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Topographic Reorganization of the Hand Representation in Cortical Area 3b of Owl Monkeys Trained in a Frequency-Discrimination Task

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SUMMARY AND CONCLUSIONS

1. Adult owl monkeys were trained to detect differences in the frequency of a tactile flutter-vibration stimulus above a 20-Hz standard. All stimuli were delivered to a constant skin site restricted to a small part of a segment of one finger. The frequency-difference discrimination performance of all but one of these monkeys improved progressively with training.

2. The distributed responses of cortical neurons ("maps") of the hand surfaces were defined in detail in somatosensory cortical area 3b. Representations of trained hands were compared with those of the opposite, untrained hand, and to the area 3b representations of hands in a second set of monkeys that were stimulated tactually in the same manner while these monkeys were attending to auditory stimuli (passive stimulation controls).

3. The cortical representations of the trained hands were substantially more complex in topographic detail than the representations of unstimulated hands or of passively stimulated control hands.

4. In all well-trained monkeys the representations of the restricted skin location trained in the behavioral task were significantly (1.5 to >3 times) greater in area than were the representations of equivalent skin locations on control digits. However, the overall extents of the representations of behaviorally stimulated fingers were not larger than those of control fingers in the same hemisphere, or in opposite hemisphere controls.

5. The receptive fields representing the trained skin were significantly larger than receptive fields representing control digits in all but one trained monkey. The largest receptive fields were centered in the zone of representation of the behaviorally engaged skin, but they were not limited to it. Large receptive fields were recorded in a 1- to 2-mm-wide zone in the area 3b maps of trained hands.

6. Receptive-field sizes were also statistically significantly larger on at least one adjacent, untrained digit when compared with the receptive fields recorded on the homologous digit of the opposite hand.

7. There was an increase in the percent overlaps of receptive fields in the cortical zone of representation of the trained skin. A significant number of receptive fields were centered on the behaviorally trained skin site.

8. The effects of increased topographic complexity, increased representation of the trained skin location, increased receptive-field size, and increased receptive-field overlap were not observed in the representations of the untrained hands in these same monkeys. Only modest increases in topographic complexity were recorded in the representations of passively stimulated hands, and no effects on receptive-field size or overlap were noted.

9. These differences in cortical representational areas, receptive-field sizes, and receptive-field overlaps probably do not by themselves account for the improvements in frequency discrimination performance with training.

INTRODUCTION

In the previous report an improvement in performance at a tactile frequency discrimination task as a result of an extended period of training in adult owl monkeys was described in detail (Recanzone et al. 1992a). The tactile stimulus in this task was applied to a small, constant skin location. The behavioral study was undertaken as a part of an experimental series designed to determine the changes in distributed cortical responses and topographic representations of a skin surface engaged in a frequency discrimination task. This study describes the topographic organization of the hand representation in area 3b of these behaviorally trained monkeys, and those of three control monkeys that were tactually stimulated in the same manner, but that were required to perform an auditory frequency discrimination task.

The normal representations of the hand in SI of the adult owl monkey have been described in detail (Kaas et al. 1979; Merzenich et al. 1978, 1987; Sur 1980; Sur et al. 1980). The representations are topographic, with receptive fields on neighboring skin locations represented by neurons at neighboring locations in the cortex. These earlier studies resulted in the identification of several "rules" of the functional organization of skin surface representations; *1*) The cortical representation of the hand is locally continuous and marked by shifted overlaps of receptive fields across the cortex. A few exceptions of this rule exists, where discontinuities in representational sequence are recorded within the body surface maps. These discontinuities separate particular body surface representations, for example those of individual digits, and those of hairy and glabrous skin. *2*) There is a roughly inverse relationship between the receptive-field size and the cortical area of representation of any given skin region. *3*) The overlap of cutaneous receptive fields defined for cortical neurons decreases as a linear function of the cortical distance of separation. These generalizations were not restricted to the representation of the hand, but applied throughout the body surface representations within SI (Sur et al. 1980).

A variety of experimental manipulations have been

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shown to result in the reorganization of the topographic representation of the hand in area 3b of adult owl monkeys (for reviews, see Edelman 1987; Kaas et al. 1983; Merzenich et al. 1988, 1990). In every case of cortical reorganization described in the owl monkey, a continuous internal topography with the expected discontinuous breaks has been conserved, and the inverse and receptive-field overlap rules have been roughly maintained. The cortical area that formerly represented a denervated skin area came to represent the surrounding skin topographically. Because these organizational principles were maintained, continuously shifting receptive fields were ultimately smaller in size in the cortical areas of representation that increased in extent after these experimental manipulations.

These consistent findings have been cited as one line of evidence that the observed reorganization was the result of normal, dynamic processes that shape the functional representation of the neocortex throughout life (see Edelman 1987; Merzenich et al. 1984, 1988, 1990). According to this view, these normal dynamic processes would also produce changes in local responses and cortical topographies as a result of changing the pattern of stimulation of the skin through the animal's behavior. This issue was initially addressed in monkeys trained to present their fingertips onto a rotating disk in an attended task (Jenkins et al. 1990). Cortical representations of the hand were found to be substantially altered by this attended behavior, with changes related to the restricted skin regions stimulated. However, there were two important limitations of this earlier study. First, while changes in cortical representations were recorded, there was no demonstration that they affected the subjects' performance of this or any other behavior. Second, while the task was attended, there was no certainty that changes of the same magnitude would not have occurred by equivalent passive stimulation.

In the present experiment adult owl monkeys were trained to detect a change in the frequency of a tactile stimulus presented to a constant location of a small part of a single finger segment (Recanzone et al. 1992a). These monkeys showed an improvement in performance at this frequency-discrimination task over the course of several weeks to months of training. In the training sessions just before the mapping experiment, the thresholds derived on the trained skin surface were approximately one-half of those derived when stimulation was applied on an adjacent, untrained skin surface, and three to four times better than the thresholds measured in the initial stages of training. In all but one trained monkey, these improvements in performance with training were shown to be the result of a true increase in perceptual acuity localized to the behaviorally engaged skin site.

This increase in temporal acuity might be expected to be reflected by changes in the representation of that skin surface throughout the somatosensory system. We sought to investigate these changes in somatosensory cortical fields 3b and 3a for four reasons. *1*) Ablation-behavioral studies have shown that SI, in general, and areas 3b and 1, in particular, are essential for this type of tactile discrimination (Carlson 1981, 1984; Cole and Glees 1954; LaMotte and Mountcastle 1979; Randolph and Semmes 1974; Semmes et al. 1972, 1974). *2*) Previous reports have provided a large data base from the hand representation of area 3b of "normal" owl monkeys. *3*) Detailed hand representation maps are necessarily derived in anesthetized monkeys. Control experiments have shown that area 3b neuronal responses derived in cortical layers III and IV differ little in anesthetized and unanesthetized owl monkeys (Stryker et al. 1987). *4*) There have been a number of reports demonstrating a capacity for representational plasticity in these cortical areas, and there is direct evidence that representations in these cortical fields can be altered by important tactual experiences (Jenkins et al. 1990; Merzenich et al. 1988, 1990).

As stated above, the behaviorally trained animals used in this study were tactually stimulated at a single skin location, and the frequency discrimination ability at this skin location of all but one monkey improved progressively with training. If cortical representational remodeling driven by this experience accounted for the observed changes in perceptual acuity, then selectively attending to the alteration-producing stimuli should be required for that cortical reorganization if attention to the task is requisite for behavioral gains. It is therefore important to determine what cortical representational changes (if any) are due to stimulation per se, and what changes are attributed specifically to attended stimulation in a behavioral task. To control for the possible effects of stimulation alone, a second set of animals were trained to discriminate differences in auditory stimuli while they were simultaneously stimulated tactually in a manner identical to the animals trained in the tactile discrimination task.

The questions that are addressed is this report are as follows. *1*) How is the topographic representation of the hand in cortical area 3b of an adult primate altered as a result of this animal learning and progressively improving at this flutter-vibration frequency discrimination task? *2*) How does the behavioral relevance of this stimulation influence these changes in the cortex?

METHODS

Behavioral training

This report describes data from five of the seven behaviorally trained adult owl monkeys that served as subjects in previous reports (Recanzone et al. 1991, 1992a) with the addition of three control animals. The psychophysical methods used to train these animals in the tactile task were described in detail in the preceding report (Recanzone et al. 1992a; also see Recanzone et al. 1991). Briefly, monkeys were trained in a modified go/no-go behavioral procedure to detect flutter-vibration stimuli >20 Hz as different in frequency from a 20-Hz standard. Hand position was strictly controlled, and all stimuli were applied to a constant finger site never exceeding 3.5 mm diam, with >90% of stimuli presented to an area ~2 mm diam. Stimuli were presented as bursts of 650-ms duration, with 650-ms pauses between bursts. The first stimulus was always 20 Hz. Up to five subsequent stimuli (bins) were presented in each trial. The animal was required to release the hand mold on detection that the stimulus was greater in frequency than the preceding (20 Hz) stimulus. The higher frequency (S2) presentation bin was pseudorandomly determined. Animals performed 500–700 trials per day, resulting in ~15–22 min of tactile stimulation per session. Six to 10 different S2 frequencies were presented on 20–50 trials to derive the frequency discrimination threshold for that single session. These thresholds, as a measure of the ability

of these monkeys to make these temporal stimulus distinctions, improved progressively with training.

Three control animals were trained to receive the equivalent tactile stimulus in a "passive" manner. They were trained in the same behavioral apparatus as were the monkeys trained at the tactile frequency discrimination task. Monkeys were required to place their hand onto the same hand mold under the same contingencies of hand placement to initiate a trial. Hand positioning was rigidly controlled, and tactile stimuli identical to those applied in the tactile discrimination task were always delivered to the same restricted surface of a segment of a single digit. Auditory stimuli were presented simultaneously with tactile stimuli, and the animal was required to make an auditory frequency discrimination to receive a reward. Higher frequency tactile stimuli (the S2s in the tactile discrimination task) were randomly presented to the tactually stimulated finger and could occur at any time including the first bin of stimulus presentation or during the presentation of the auditory S2 stimulus. As in the frequency discrimination behavioral trials, a higher frequency tactile stimulus was presented once during each trial. Tactile stimuli of 20 Hz only were presented exclusively on a small percentage of trials, corresponding to the Catch Trial and False-Positive rate for animals trained in the tactile discrimination task.

The tactile stimulus in no way predicted the availability of a reward, and these monkeys never responded at above-chance rates to these tactile "S2" stimuli. The tactile stimulus was therefore presumed to be unattended, whereas the overall schedule of tactile stimulation was essentially identical to that presented to tactile discrimination animals. One simple control to ensure that these control animals were not influenced in their behavior by the tactile stimulus was to turn the tactile stimulus off for brief periods of time during auditory discrimination. Consistently close matches between these performance functions indicated that concurrent tactile stimulation had no significant influence on auditory discrimination behavior.

Electrophysiology

The primary goal of the electrophysiological study was to define the distributed neuronal responses, and thereby the cortical representations or "maps" of the hand surfaces, in the SI cortical fields in both cerebral hemispheres of these monkeys. The hemisphere contralateral to either the trained hand in experimental animals or to the passively stimulated hand in control animals was studied first. Opposite hemispheres were studied as time permitted. In one tactually trained and in two passively stimulated cases, only a partial map of the second hemisphere was derived. Area 3a was mapped in a broad region rostral to the area 3b hand representation in every case (see Recanzone et al. 1992b). After the somatosensory maps were completed, auditory cortical areas were also studied in several monkeys, as a part of a different experimental series.

Anesthesia was induced with a 3% halothane–25% oxygen–72% nitrous oxide mixture. After the femoral vein was cannulated, the gas anesthetic was withdrawn, and pentobarbital sodium was administered intravenously as needed to maintain a surgical level of anesthesia. Doses of pentobarbital were 28 mg/kg infused over 20–30 min for induction, and 1–5 mg/h during the course of the experiment. These values varied among individual monkeys and within monkeys over the long time course of these experiments. Lactated Ringer solution with 5% dextrose was continuously infused intravenously (2–5 ml/h). Animals were anesthetized for up to 56 h, and every effort was made to maintain them in a constant physiological state. Animals gave no sign of discomfort and were maintained areflexic throughout these long experiments. Atropine sulfate (0.1 mg/12 h) and penicillin G (30,000 U/24 h) were administered intramuscularly. Body temperature was maintained at 37°C with a thermostatically controlled heating blanket. Heart rate and respiration rate were monitored. Blood pressure, pulse, and hydration level were continually assayed by viewing the cortical microvasculature at high magnification, and by monitoring skin turgidity. The bladder was evacuated at regular intervals.

The head was stabilized in a stereotaxic apparatus. A wide craniotomy exposed the relevant anterior parietal cortical area. The dura was resected, and a silicon oil well was constructed. The cortical vasculature was photographed, or a computer image of it was recorded by use of a Cohu video camera mounted on a Zeiss operating microscope. This image was magnified $>\times 40$. Images of the dorsal and volar glabrous surfaces of the hands of each monkey were also produced.

Microelectrodes were either glass micropipettes filled with 3.6 M KCl solution ($\sim$22- to 28-μm-diam beveled tips) or parylene-coated tungsten-iridium electrodes (BAK). In either case, impedances measured 1–3 MΩ at 1 kHz. All microelectrode penetrations were parallel and were introduced roughly perpendicular to the cortical surface. Each insertion point was marked on the image of the cortical surface with reference to vascular details. All data were collected at a depth of 700–900 μm below the cortical surface, which corresponds to cortical layers III and IV in these cortical fields in this species. Multiple-unit recordings were amplified, band-pass filtered, and displayed by the use of conventional methods.

Cortical receptive fields were defined by the use of fine-tipped opaque glass probes (tip diameter $<$1 mm). The skin stimulus criterion of just-visible skin indentation was used for all receptive-field definitions. Other studies have shown that just-visible indentation is in the range of $\sim$250–500 μm, which is in the middle of the dynamic ranges of cutaneous mechanoreceptors (see Gardner 1989; Iggo and Andres 1982; Johnson 1974; Talbot et al. 1968). Receptive-field boundaries were carefully drawn on magnified images of the hand surfaces.

Data analysis

All maps were reconstructed by use of a Macintosh II computer. Electrode penetration locations were either reproduced by optically scanning the brain photograph or placed directly onto a computer image of the brain surface during the recording experiment. Boundaries between areas of representation of different hand surfaces were drawn between sampled cortical locations at which receptive fields of neurons were located on different designated skin surfaces. The physiological boundary between areas 3a and 3b was drawn between cortical locations progressing in the posterior-to-anterior direction in which the posterior location had a cutaneous response with a small receptive field near the extreme fingertip and the adjacent anterior location had *1*) a noncutaneous (deep) response, *2*) a significantly enlarged receptive field, or *3*) a sequence reversal in the topographic location of a cutaneous receptive field on the fingers. The physiological definition of this border was usually straightforward, and physiologically defined borders matched the cytoarchitectonically defined borders between these two cortical areas (see Recanzone et al. 1992b).

The receptive-field center was estimated by eye. A small number of receptive fields that included multiple digits or extended onto the palmar pads were not considered in this analysis. Most receptive fields were elliptical in shape, which made shorthand definitions of their locations appropriate. Receptive-field areas were measured on the Macintosh II with the use of the software Canvas. All statistical analysis was done with Statview 512+. The specific statistical tests are described where appropriate in the RESULTS or in figure or table legends. P values <0.01 were taken as demonstrating statistical significance.

Receptive-field overlap was defined with respect to specific comparison receptive fields. Percent overlap was then defined as (area

of skin represented by both receptive fields)/(area of skin represented by the comparison receptive field) × 100.

