a stable sensory function. Any variations or improvements in discriminability have been viewed as because of changes in "motivation," "attention," "criterion," "familiarity," with, or "learning" the specific requirements or contingencies of the specific behavioral task used to measure discrimination capacity. Certainly these variables do affect measurements of discrimination capacity. However, it has been clear for more than a century that even the fundamental resolving capacity of the perceptual machinery improves with experience, with gains in acuity achieved over a practiced skin surface not applicable to a nearby, untrained skin surface (Dresslar 1894; Jones et al. 1973; Vierck and Jones 1970; Volkmann 1858).

The data from the present experiments suggest that extensive stimulation to a restricted patch of skin under behaviorally controlled stimulation is "locally expressed" in the functional representation of that skin surface within area 3b. Gains in acuity and/or sensitivity would be expected to result from practiced performance of this task.

Whatever the correct interpretation as to the contributions to area 3a and 3b to these changes, it is clear that the topography and selected effective cortical inputs have been dramatically altered in two functionally defined cortical fields. In any event, all sign of normally large deep multiple-digit receptive fields has been lost over a substantial area 3a zone. These changes along the 3a-3b border presumably require topographic adjustment elsewhere in both fields 3a and 3b.

All of these studies imply that there should be clear evidence of physiological changes at the neuron level that can account for these improvements in perceptual and motor capacities. As a monkey performs the simple behavioral task described in this report over a period of a few to many weeks, a dramatic representational alteration reflecting this specific hand use was recorded within the cortical areas 3b and 3a. It is reasonable to hypothesize that 1) these representational changes have operational (behavioral) consequences for these monkeys; and 2) these representational changes manifest the area 3b and 3a contributions to the successful performance of this behavioral task, and to alteration of the ability to perform other tasks, given this special experience.

Area 3b is almost certainly the least alterable, by use, of somatosensory cortical representations (see Jenkins and Merzenich 1987; Merzenich et al. 1987, 1988). Performance of a simple repetitive task like this one must result in reorganizational changes within many cortical areas excited differentially by these special, repetitive, sequenced motor and sensory events. It appears reasonable to hypothesize that use-driven changes in the many areas necessarily engaged by any such task collectively constitute the cortical contributions to the acquisition of skill and perceptual capacity in developing and adult mammals. These ideas are consistent with the view that the nervous system and cerebral cortex in particular are capable of selfregulation and adaptive reorganization, as previously expressed by Lashley (1930, 1933, 1951) and Hebb (1949).

Our behavioral experiments now turn toward a more direct consideration of a determination of the significance of behaviorally driven cortical representational changes in studies in which we can track performance gains in parallel with alterations in cortical representational details and suprathreshold neuronal response characteristics.

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