RESULTS

This report describes the results of experiments that were conducted to investigate the consequences of discrimination training on the response properties of neurons within the hand representation in somatosensory cortical area 3b. Results are presented by comparing the cortical representations of the trained digit with the representations of five classes of controls: *1*) the cortical representation of an adjacent finger on the same hand (this digit was also tested psychophysically; see Table 1); *2*) the cortical representation of the corresponding digit on the opposite, untrained hand; *3*) the cortical representation of an adjacent digit on the untrained hand; *4*) the cortical representation of the digit stimulated in the passive stimulation (auditory discrimination) control monkeys; and *5*) the cortical representation of a digit adjacent to the stimulated digit in this passive stimulation control group. The cortical representation of the trained digit was therefore compared with that of three sets of digits that had never been stimulated in training sessions, with that of one set of digits that were trained only in two or three widely scattered sessions to define the frequency discrimination thresholds at these control locations, and with that of one set of digits that were stimulated with behaviorally unimportant stimuli on the same schedule as the tactually trained animals.

The following nomenclature is adopted: the cortical representations of the hands stimulated in tactually trained animals will be designated as "EE" with the corresponding animal number designated in the previous report and summarized in Table 1 (Recanzone et al. 1992a). The opposite control hemispheres of these same animals are designated "EC." Thus EE-1 denotes the hemisphere representing the experimental, or trained, hand of *animal E1*, whereas EC-1 denotes the hemisphere representing the opposite, untrained hand of *animal E1*. The cortical representations of the stimulated hand in passive stimulation control animals are designated "PS." The hemisphere contralateral to the representation of the passively stimulated hand representation is designated as "PC." The cortical representation of the trained hand in the one animal that did not show an improvement in performance with training is designated "ED-4." The restricted areas of skin described in this report that were stimulated in monkeys trained at the tactile discrimination task are termed "trained" skin, whereas the corresponding skin location on the opposite hand that never received this sinusoidal tactile stimulation are termed "homologous" skin. The areas of skin stimulated in animals trained at the auditory discrimination task are termed "stimulated" skin.

Psychophysically measured thresholds defined in these animals are summarized in Table 1 (Recanzone et al. 1992a). Thresholds on the trained digit are taken as the mean of the three sessions just before the electrophysiological study. Thresholds on the adjacent digit were derived in a single session a few days before the electrophysiological experiment. Four of these five animals achieved thresholds of ~2–3 Hz (mean, 2.27 Hz) on the trained digit. By contrast, all measured thresholds were >3 Hz (mean, 4.35 Hz) when stimuli were applied to a corresponding location on an adjacent control digit in a well-trained animal. The discrimination abilities of one animal did not improve with training even though this monkey (*E4*) received an equivalent number of training sessions and could clearly make appropriate discriminations for frequencies separations >6–8 Hz above the 20-Hz standard (see Recanzone et al. 1992a). The data derived from this unique case will be described separately.

Cortical representational maps

The cortical mapping data shown in this and the following reports were derived in cortical areas 3b and 3a. Cortical area 3b is the focus of this report. The details of the cutaneous representation in area 3a of these animals is the subject of the next report in this series (Recanzone et al. 1992b).

All of the cortical area 3b and 3a hand representations derived in this study are shown in Figs. 1–6. In each figure the electrode penetration locations are indicated by filled dots in the *left panels*, and the hand surface representations reconstructed from this dense cortical receptive-field sample are shown to the *right*. For all drawings, rostral is upward, and the horizontal scale bar represents 500 μm. The hatched region denotes the cortical area of representation of the digit stimulated in the task for experimental and passive-stimulation control hemispheres, and the homologous digit in contralateral control hemispheres. The hand representations of the trained and untrained hands of two monkeys are shown in Figs. 1 and 2, respectively; Figs. 3 and 4 similarly show the representations of trained and untrained hands of two other monkeys. Passive-stimulation control hemispheres from each of these three control monkeys are shown in Fig. 5. Finally, the representations of both hands of the single monkey that did not show a progressive improvement in frequency discrimination performance with training are shown in Fig. 6.

TABLE 1. *Summary of tactile frequency discrimination thresholds*

Animal	Trained Digit	Threshold	Adjacent Digit	Threshold	Number of Sessions*
E1	D3-Right	1.95 ± 0.25	D4-Right	3.75	58
E2	D3-Left	2.22 ± 0.14	D2-Left	3.10	131
E3	D4-Right	2.69 ± 0.24	D3-Right	4.34	110
E4	D3-Right	7.84 ± 5.5	D4-Right	7.67	80
E5	D2-Right	2.20 ± 0.71	D3-Right	6.22	30

Values are means ± SD for the final 3 consecutive days of training on the trained digit, and the single threshold measurement on the session preceding the electrophysiological experiment for the adjacent digit. *Total number of consecutive days from the first session in which thresholds were derived, to the final session on the day before the electrophysiology experiment.

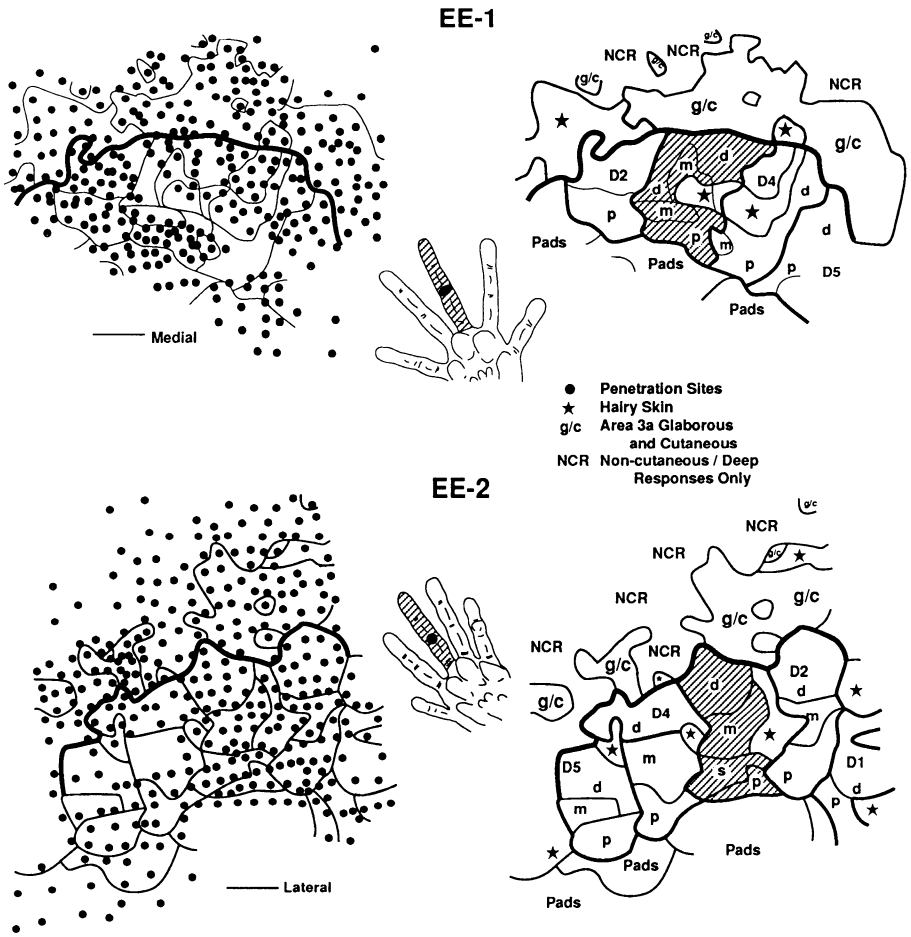

FIG. 1. Cortical representation of the hand surfaces in the hemisphere representing the trained hand in 2 different owl monkeys, *E1* and *E2*. The location of each cortical penetration is shown by the large circles in the *left panel*. The reconstructed representation, or map, of the different hand surfaces are shown in the *right panel*. *Inset*: the hand represented, where the black mark denotes the area of skin stimulated in the behavior, and the hatching indicates the digit stimulated. All cortical locations that responded to stimulation of this digit are also enclosed by hatching. The thick line denotes the physiologically defined area 3a–area 3b border in all figures. Rostral is upward, and the bar represents 500 μm. Lines denote boundaries between different digits and digit segments within each hand representation. d, distal phalanx; m, middle phalanx; p, proximal phalanx; s, receptive fields centered on the stimulation site for case EE-2; Pads, palmar pads; stars, representations of hairy skin in both area 3b (below heavy line) and area 3a (above heavy line). g/c, cortical locations in area 3a that were responsive to cutaneous stimulation of the glabrous skin; NCR, regions in which noncutaneous responses were recorded.

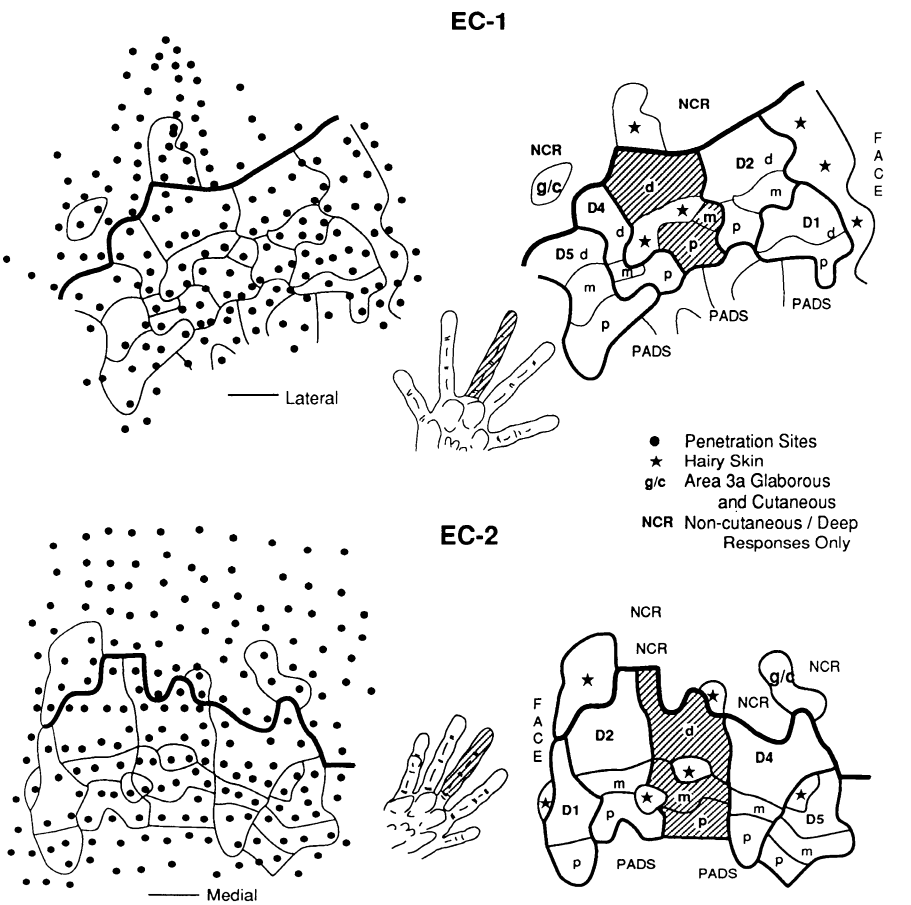

FIG. 2. Cortical representations of the contralateral hand of the 2 monkeys shown in Fig. 1. These hemispheres represent the hand that was not used to discriminate the frequency of the tactile stimulus. Conventions as in Fig. 1.

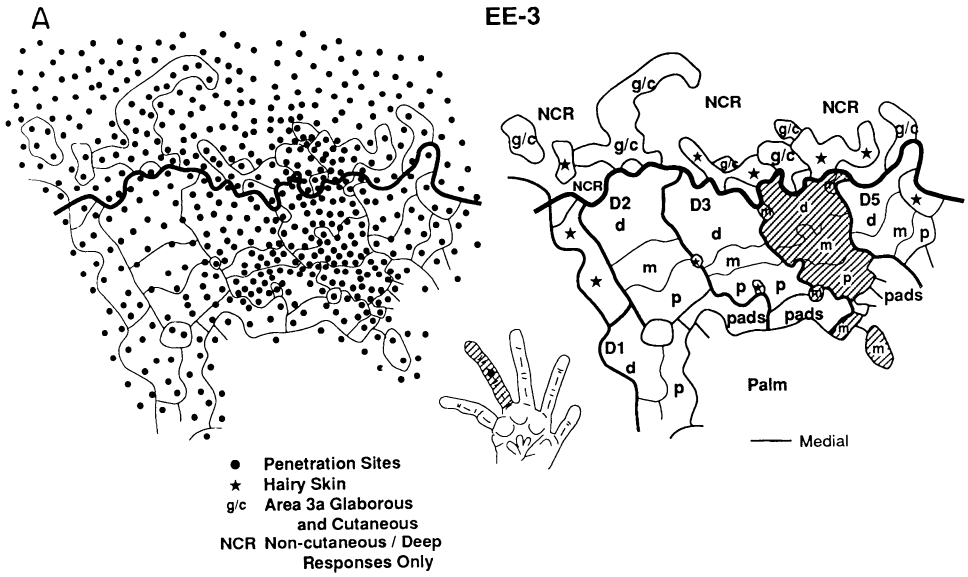

FIG. 3. Cortical representations of the trained hands in the 2 other monkeys that showed significant improvements in performance with training, *E3* (*top*) and *E5* (*bottom*). Conventions as in Fig. 1.

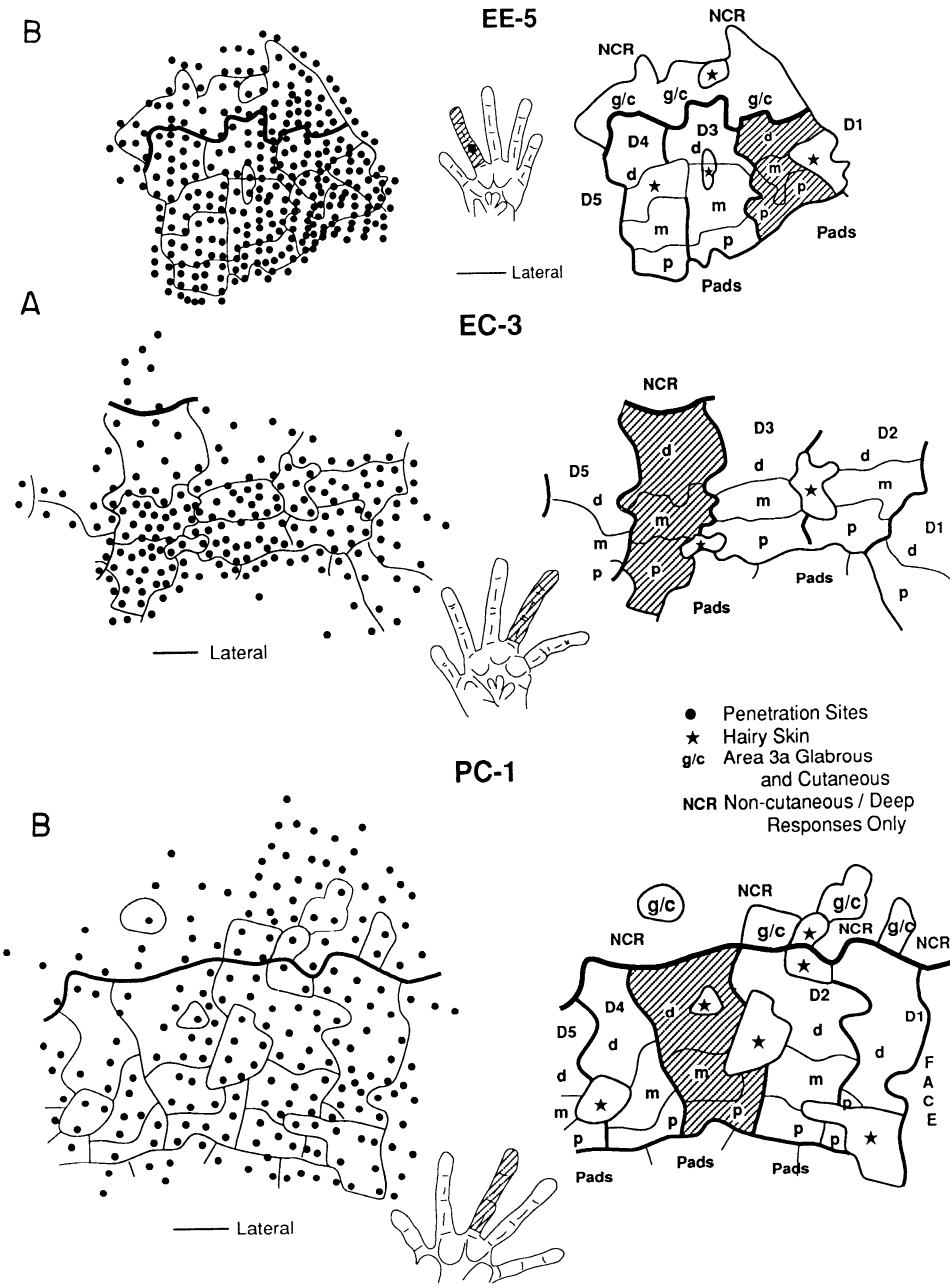

FIG. 4. Cortical representations from the opposite, unstimulated control hand of *monkey E3* (*top*) and from the unstimulated hand of a passively stimulated control, *monkey P1* (*bottom*). These representations are from hands that were never stimulated by the tactile probe, as in the representations shown in Fig. 2.

At first viewing of these representations, there seems to be little difference between experimental and control hemispheres. However, when examined in detail, the topographies of hand surface representations were consistently more complex in experimental hemispheres than in control hemispheres. In every experimental hemisphere, discontinuities were recorded within the representations of individual digits. To cite a few examples, in case EE-1 (Fig. 1, *top*) there was a split representation of the middle phalanx of digit 3, and the representation of the middle phalanx of digit 4 was not located between the proximal and distal phalanges as is usually the case. In case EE-2 (Fig. 1, *bottom*) there was a very large representation of the skin centered on or near the proximal-middle phalangeal joint of digit 3 that spread roughly equally between these two digit segments. This region of skin was stimulated in the behavioral task and is labeled "S" in this cartoon drawing. In case EE-3 (Fig. 3, *top*) there were discontinuous islands of representation of the middle segment of digit 4 located caudally and surrounded by the representation of the palmar pads, and located anteriorly, there surrounded by distal digit representations and area 3a. Finally, in case EE-5 (Fig. 3, *bottom*) the representation of the proximal segment of digit 2 was divided by a representation of the middle segment of the same digit.

A preliminary quantification of this complexity was made for each cortical representation. The number of discontinuities within a single digit was counted, excluding discontinuities between glabrous and hairy skin, and between individual digits. Cases EE-1, EE-2, and EE-3 contained 6, 10, and 7 discontinuities, whereas the more topographically ordered experimental case EE-5 contained only 2. By contrast, the contralateral control hemispheres of these same monkeys were continuous with rare exception, and receptive fields progressed in an orderly, topographic manner all across these cortical hand maps. These control hemispheres contained only 1, 0, and 0 discontinuities (cases EC-1, EC-2, and EC-3, respectively).

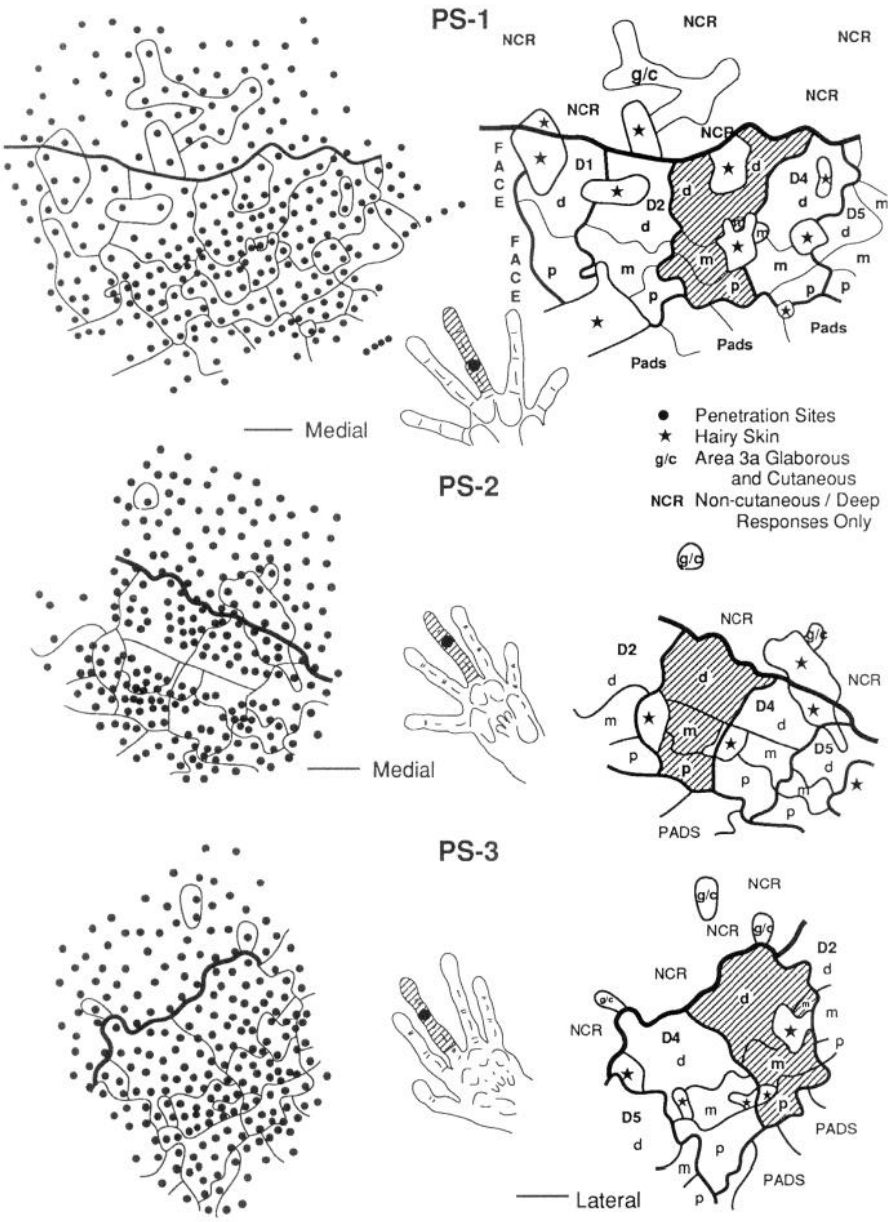

FIG. 5. Cortical representations of each of the 3 passively stimulated control hands studied in these experiments. In each case, the area of skin stimulated in this passive manner is shown in the *inset*. *Monkeys P1, P2*, and *P3* were stimulated on 64, 118, and 108 sessions, respectively. Conventions as in previous figures.

Anomalies of representation were recorded in a less remarkable form in passively stimulated control animals. In case PS-1 (Fig. 5, *top*) a representation of the middle phalanx of digit 3 was split by a representation of the hairy skin, and in case PS-3 (Fig. 5, *bottom*) there was a similar split in the middle phalangeal representation of digit 3 by a zone of representation of hairy skin. The number of nonconventional discontinuities in these hemispheres were 4, 1, and 2 for cases PS-1, PS-2, and PS-3, respectively. Finally, in both of the hand representations in the monkey in which discrimination performance did not improve, no equivalent examples of such topographical anomalies were seen (0 discontinuities, Fig. 6).

Territories of representation of digits in area 3b

Although the cortical representations of the trained hands showed more topographic complexities than control hemispheres, and other representational changes were noted as described in subsequent sections, the areas of representation of stimulated digits were not appreciably different from the areas of representation of any other long digit on the same hand. The total areas of representation for each of the digits in which the entire extent of the digit representation was defined are summarized in Fig. 7. Histogram bars representing trained digits are filled (Fig. 7*A*), and bars representing the passively stimulated digits are cross-hatched (Fig. 7*C*). In all cases, the representation of any single digit was on the order of 1 mm^2, a value consistent with other reports of normal digit representation of the adult owl monkey (Merzenich et al. 1987).

An important issue in measuring cortical areas of representation is the error inherent in the measurement. Cortical locations sampled in these electrophysiological maps were separated by distances on the order of 100–200 μm (see Figs. 1–6). Boundaries of representations were drawn between cortical penetration sites, the neurons of which had receptive fields centered on different hand surfaces, or were scaled between penetration sites proportionally if they included both hand surfaces. This led to a possible error of the estimation of boundary position of 50–100 μm at any given boundary location. However, this error will tend to cancel because there are many sites of determination of these boundaries in the representation of any given skin surface. Given this sampling density, the errors in estimating cortical areas of representation are small (see Merzenich et al. 1987; Stryker et al. 1987) (also see DISCUSSION).

Enlarged representation of the trained skin

The central issue of this electrophysiological study is how the behavioral training affected the cortical representation of behaviorally engaged skin. This question was addressed by defining the cortical territory of representation of the skin stimulated directly in the behavior. The representations of skin areas of corresponding size and location on an adjacent digit as well as on the homologous digits on control hands were used for comparison. This analysis revealed that *the representation of the stimulated skin was larger than control skin sites in all trained monkeys*. Figure 8 shows reconstructed maps highlighting all cortical penetrations that included some or all of the trained skin (dark stipple), the homologous skin on the adjacent digit (light stipple), or both skin surfaces (cross-hatched). The *inset* shows the stimulated skin site (black dot) and its equivalent on an adjacent finger (stippled dot). The expanded repre-

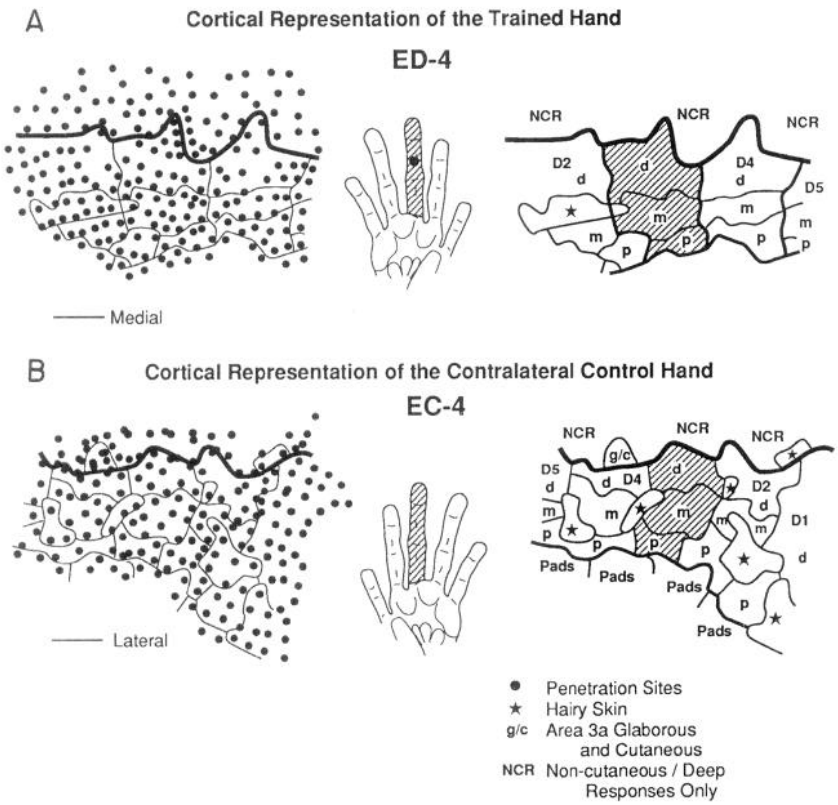

FIG. 6. Cortical representations of the hand trained in the tactile task (*top*) and the opposite, unstimulated control hand (*bottom*) from the 1 monkey that did not show an improvement in performance with training (*monkey E4*).

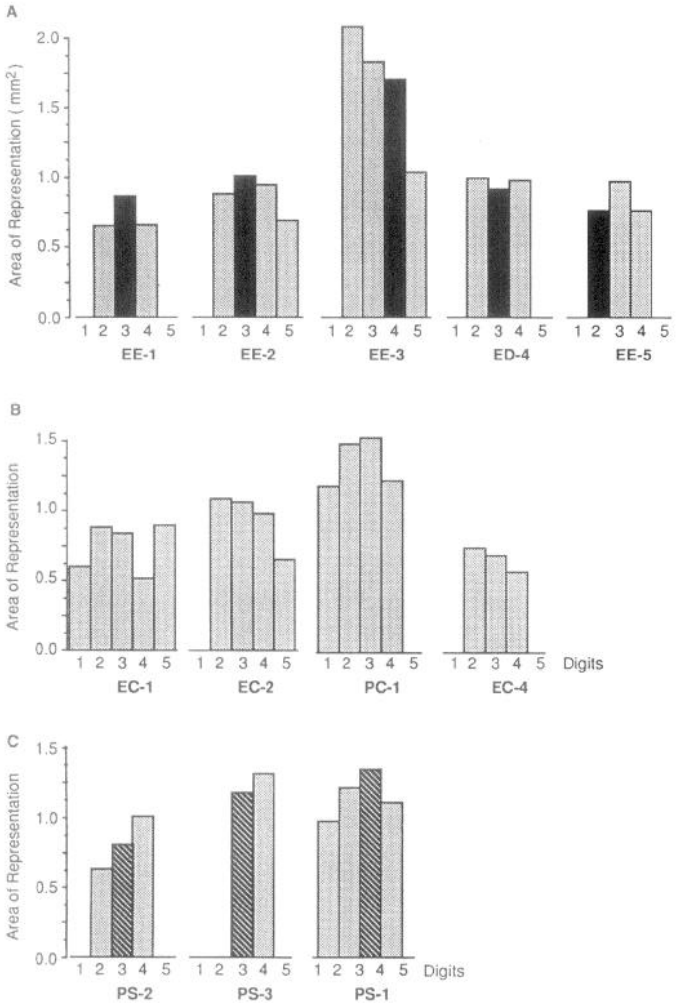

FIG. 7. Total area of representation (in mm^2) of the entire glabrous surface of each digit in all studied monkeys. The representations of the hands trained in the tactile task are shown in *A*, the representations of the opposite, unstimulated control hands are shown in *B*, and the representations of the passively stimulated hands are shown in *C*. The filled bars represent digits that were trained in the task (*A*); dark hatched bars represent digits that were stimulated in the passive stimulation paradigm (*C*).

sentation of the trained digit was not restricted to a topographically continuous region of cortex but could be discontinuous. Examples are illustrated in the *top left* of Fig. 8 (case EE-1), where two penetrations had formed an island of digit 3 representation within the representation of digit 2, and one rostral near the area 3a–area 3b border. Similar discontinuities occurred forming islands of representation displaced rostrally (cases EE-1, EE-2, and EE-5) as well as caudally (case EE-3).

The representation of corresponding areas of skin on the opposite, untrained hand were smaller than the representations of the trained digit (Fig. 9). The representation of the homologous skin in the other hemisphere generally occupied a discrete region. This region was topographically appropriate, reflecting the orderly progressions of receptive-field locations encountered in the control hemispheres. In the control hemisphere of one monkey (*E1; top left*), there were no receptive fields that extended over a skin location on digit 3 that was equivalent to that engaged in the behavior in experimental cases.

Reconstructions from passive-stimulation control animals are shown in Fig. 10. Discontinuities were recorded in one of these monkeys (PS-3, *top right*). In all of the passive-stimulation control hemispheres, the representations of these restricted skin surfaces were small and confined to an area within the "appropriate" region of 3b. They were, in every case, smaller than representations of the trained digit in experimental hemispheres. At the same time, they were generally very modestly (but with this small sample, not statistically significantly) larger than representations recorded in naive controls.

Finally, Fig. 11 illustrates the cortical representations of the stimulated and unstimulated hands for *animal E4*, the discrimination thresholds of which did *not* substantially improve with training. The stimulated hand (*left*) showed small discontinuities for both digits 3 and 4; in both cases these discontinuities were separated by a single electrode penetration. There was a smaller representation of these restricted skin regions for both digits in the control hemisphere (*right*), when compared with their representation in the cortex contralateral to the stimulated hand (*left*).

This analysis shows that the cortical territory of representation of the stimulated skin expanded differentially when compared with similar skin areas on other, nonstimulated digits. This difference is summarized by comparing the absolute cortical areas of representation of these restricted skin areas (Fig. 12). The representation of the stimulated skin in hemispheres representing trained digits (TD; filled bars) is 1.4–3.2 times larger than the area of cortex contributing to the representation of an adjacent digit (AD; stippled bars). The area of representation of the homologous skin area in the contralateral hemisphere (CD; light cross-hatching) was always less than that of the experimental hemisphere, and equivalent in area to the representation of its own adjacent digit (ACD; open bars). The area of representation of the trained skin was the smallest for the monkey with the poorest behavioral performance (ED-4 in Fig. 12*B, left*). The passive-stimulation control hemispheres (Fig. 12*C*) showed a similar result, i.e., representations were small, but were modestly larger than those of corresponding skin surfaces in the opposite hemisphere. In every case the representation of the skin area stimulated in the behavioral task was larger than the representation of adjacent digits.

Inspection of the data summarized in Fig. 12 shows that the absolute area of representation of these skin surfaces varied considerably among cases. This was also true for the representations of equivalent skin regions on adjacent digits, and on corresponding skin sites on the opposite hand. The behavioral discrimination thresholds for the trained and adjacent skin surfaces also varied, although over a smaller range (see Table 1). These data were subjected to regression analysis. The correlation between the behavioral threshold and the cortical representation of the entire digit is shown in Fig. 13*A*. These two parameters were not correlated ($r = 0.045$; $P = 0.913$). *B* shows the correlation of the behavioral threshold with the cortical representation of the entire restricted skin region. This correlation coefficient is much larger, increasing to 0.749 with the slope of the best-fit line equal to −10.125, but did not reach statistical significance by our criteria ($P = 0.0126$). This analysis suggests

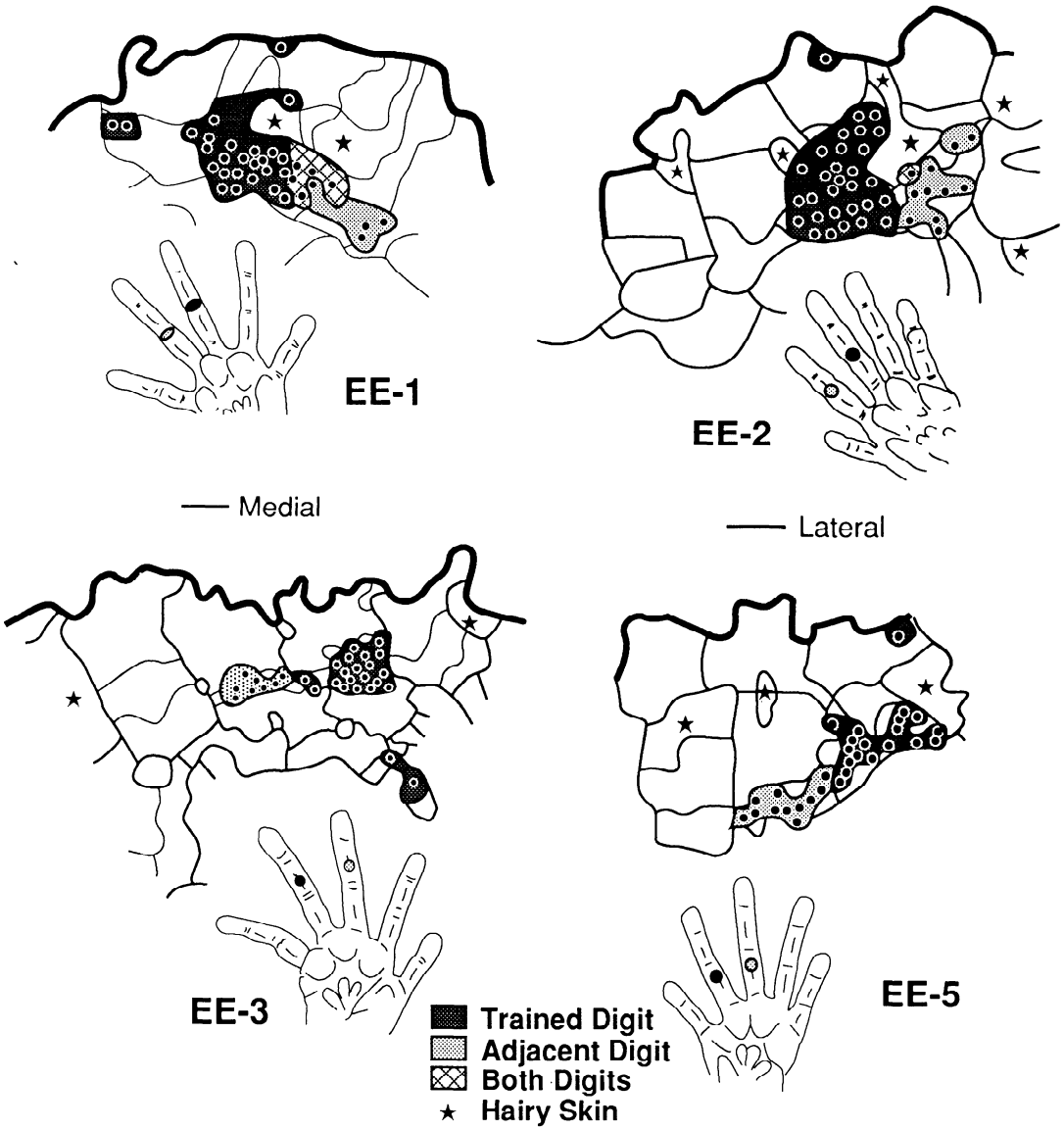

FIG. 8. Cortical representations of the small area of skin trained in the tactile discrimination task (dark stippling), the corresponding location on an adjacent, untrained control digit (light stippling), or to both digits. Each panel represents a different monkey that showed an improvement in performance with training. Stars denote locations of hairy skin representation.

that there may be a rough correlation between the area of representation and the improvement in behavioral performance with training.

Receptive-field sizes

The previous analysis revealed that the cortical area of representation of a restricted skin area expanded in trained hemispheres, even though the cortical area of representation of the entire digit was equivalent to those of control digits. One might expect that the increase of the cortical representation of a restricted skin field would result in a corresponding decrease in receptive fields over this skin region. That prediction is based on the "inverse rule" that applies to normal animals, by which receptive-field sizes are inversely related to the areas of the cortical representation of specific skin sectors (Sur et al. 1980).

In contrast to this expectation, the sizes of receptive fields increased in the zone of representation of the trained digit when compared with receptive fields representing the adjacent digits and the control hands. A random sample of receptive fields defined within area 3b representing hands trained in the task is shown in Fig. 14. The only exception was seen in *animal E5* (*bottom right*). This monkey's performance did improve (Table 1), and in this monkey there was an increase in the cortical territory of representation of the behaviorally engaged skin in area 3b (see Fig. 12). In all of the successfully trained animals, receptive fields were more densely located on the stimulated digit (stimulation sites are marked by black dots; digit 3 for cases EE-1 and EE-2, digit 4 for case EE-3, and digit 2 for case EE-5 in Fig.

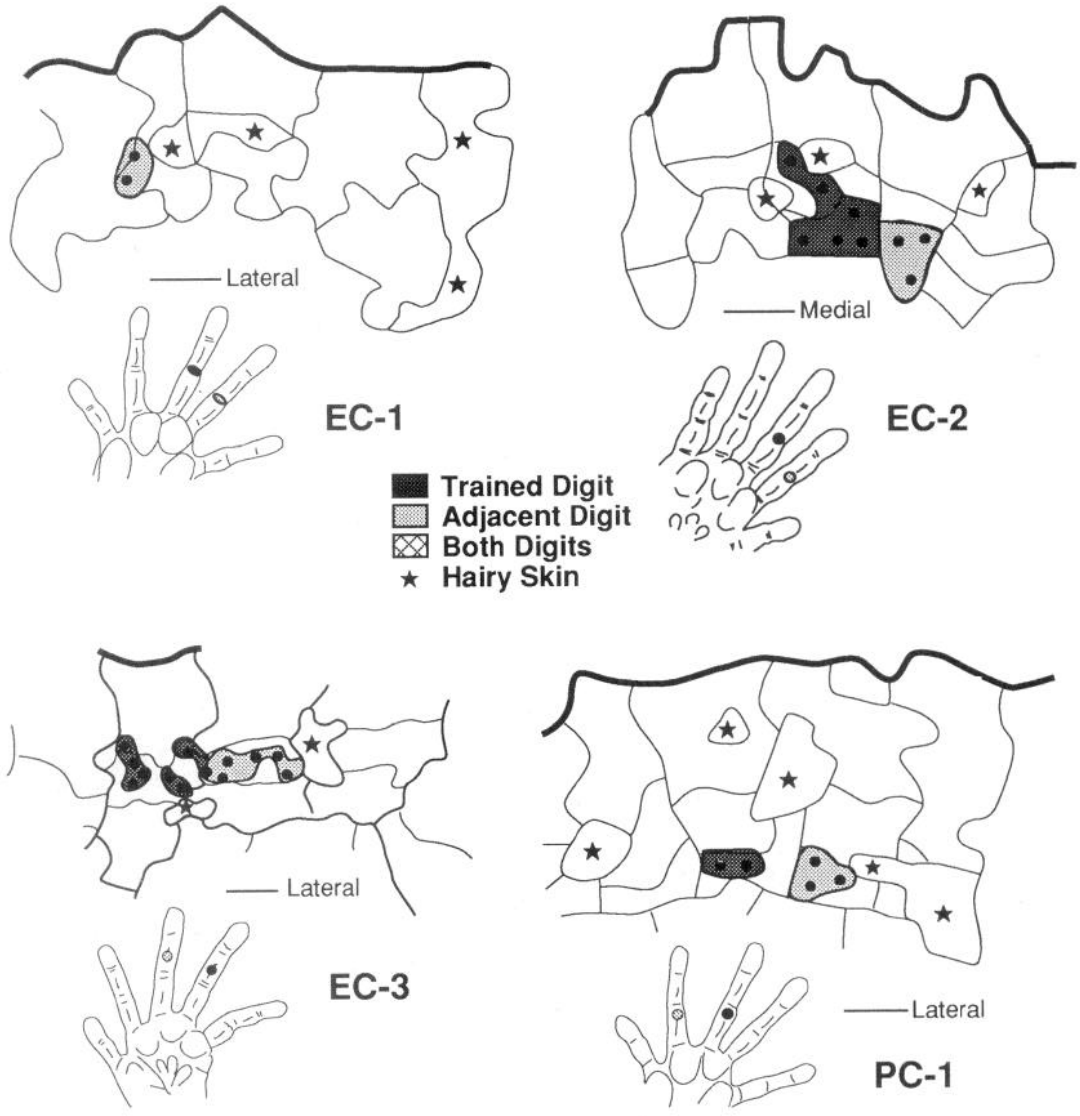

FIG. 9. Cortical representations of the corresponding skin locations as shown in Fig. 8 for the opposite, unstimulated control hands. Cases EC-1, EC-2, and EC-3 represent the unstimulated hands of monkeys trained in the tactile discrimination task; case PC-1 represents the unstimulated hand from a monkey trained in the auditory discrimination paradigm. Conventions as in Fig. 8.

14). By comparison, the contralateral control hands had receptive fields that were more evenly distributed across the glabrous surface and were generally smaller in size (Fig. 15).

The receptive fields representing the stimulated digit of *animal E4*, which never showed improvements in tactile frequency discrimination despite intensive training, were also increased in size (Fig. 16). This animal was stimulated for 80 training sessions, so one possibility is that either stimulation alone or behaviorally attended stimulation alone can result in this enlargement of receptive-field sizes. If the former was the case, similar receptive-field size increases should be observed in the representations of passively stimulated hands. In fact, in these hemispheres the receptive fields were more similar to those of control hemispheres, although there were limited pockets of dense representations for each hand (Fig. 17).

Statistical analyses were performed to quantitatively compare receptive-field sizes within and between these cases. The receptive-field size means and standard errors are summarized for each digit in each case in Table 2. In all experimental hemispheres except EE-5, the receptive-field sizes over the trained digit were statistically significantly larger than those on other digits (unpaired 1-tailed t test, $P < 0.01$). In case EE-1, the receptive-field sizes on digit 4 were also significantly different from control digits 1, 2, and 5 but were not significantly different from the behaviorally engaged digit 3. In every other case there were no statistically significant differences between the receptive-field sizes on untrained digits of the same hand. This was true of both the opposite hemisphere controls and the passively stimulated controls.

Receptive-field sizes were also compared between hemispheres in cases in which both hemispheres were mapped.

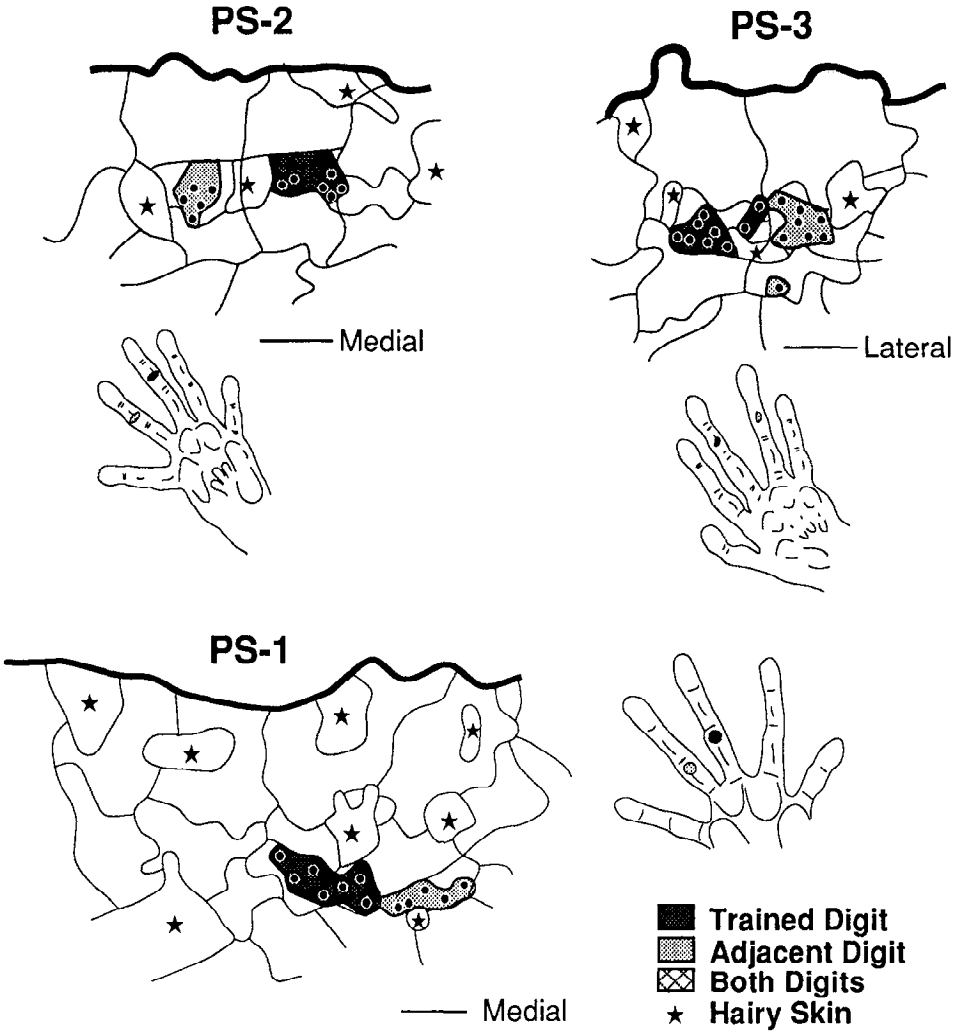

FIG. 10. Cortical representations of the areas of skin stimulated in the passive stimulation paradigm (dark stipple) and the corresponding skin on an adjacent, unstimulated digit (light stipple). In no cases were there cortical locations that had receptive fields encompassing both skin regions. Conventions as in Figs. 8 and 9.

The results of this analysis are summarized in Table 3. In every case, receptive-field sizes measured on the digit trained in the task (bracketed) were significantly larger than those measured on the corresponding, unstimulated digit on the contralateral hand. This cross-hemisphere comparison also revealed a statistically significant increase of receptive-field sizes on several of the adjacent, unstimulated digits on the trained hand. Only one hemisphere was investigated in passive stimulation control *animals P2* and *P3*.

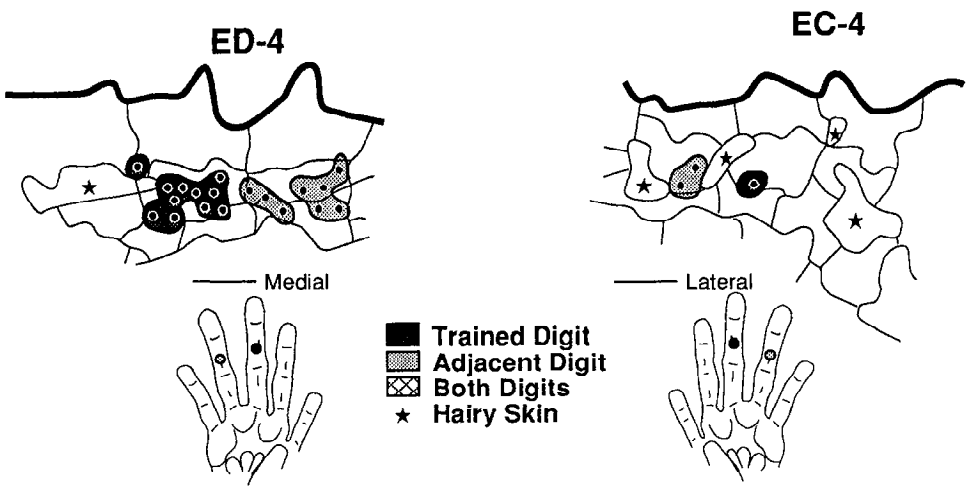

FIG. 11. Cortical representations of the hand trained in the tactile discrimination task (*left*) and the opposite, unstimulated hand (*right*) for the 1 monkey that did not show an improvement in performance with training, *E4*.

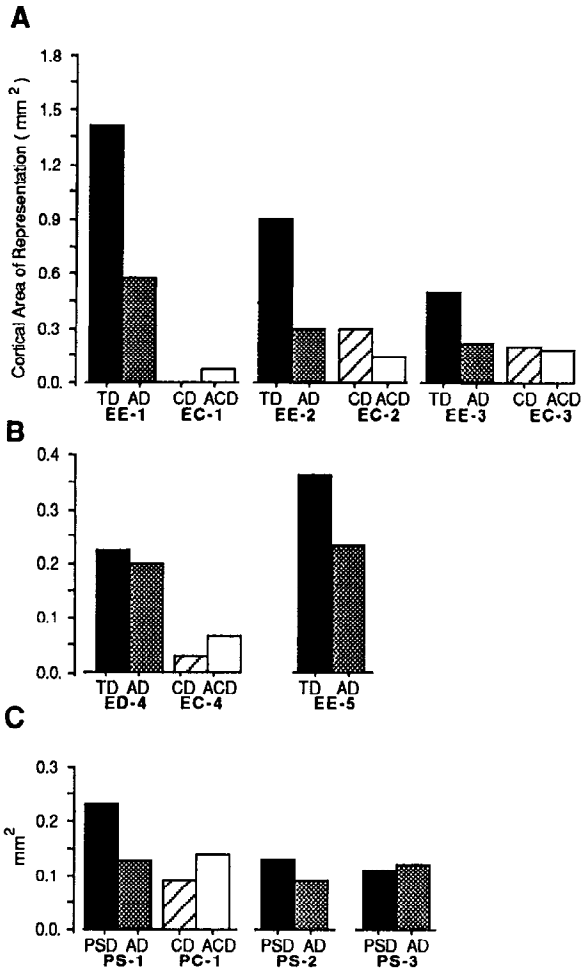

FIG. 12. Cortical areas of representation of the restricted skin regions shown in Figs. 8–11. *A* and *B*: results from monkeys trained in the tactile discrimination task. *C*: results from the passive stimulation monkeys. Filled bars denote the area of representation of the trained skin (TD) in experimental hemispheres, or the stimulated skin (PSD) in passively stimulated monkeys. Light hatched bars denote the corresponding skin of the opposite hand (CD). The stippled bars denote the area of representation of the skin on the digit adjacent to the stimulated digit (AD), and the open bars denote the corresponding skin location on the opposite, unstimulated hand.

Distributions of receptive-field sizes

The apparent training-induced increase in receptive-field sizes raises the question of whether all, or only a subset of, receptive fields increased in size. The receptive-field size distribution for all neurons recorded in area 3b in four representative cases are shown in Fig. 18. In this figure the distribution of size for receptive fields located on either the stimulated digit or the homologous digit in the contralateral hemisphere are shown in the *left column*. Results of the same analysis for receptive fields located on an adjacent digit of the same hand are illustrated in the *right column*. The receptive fields located on the trained and adjacent digits from the experimental hemisphere of *animal E1* (Fig. 18*A*) had a broad distribution when compared with the receptive fields defined for neurons in the contralateral control hemisphere from this same animal (Fig. 18*B*) or to those defined in the control hemispheres of a passive-stimulation control animal (PS-3 in Fig. 18*D*). The number of large receptive fields located on the stimulated digit was greater in the experimental hemispheres, yet distributions for receptive fields on adjacent digits were also clearly broadened. Results in *animals E2, E3*, and *E4* were similar to those for *animal E1*.

Paradoxically, the well-trained *animal E5* did not show a statistically significant increase in the size of receptive fields defined on digits of the trained hand, and the receptive-field size distributions were essentially equal for those located on stimulated and control digits (Fig. 18*C*). In passive stimulation hemispheres, receptive-field size distributions were essentially identical to those of the control hemispheres (Fig. 18*D*). In every case studied, including all experimental hemispheres, there were a significant number of receptive fields that were small and that fell into size bins of <30 mm^2. The largest differences between experimental and control hemispheres was the number of receptive fields that were >30 mm^2. From these analyses, it is concluded that only a subset of receptive fields increased in size as a result of the behavioral discrimination training.

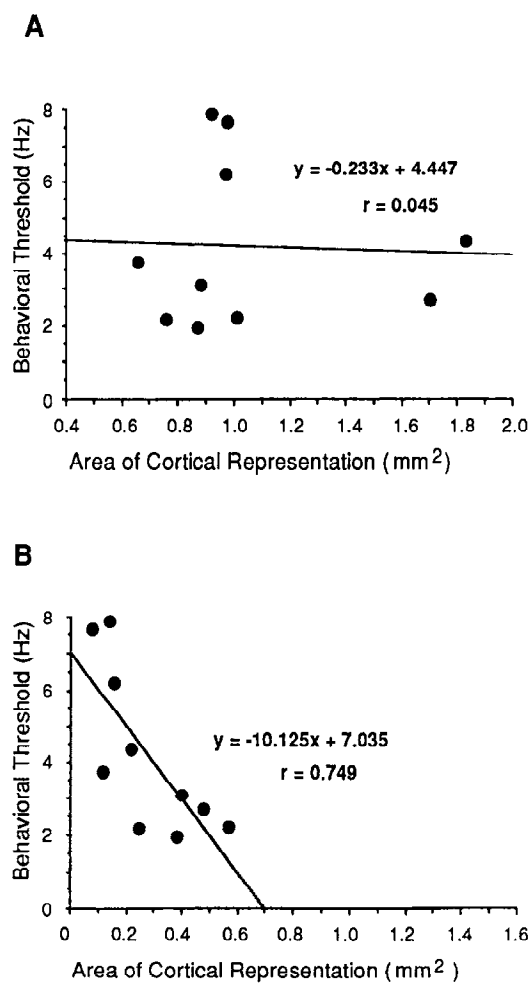

FIG. 13. Regression analysis of the behavioral threshold measured at each of 10 different skin locations in the 5 tactually trained monkeys (*x*-axis) vs. the cortical area of representation of either the entire glabrous surface of the digit (*A*) or just the restricted skin region stimulated (*B*).

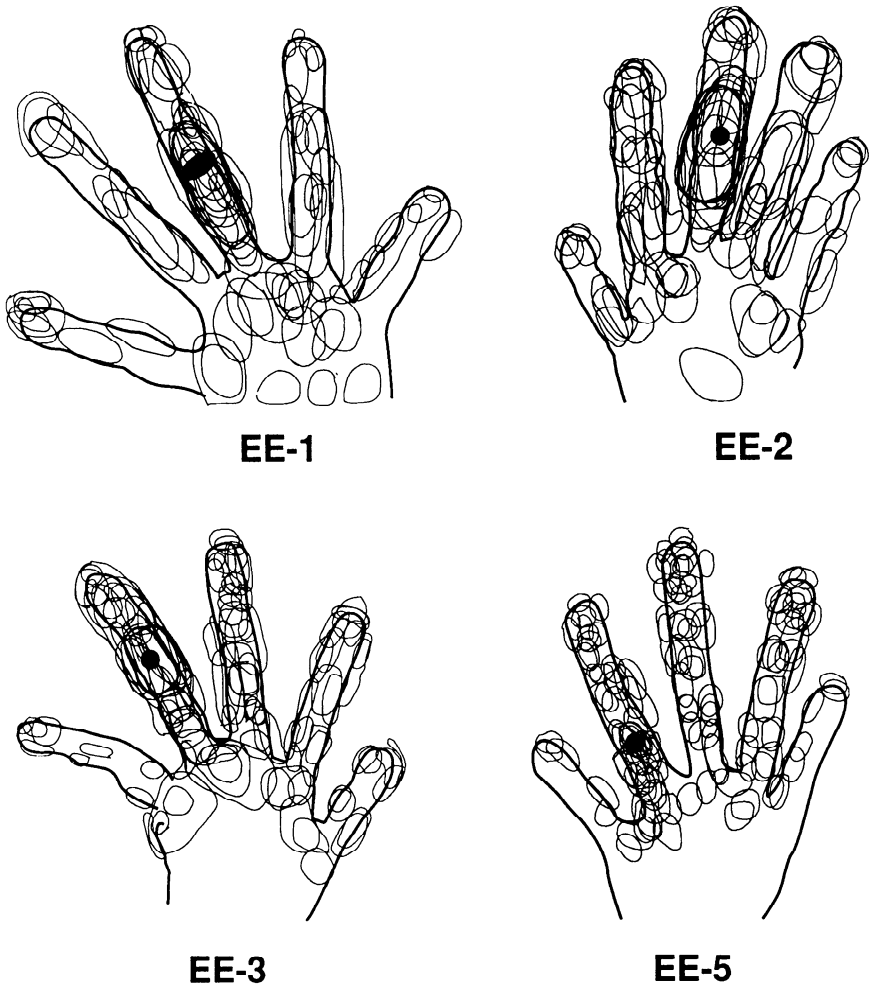

FIG. 14. Representative receptive fields defined in area 3b on the trained hands of each of the 4 monkeys that showed an improvement in performance with training. The probability that the receptive field for any cortical location is included in this figure was 33–50%. This probability was set to give approximately the same number of receptive fields in each figurine. Filled circle denotes the area of skin trained in the behavioral task. This skin location was on digit 2 for cases EE-1 and EE-2, digit 4 for case EE-3, and digit 2 for case EE-5.

Topographic distribution of larger receptive fields

The cortical locations of receptive fields of different sizes are illustrated with reference to the area 3b map for two representative experimental hemispheres in Fig. 19. In this figure the locations of cortical penetrations are illustrated in the *top panels*. The lines running through the large symbols are labeled to correspond to the graphs illustrated in the *bottom panels*. Receptive fields located on different digits are indicated by the different symbols (filled circles, digits 1, 3, and 5; open circles, digits 2 and 4; squares, receptive fields representing the stimulated skin). Graphs are offset in the *bottom panels* for clarity. The *left panel* shows the data from case EE-2. The largest receptive fields corresponded to an area of representation of the stimulated skin (squares). There was also some increase in receptive-field sizes recorded for neurons sampled in immediately adjacent cortical penetrations. In each case there were a few examples of cortical receptive fields that included the trained skin that were no larger than receptive fields that were far removed from the representation of this skin site. A second example (case EE-3) is shown in the *right panel*. Again, *the largest receptive fields were centered on locations representing behaviorally engaged skin*. The receptive fields neighboring this region were also somewhat larger in size, whereas the smaller receptive fields were most commonly observed distant to the representation of the stimulated skin.

Internal topography of the representation of individual digits

These topographically localized receptive-field size increases could be accounted for in many different ways. For example *1*) all of the receptive fields near the stimulated skin could have expanded symmetrically. *2*) Receptive fields originally representing skin surfaces near the stimulated skin could have expanded asymmetrically to incorporate this skin into a larger receptive field. *3*) Receptive fields could have enlarged and moved to become centered on the stimulation site. The obvious clustering of receptive fields over the stimulated skin (Fig. 14) is more consistent with the second or third of these possibilities.

To further address this question, the distances from the base of the digit to the geometric center of each receptive field were plotted as a function of the distance of the electrode penetration measured from a line drawn orthogonal to the representation of this axis of the digit. This straight line was roughly parallel to and was located slightly caudal to *lines E* and *F* of the *left* and *right* panels of Fig. 19, respectively. This compressed the data so that it could be plotted as a function of linear distance. If receptive fields

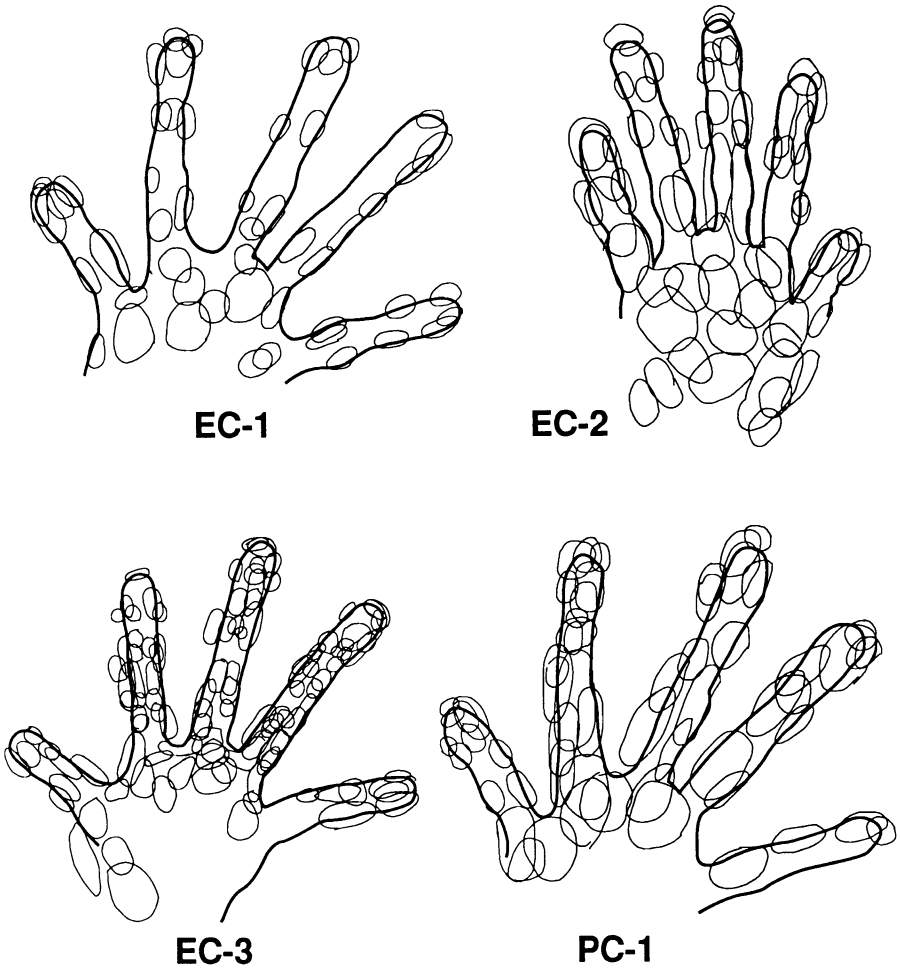

FIG. 15. Representative receptive fields defined in area 3b on the opposite, untrained hand of 3 monkeys trained in the tactile discrimination task (cases EC-1, EC-2, and EC-3) and the unstimulated hand of 1 monkey trained in the auditory discrimination task (PC-1). The probability that a receptive field would be shown in this figure was 50%. These hands did not receive sinusoidal tactile stimulation.

expanded symmetrically, the geometric centers of the receptive fields would not change, and this function would roughly follow a straight line. If the expansion was asymmetric, the geometric centers would cluster around the stimulated skin, and the slope of the receptive-field center versus cortical distance function should be decreased. If the receptive fields moved to incorporate the stimulated skin, the same geometric center of receptive fields should be recorded over a large cortical distance.

The results of this analysis suggest that many receptive fields moved to become centered on the stimulated skin of the trained digit. The receptive fields centered on the

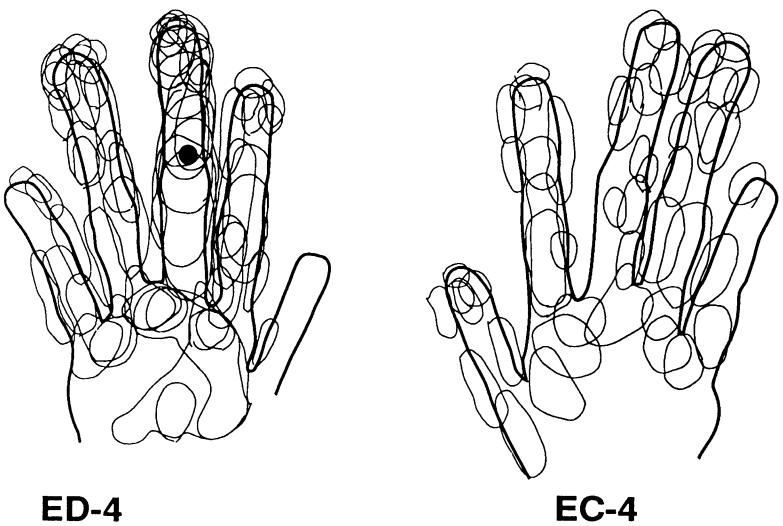

FIG. 16. Representative receptive fields defined on the hand trained in the tactile discrimination task (*left*) and on the opposite, unstimulated control hand (*right*) from the 1 monkey that did not show any improvement in performance with training.

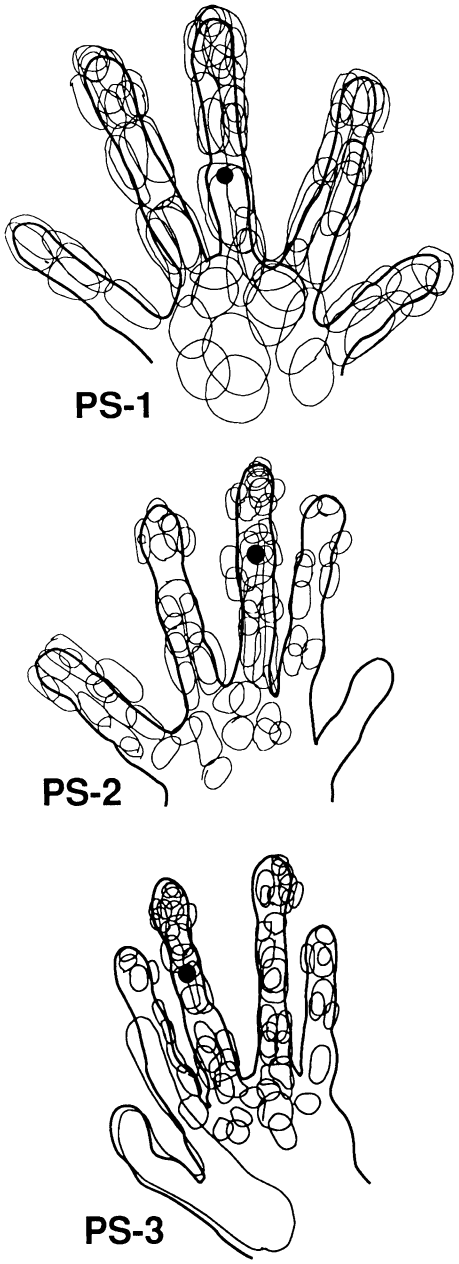

FIG. 17. Representative receptive fields defined on the hands that were passively stimulated in animals trained at the auditory discrimination paradigm. Probabilities determined as in Fig. 1. Black regions denote the small area of skin stimulated in the task.

trained digit (Fig. 20*A*) clustered at a skin distance corresponding to the stimulus probe location, centered 11 mm from the base of the finger (arrow). Receptive fields with geometric centers at this location were represented over a cortical distance of >500 μm. The control digits (Fig. 20, *B* and *C*) had a fairly linear distribution in comparison. The same analyses in the other monkeys yielded similar results.

Percent overlap of receptive fields as a function of cortical distance

A second method to test how receptive fields expanded over the trained skin representation is to measure the percent overlap of receptive fields representing these digits. The percent overlap between the receptive fields at two cortical locations is normally roughly inversely related to the cortical distance between them, regardless of the body surface representation or receptive-field size (Merzenich et al. 1983a; Sur et al. 1980). If receptive fields expanded asymmetrically to include the trained skin, there should be a modest increase in overlap between receptive fields located near the stimulation site, but this overlap would not be complete because the expanded receptive fields would still retain their original, nonoverlapping parts. Alternatively, if receptive fields moved to be centered on the stimulation site, the percent overlap should approach 100% for receptive fields representing the stimulated skin throughout a large area in the cortex.

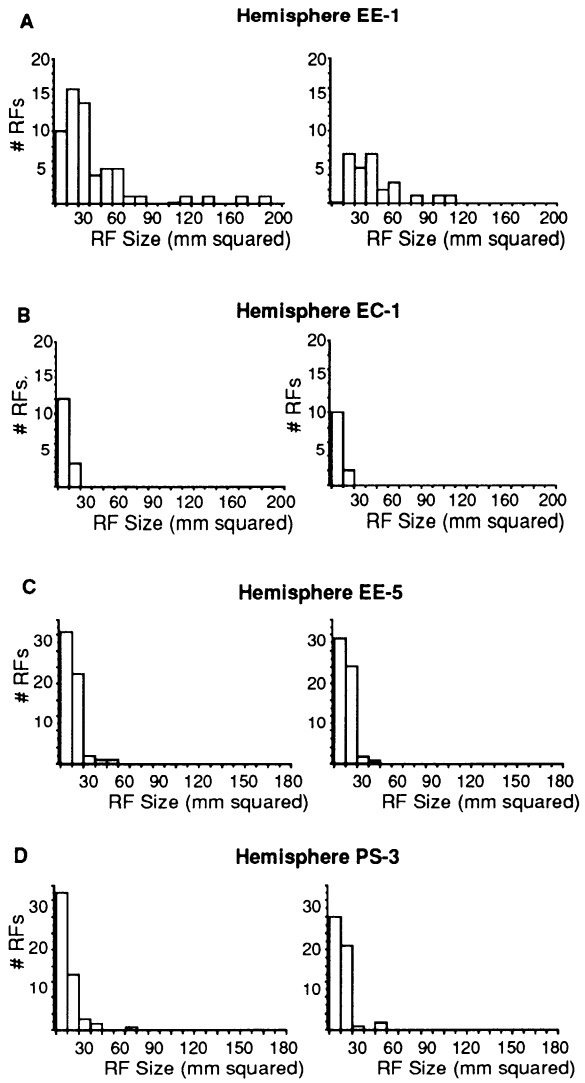

FIG. 18. Distribution of receptive-fields sizes located on 8 different digits represented in 4 hemispheres. The *top panel* shows the receptive-field size distributions from the trained hand of *monkey E1*. The trained digit is in the *left panel*; the untrained, adjacent digit is in the *right panel*. The homologous digits on the opposite, unstimulated hand from this same monkey are shown in *B*. Distributions for the trained (*left*) and adjacent (*right*) digits of the 1 monkey with small receptive fields (*E5*) is shown in *C*. *D*: distributions for the stimulated (*left*) and adjacent (*right*) digits for a passively stimulated control monkey (*P3*).

TABLE 2. *Summary of receptive-field size statistics*

Case	D1	D2	D3	D4	D5
			Experimental hemispheres		
EE-1	14.2 ± 3.7	20.7 ± 4.6	[32.1 ± 5.4]	30.5 ± 3.6*	21.2 ± 4.0
EE-2	12.3 ± 1.7	28.4 ± 3.7	[52.8 ± 5.0]*	28.3 ± 24.7	16.9 ± 2.8
EE-3	13.5 ± 1.5	14.1 ± 1.2	15.2 ± 1.4	[43.3 ± 5.5]*	8.9 ± 2.3
ED-4	ID	23.5 ± 3.3	[45.4 ± 4.21]*	25.7 ± 3.0	23.5 ± 8.9
EE-5	18.8 ± 8.9	[11.5 ± 0.8]	10.5 ± 0.6	1.1 ± 0.6	9.2 ± 0.4
			Control hemispheres		
EC-1	18.9 ± 5.4	10.7 ± 2.5	7.6 ± 0.6	9.1 ± 0.9	7.9 ± 0.5
EC-2	14.3 ± 2.3	11.8 ± 1.2	12.5 ± 1.8	9.5 ± 1.5	7.9 ± 0.5
EC-3	7.8 ± 1.0	6.0 ± 0.6	8.5 ± 1.1	9.07 ± 1.3	10.0 ± 1.23
EC-4	ID	19.6 ± 2.3	16.2 ± 3.0	18.2 ± 2.3	19.3 ± 3.5
PC-1	9.7 ± 1.4	13.7 ± 1.7	16.6 ± 1.3	20.0 ± 2.5	14.4 ± 2.1
			Passive-stimulation hemispheres		
PS-1	21.4 ± 2.1	24.1 ± 2.4	[19.0 ± 1.4]	23.9 ± 1.8	20.8 ± 1.7
PS-2	ID	9.9 + 0.8	[15.6 ± 1.8]	15.4 ± 1.9	18.9 ± 2.4
PS-3	ID	11.5 ± 2.8	[9.5 ± 0.7]	10.5 ± 1.3	8.0 ± 0.9

Values are means ± SE of receptive-field areas and are measured in millimeters squared. Brackets indicate the digit either trained in the task (*Experimental hemispheres*), the homologous digit (*Control hemispheres*), or passively stimulated (*Passive-stimulation hemispheres*). Data from digits 1 through 5 are shown (D1–D5). ID, insufficient data. *$P < 0.01$ 1-tailed unpaired t test.

This analysis was restricted to a sample of cortical locations with receptive fields on the central third of the glabrous skin of the digit, thus eliminating receptive fields located on the far ulnar and radial aspects of the digit. The percent overlap was then measured for every cortical location with respect to six to eight cortical locations with their receptive fields (reference receptive fields) scattered throughout the proximal-distal aspect of the digit. These reference receptive fields were chosen by selecting cortical locations that were uniformly scattered throughout the representation of the digit, without prior knowledge of their specific receptive fields. The percent overlap was taken as the area of overlap divided by the area of the reference receptive field × 100. This percent overlap was then plotted against the cortical distance between the two locations. The combined results from all of the reference cortical locations plotted for three different digits from *animal E2* are shown in Fig. 21. Included in these plots are the theoretical functions of receptive-field overlaps ranging from 100% at zero cortical distance to 0% overlap at a cortical distance of 600 μm (see Sur et al. 1980). The percent overlap with cortical distance does not decrease uniformly for the trained digit (Fig. 21*A*). There were several instances in which receptive fields on the trained digit overlapped by 100% at cortical distances of up to 500 μm. Significant overlap was observed beyond 600 μm in cortical distance. All overlap was down to zero beyond 1,000 μm, with one exception.

The same analysis on the adjacent digit of this monkey revealed a slightly more organized and very crudely inverse relationship between overlap and cortical distance (Fig. 21*B*). In only four instances was there any overlap of receptive fields recorded for cortical locations separated by >600 μm. The percent overlap functions for the contralateral hemisphere were more reasonably inversely related to cortical distance (Fig. 21*C*). The function shown in this graph is in rough agreement to that of the normal owl monkey (Sur et al. 1980).

Further analysis revealed that the high degree of overlap was mainly confined to the representation of the trained digit. This is illustrated for two digits in case EE-2 in Fig. 22. Three cortical locations were selected that had receptive fields on the proximal (filled circle), middle (filled diamond), or distal (filled star) segments of the digit (see cartoons at the *top* of Fig. 22). The percent overlap was measured as the distance along the long axis of the finger with respect to the selected cortical locations of reference receptive fields shown in the graphs below. The representation of the trained digit is to the *left*. The *middle panel* (filled diamonds) represents results from the overlaps onto a receptive field that was centered on the trained skin. The greatest overlap of receptive fields with cortical distance was seen within the representation of the trained skin in each studied monkey with increased receptive-field sizes. The results from the adjacent digits and those in untrained hemispheres were better described by a roughly inverse function.

TABLE 3. *Summary of receptive-field size comparisons between hemispheres*

Animal	Digit 1	Digit 2	Digit 3	Digit 4	Digit 5
E1	NS	NS	[†]	†	*
E2	NS	NS	[†]	*	NS
E3	NS	†	†	[†]	NS
E4	ID	NS	[†]	*	NS
P1	†	†	[NS]	NS	*

Unpaired 2-tailed t test using the population of receptive fields shown in TABLE 2. Brackets denote the digit either trained (*E1–E4*) or passively stimulated (*P1*). NS, not significant; †, $P < 0.01$; *, $P < 0.05$; ID, insufficient data.

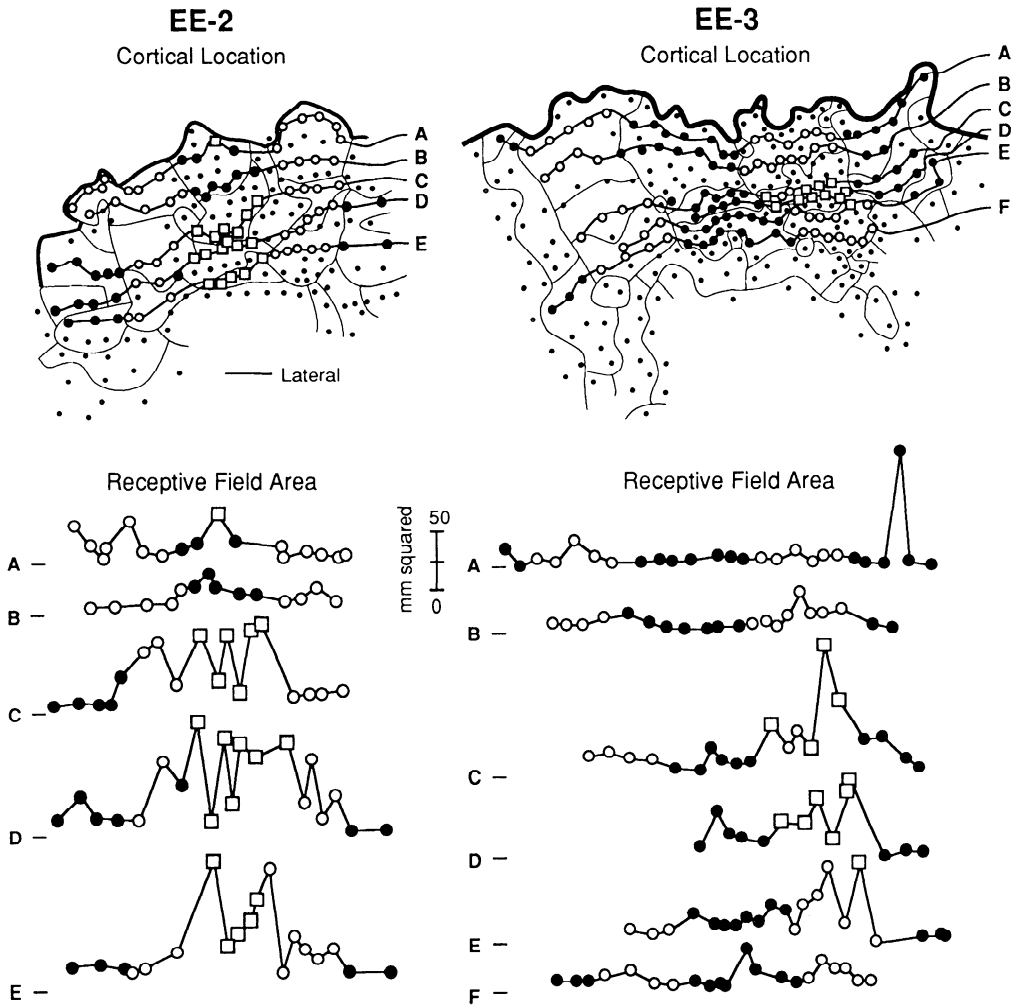

FIG. 19. Cortical location of receptive-field sizes in 2 experimental hemispheres, EE-2 (*left*) and EE-3 (*right*). *Top panel* shows all cortical penetration locations. Large symbols connected by solid lines mark the cortical locations used to plot receptive-field sizes in the *bottom panel*. Small dots denote cortical locations not used in this analysis. The different symbols represent different digits: filled circles, digits 5, 3, and 1; open circles, digits 2 and 4; open squares, receptive fields on the trained skin. *Bottom panel* shows the receptive-field size for each cortical location indicated in the *top panel*. These graphs are offset for clarity. See text for details.

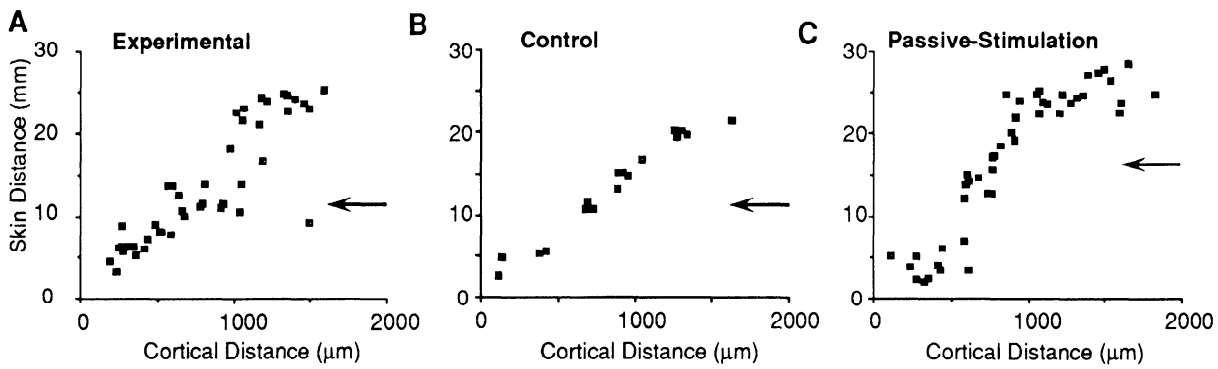

FIG. 20. Functions of the geometric center of receptive fields plotted against the linear location of the corresponding cortical location. Arrow indicates the approximate location of the trained (*A*), homologous (*B*), or stimulated (*C*) skin location. *A* and *B*: from the trained digit and the homologous digit on the opposite hand of *monkey E2*. *C*: the stimulated digit of a passively stimulated control monkey (*P3*).

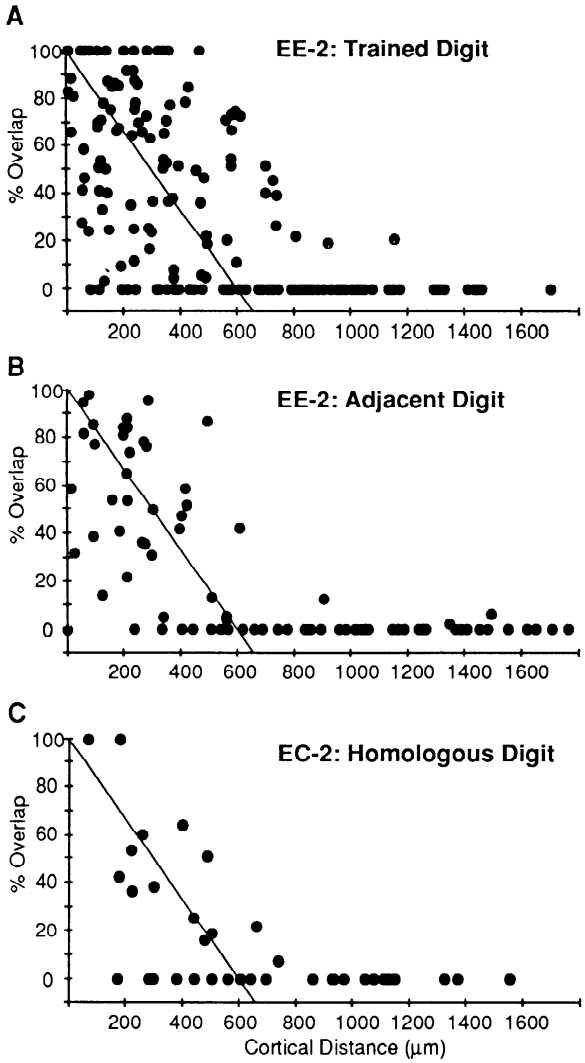

FIG. 21. Percent overlap of receptive fields as a function of cortical distance between the 2 locations. Comparisons were made with reference to 6–8 reference receptive fields located throughout the central 3rd of the digit representation, which excludes the most radial and ulnar aspects of the digit. *A*: this function for the trained digit. *B*: from the adjacent, untrained digit. *C*: from digit 3 of the opposite, unstimulated digit of *monkey E2*.

Correlation of receptive-field sizes with behavioral thresholds

Increases in receptive-field sizes could plausibly contribute to the improvement in behavioral performance documented in the previous study (Recanzone et al. 1992a). This seemed unlikely to be the primary determinant of improved behavioral performance because *1*) receptive-field sizes enlarged in *animal E4*, which had very high-frequency discrimination thresholds; and *2*) receptive fields remained at virtually normal small sizes in *animal E5*, which had very low behavioral thresholds. Regression analysis of receptive-field size with behaviorally measured thresholds showed no correlation between these two parameters (slope = -0.026; $r = 0.176$; $P = 0.626$). It is concluded that the simple expansion of receptive fields cannot in itself account for the improvement in performance with training.

DISCUSSION

The goal of this study was to determine the consequences of tactile discrimination training on the topographic representations of the hand surface in somatosensory cortical area 3b in an adult monkey. The cortical representations of the hand surface defined in animals trained to discriminate frequency differences for a tactile stimulus applied to a small, constant skin location were compared with the representations of the contralateral hand from these same animals, and to the representation of the hands from other monkeys that received the same tactile stimulation but attended to an auditory discrimination task. Analysis of the receptive-field properties and topographies of these cortical representations in these monkeys revealed several interest-

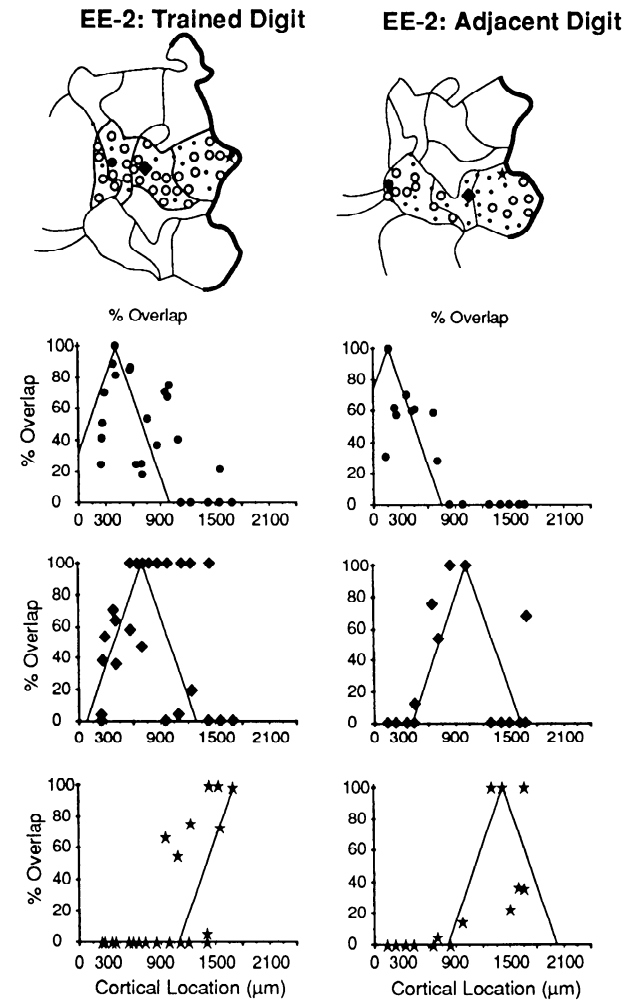

FIG. 22. Percent overlap of receptive fields as a function of their cortical location for 2 digits of *monkey E2*. *Left panel*: the digit trained in the tactile frequency discrimination task. *Right panel*: the adjacent, untrained digit. *Top panel*: representation of these digits; rostral is to the right, and the heavy line represents the 3a–3b border. Small dots denote cortical locations not used in this analysis. Open circles denote cortical locations used to define percent overlap relative to the 3 different filled symbols in each representation. These locations are projected directly downward to mark the *x*-axis location for these sites in the graphs shown in the *bottom panels*. The filled circle denotes a proximal receptive field, the filled diamond a receptive field near the middle of the digit, and the star a receptive field at the distal portion of the digit. The filled diamond in the *left panel* was centered on the trained skin. See text for details.

ing findings. *1*) The topographies of the representations of the trained hands were more complex than those of control hands. *2*) There was an increase in the cortical area of representation of the skin that was engaged in the behavioral task in animals in which performances at the tactile discrimination task improved with training. This effect was the smallest in the one animal which did not significantly improve. *3*) Receptive fields defined over the trained skin were substantially larger in size when compared with either those representing the adjacent digit of the same hand, or with those representing the same digit of the opposite, untrained hand, in four of five trained animals. *4*) The receptive fields defined on the digit adjacent to the trained digit were also significantly larger than receptive fields defined on the same digit of the opposite hand, in the same four of five trained animals. *5*) Receptive-field overlap was increased over a cortical map region roughly centered on the zone of representation of the behaviorally engaged skin site. *6*) These effects of increased cortical representation, increased receptive-field sizes, and local changes in receptive-field topographies and overlaps were observed only on a very modest scale in monkeys that received equivalent but behaviorally irrelevant tactile stimulation.

On the basis of these results, the following can be concluded. *1*) The details of topographic representations are substantially altered by a period of discrimination training. *2*) The training-induced topographic reorganization of the cortical representations of the skin surface is gated by attention, because only limited-scale changes emerged in monkeys stimulated in an equivalent but behaviorally irrelevant manner. *3*) Consistent with earlier results and conclusions (see Jenkins et al. 1990; Merzenich et al. 1988, 1990), with respect to the spatial response properties of neurons, the details of the functional organization of somatosensory cortical field 3b defined at any given time in the life of any adult monkey reflects the behavioral experiences of that animal.

Some technical considerations

AREA OF REPRESENTATION MEASUREMENTS. The areas of the cortical representation of selected skin locations were estimated by drawing the boundaries of representation at the midpoints between electrode penetrations centered on different designated skin zones. The maximum possible error in these map measurements was determined by including only those points with receptive fields including the stimulated skin, to obtain an estimate of the minimum area of representation, and then defining the area by the boundary of the next electrode penetration, which provides the maximum measurement of representation of this area. These measurements define the largest and smallest possible errors and are undoubtedly a gross overestimate of the actual error. The results of this analysis showed that the absolute areas of representation in these cases could be in error by up to 20–40%, with the smallest and largest errors of 17 and 49%, respectively (data not shown). In reality, underestimates and overestimates of boundary positions cancel, leaving a predicted error of measurement that is dependent on the number of locations at which boundary locations are determined. The estimates of representational territories relative to the estimates of other skin surfaces within and between hemispheres are within at least 5–18%, with the majority within 10% of these estimated values. These estimations of possible error are consistent with those defined mathematically and empirically by other investigators (Merzenich et al. 1987; Stryker et al. 1987). Such small errors cannot account for differences in the measured sizes of representation of trained and untrained digit skin, which were on the order of 150–300%.

Measures of percent overlaps of receptive fields can be ambiguous, because receptive fields with different sizes result in different measures depending on which receptive field is used as the "comparison" receptive field. We were able to partly circumvent this problem by measuring all receptive-field overlaps with respect to a subset of comparison receptive fields. This subset of receptive fields were selected to evenly represent the entire proximal-distal extent of the central glabrous region of the digit. This resulted in an increased sample when compared with a simple, nearest-neighbors analysis, yet did not require comparing every possible combination of locations. By using a significant subset of all possible receptive fields, a reasonable estimate of receptive-field overlap within a given digit representation was obtained.

LIMITATIONS OF MULTIPLE-UNIT RECORDING. All neural responses were recorded extracellularly, and although single units were sometimes sampled, recording at most sites was from a small cluster of neurons. Inspection of the oscilloscope tracings indicated that at most recording locations only two to five neurons were sampled simultaneously.

One advantage of multiple-unit recording is the ability to survey several hundred locations in a single hemisphere, because receptive-field definitions can be derived more rapidly then with use of single-unit recording methods. A second advantage is that multiple-unit recording procedures provide a more complete reconstruction of excitatory responses integrated at each cortical location. One consideration is the potential integration of cortical activity over the horizontal dimension of the cortex at the electrode. This potential problem can be evaluated empirically by exploring discontinuities among representations of different skin surfaces. The cortical locations that respond to stimulation of only hairy or only glabrous skin, or to stimulation of one or to the other of two adjacent fingers, are separated by <100 μm in the great majority of cases. Thus the effective "seeing distance" of these electrodes in these preparation is well below 50 μm, and these maps are contaminated by little horizontal integration of receptive-field responses.

If multiple-unit recording leads to any erroneous definition of receptive-field areas, they would be expected to result in overestimates of sizes, because a few neurons that may have slightly different receptive fields are recorded simultaneously. In fact, examination of data from other studies in which receptive fields have been derived from the middle cortical layers of area 3b in anesthetized or unanesthetized primates reveals that single-unit and multiple-unit receptive fields are of approximately corresponding sizes (e.g., see Mountcastle and Powell 1959; Stryker et al. 1987;

Sur 1980; Sur et al. 1980). In any event, small overestimates in receptive-field sizes should not affect the present representational plasticity results, because all cortical receptive fields were defined by the use of identical recording and tactile stimulation methods.

ANESTHETIC STATE. These extensive mapping experiments were necessarily performed on animals that were anesthetized. Barbituates have been described as having only minimal effects in cortical area 3b in monkeys on excitatory cutaneous receptive fields defined by the use of the techniques employed in this study (Mountcastle and Powell 1959; Stryker et al. 1987) but do affect inhibitory receptive fields (Mountcastle and Powell 1959). This analysis of topographic representation based on excitatory responses recorded extracellularly in deep cortical layer III and layer IV almost certainly provides a valid survey of area 3b representation topography that applies to the unanesthetized case. The effects of anesthetic state on layer III–IV receptive-field measurements and absolute locations of receptive fields using the techniques employed in this study were specifically addressed in this species in a study conducted by Stryker and colleagues (1987). They found very little difference between middle-layer receptive fields among samples derived at the same locations in unanesthetized or sodium pentobarbital–anesthetized owl monkeys. This conclusion does not necessarily apply to other somatosensory fields, cortical layers, or anesthetics (e.g., see McKenna et al. 1981; Duncan et al. 1982).

A second concern was how the relatively long times that these animals were anesthetized might affect cortical responses. The anesthetic level was closely monitored throughout the course of these experiments, as were indicators of the physiological state of the animal (see METHODS). Neural responses were equivalent in responsiveness throughout this extended period of anesthesia. There was no indication from either on-line monitoring of neural responses while mapping the receptive fields or from recorded suprathreshold responses to sinusoidal tactile stimulation of the skin (see Recanzone et al. 1992c) that the anesthetic affected the neural response sample differentially over time.

POSSIBLE CHANGES IN THE HAND. Changes in the topographic representations of the hand measured at the cortical level could reflect changes arising at any level of the somatosensory system. In fact, changes in the skin itself (for example, changes in skin mechanics) could possibly contribute to these effects. In fact, small calluses were recorded in several monkeys (as they are sometimes seen in behaviorally untrained monkeys), but they were not related to the behaviorally engaged skin site. Despite the daily tactile stimulation, there was no indication of skin thickening or callusing over this skin location in any trained monkey.

OTHER POSSIBLE SUBCORTICAL ORIGINS OF OBSERVED CORTICAL REPRESENTATIONAL CHANGES. It is also possible that subcortical somatosensory nuclei make a contribution to these representational changes recorded in area 3b. Changes in somatotopic representations after peripheral nerve transection or lesions to central fiber tracts have been documented in the dorsal column nuclei and ventrobasal thalamus (McMahon and Wall 1983; Millar et al. 1976; Pollin and Able-Fessard 1979). The greater divergence of anatomic connections in the cerebral cortex as compared with subcortical nuclei has been argued to be an indication that the cerebral cortex is the focus of dynamic self-organization in this system. Moreover, we have argued earlier that the behavioral modulation that gates these changes is primarily expressed at the cortical level (see Merzenich et al. 1988, 1990), a conclusion that has been directly demonstrated to apply to the auditory system (Ryugo and Weinberger 1978). In fact, cortical reorganization has now been observed with direct cortical stimulation by the use of experimental strategies by which the normal subcortical nuclei are bypassed (see Dinse et al. 1990; Nudo et al. 1990; Recanzone and Merzenich 1988). Although these studies directly demonstrate a capacity for direct stimulation-induced reorganization at the cortical level, they do not eliminate the possibility of subcortical contributions to this behaviorally induced reorganization. This question warrants further serious study.

Opposite-hemisphere 3b maps are not altered by this behavioral training

One set of control data was derived from the hemisphere ipsilateral to the trained digit in the same animal. An opposite-hemisphere control provides the advantage that it is from the same animal as the experimental maps. These opposite-hemisphere maps provide data from hands that were neither stimulated nor directly engaged in this behavioral task, and were derived by the use of the same methods as for experimental hemispheres. The disadvantage is that these contralateral representations may be affected by these behaviors, either via callosal projections of cortical neurons, or indirectly, as a result of the opposite hand being used in some stereotyped way in the animal's performance of this trained behavior.

The callosal projections between the hand areas of SI are modest if not entirely nonexistent in primates (see Killackey et al. 1983 for owl monkey; Shanks et al. 1985 for macaque). On the other hand, there are projections of SII to its homologue on the contralateral hemisphere, as is true of most of the parietal cortex. The indirect influence of the stimulated SI on opposite-hemisphere hand representations surely exists to some extent, because area 3b does project reciprocally to the ipsilateral SII in this species (Cusick et al. 1989), providing a 3b-to-SII-to-opposite SII-to-opposite SI projection. Although the extents and functions of these direct and indirect interhemispheric projections are unclear, it should be stressed that the representations of the hand surface in areas 3a and 3b in these control hemispheres were, by these limited physiological criteria, equivalent to those in normal hemispheres. It is concluded from this data that there is no significant interhemispheric transference of changes to the contralateral area 3b hand representation conferred as a result of the performance of this task.

Experience-driven changes in cortical representational topographies

Several features of the topographic representations of the hand trained in the behavioral task were notable in light of earlier findings. The control hemispheres representing the hand that was not used in the task were exceptionally orderly in topographic detail. Receptive fields were small, their geometric centers progressed along the digits as a roughly linear function of cortical distance, and the percent overlaps of their receptive fields dropped off roughly linearly with distance. By contrast, in the four monkeys studied electrophysiologically in which performance improved at the tactile frequency discrimination task, the topographic representation of the hand was less orderly than was seen in other normal hemispheres in this or in earlier studies (Kaas et al. 1979; Merzenich et al. 1978, 1987; Sur et al. 1980). The topographic complexities in these trained monkeys were not all obviously related to the behavioral stimulation of the hand. They may be partly attributable to the stereotyped hand-placement and response behaviors that were a part of this behavioral task.

A seemingly paradoxical finding in this series was that, in addition to the increased areas of cortical representation of the trained skin, receptive-field sizes over this region also increased. Previous reports have defined an inverse relationship between receptive-field size and cortical representational area for normal monkeys (Merzenich et al. 1984; Sur et al. 1980). At the same time, increases of receptive-field sizes in SI have been earlier described after acute peripheral nerve stimulation (Recanzone et al. 1990), denervation (Calford and Tweedale 1988, 1991; Merzenich et al. 1983a,b), cortical lesions (Doetsch et al. 1990; Jenkins and Merzenich 1987), and iontophoresis of γ-aminobutyric acid antagonists (Alloway et al. 1989; Beatuev et al. 1982; Hicks and Dykes 1983).

There are several possible interpretations of the origins of the dramatic receptive-field size increases recorded in the present cases. Receptive-field size enlargements recorded in these experiments might be accounted for by a local release from tonic inhibition within the zone of representation of the stimulated skin. The iontophoresis data of others suggest that receptive fields can increase in size substantially after the release of tonic inhibition (Alloway et al. 1989; Hicks et al. 1983, 1986). This mechanism has been proposed to account for receptive-field size changes that immediately follow denervation (see Calford and Tweedale 1991). If inhibition in the cortical sector representing the trained skin region would be reduced or eliminated, one might expect general increases in receptive-field sizes in these sectors, with a result that larger receptive fields would more often include the trained skin spot. However, *1*) by this model alone, one would not expect to see the *shifts* in receptive-field locations recorded as a major feature of these results, or the emergence of cortical zones several hundred micrometers across in which all receptive fields are closely equivalent. *2*) Analyses of the magnitudes of suprathreshold responses evoked by behaviorally important stimuli in our experiments reveal little difference in evoked discharge rates in cortical map sectors with enlarged cortical fields as compared with control sectors, indicating little difference in general excitability levels among cortical regions with enlarged or normal-sized receptive fields. *3*) Training of monkeys in a different task in which a similarly restricted skin surface was engaged in the behavior but in which stimuli were moving across this small skin sector (Jenkins et al. 1990) resulted in a severalfold *decrease* in receptive-field sizes. Thus there can be opposite cortical receptive-field consequences of the equivalently intense behavioral engagement of a restricted skin surface. These findings are inconsistent with the interpretation that behavioral engagement of any restricted cortical sector results in a general, constant, and predictable change in the strength of inhibition in differentially engaged cortical regions. For these and other reasons elaborated in subsequent reports (see Recanzone et al. 1992c), it is unlikely that a release from inhibition can by itself account for the changes recorded in this study. For the same reasons, enduring positive changes in excitability induced, for example, by long-term positive changes in cholinergic inputs also cannot, by itself, account for the representational changes recorded in these experiments.

A second possibility is that inputs from other, larger receptive-field afferent sources emerge to contribute to the receptive fields recorded in these multiple-unit samples. However, careful examination of the responses sampled at any given cortical location revealed that all neurons usually responded roughly equally across these large receptive fields. There were no detectable differences in the character of responses in the zone of large receptive fields, for example consistent with an emergent expression of Pacinian or other larger receptive-field afferent inputs. Moreover, such changes resulting in a simple addition of topographically in-register larger field afferents cannot easily account for topographically peculiar details of these behaviorally remodeled representations. It is therefore unlikely that an emergent population of larger receptive-field neurons was responsible for the increase of receptive-field size.

A third possibility, which is most consistent with these and earlier results, is that *1*) this behaviorally important stimulation at a constant skin location resulted in increased synaptic effectiveness for all of those thalamocortical inputs, the receptive fields of which include the stimulated skin site, with the resulting creation of enlarged cortical receptive fields representing a greater-than-normal amalgamation of thalamic receptive fields; and *2*) synaptic effectiveness changes within the cortical network itself account for distributed representational anomalies: for example, the emergence of discontinuous representational patches, the creation of a zone several hundred micrometers across in which receptive fields closely correspond, and the emergence of larger-than-normal receptive fields in a broad cortical zone surrounding the behaviorally engaged cortical region.

The panoply of changes recorded in these experiments are completely consistent with the operation of Hebb-like synapses driven to change by temporally coherent inputs in a competitive cortical network (see Recanzone et al. 1992c; Grajski and Merzenich 1990). The emergence of intrafield irregularities in representational topography, the increases

in receptive-field sizes, and the movements of receptive fields that came to be roughly centered on the stimulation site constitute interesting exceptions to three general principals of normal somatotopic representations: *1*) the conservation of representational continuity, *2*) the linear decrease in receptive-field overlap with increasing cortical distance, and *3*) the inverse relationship of receptive-field size with the cortical area of representation of a given skin surface. Models in which the temporal coherence of inputs is a major contributor to the functional organization of a dynamically representationally modifiable cerebral cortex are consistent with the emergence of such anomalies (see Edelman 1978, 1987; von der Malsburg and Singer 1988; Merzenich 1987; Merzenich et al. 1988, 1991; Palm 1990; Recanzone and Merzenich 1992; Singer 1990). The repetitive low-frequency stimulation applied to an invariant location on the skin presumably results in temporally synchronous inputs delivered over a significant cortical zone. This behaviorally important, temporally coherent activity delivered into this cortical sector over a prolonged training period would be expected to affect synaptic strengths not only within the cortical region originally representing the stimulated skin by overt neuronal discharges, but also at locations at which this input is initially below threshold (see Merzenich et al. 1984, 1987). The anomalies of the somatotopic organization of area 3b described in this study are consistent with the results expected from altering the synaptic efficacies of both thalamocortical and intrinsic cortical network connections over what is ultimately a relatively large cortical region. These processes would result in *1*) an increased zone of representation of the stimulated skin; *2*) a significant core sector in which neurons have nearly identical receptive fields roughly centered on the stimulated skin spot; *3*) distortions in receptive-field overlaps; and *4*) the potential emergence of representational discontinuities (representational "complexities") observed in all trained animals.

It is important to emphasize that, by operation of Hebb-like synapses in a competitive cortical network, there is no important inconsistency with the results obtained in an earlier study (Jenkins et al. 1990), in which extensive training on a restricted skin surface consistently resulted in the emergence of significantly *smaller* receptive fields. In the present study stimulation was restricted to a constant, stationary skin spot. In the study of Jenkins and colleagues, stimuli moved across a small fingertip skin surface. In the former case there is a single, stationary source of coherent inputs, and the cortical network creates amalgamated and thereby enlarged receptive fields because it has no basis for excluding any thalamic contributor to cortical receptive fields. In the latter case any small skin locus within the stimulated skin sector is a source of coherent inputs that will compete with others in the cortical network and thereby generate smaller-than-normal cortical receptive fields.

As noted above, several features of these distributed representations indicate that synaptic efficacy changes are also occurring for the intrinsic intracortical connections within the behaviorally engaged cortical zone. Thus, for example, *1*) over a cortical zone several hundred micrometers across, all neurons could have nearly identical cortical receptive fields. *2*) Increases in receptive-field sizes were not restricted to the representation of the trained digit. Receptive fields were also enlarged for the representations of other nearby hand surfaces. *3*) Widely separated, discontinuous patches of representation of the behaviorally engaged skin were seen in all experimental cases.

These distant experience-induced alterations, extending well away from the immediate zone of representation of the behaviorally stimulated skin spot, appeared to fall off as a function of cortical distance. These changes in the cortical region surrounding the representation of the trained skin may be related to the transference of the improvements in behavioral performance on untrained, adjacent digits. Further elaboration of how this mechanism can account for the results described herein, as well as the results seen within cortical area 3a and for the temporal response properties of neurons in both cortical areas, is deferred to the final report of this series (Recanzone et al. 1992c).

Again, these findings indicate that, over a large cortical area, all neurons came to respond to identical or nearly identical cutaneous inputs. This expanded area of extensively overlapping receptive fields was restricted to ~600–1,000 μm, with no overlap recorded beyond this distance. In previous reports on cortical somatotopic plasticity, the representations of specifically stimulated skin surfaces have been shown to increase within sharply limited distance limits (e.g., see Jenkins et al. 1990; Merzenich et al. 1983a,b). This distance limit ($\pm$1,200–2,000 μm) is within the limits of anatomic divergence, as estimated by the tracing of single thalamic afferents (Garraghty et al. 1989; Garraghty and Sur 1990; Landry and Deschênes 1981) by locally injecting anatomic tracers (Cusick and Gould 1990; Jones and Friedman 1982; Lin et al. 1979; Mayner and Kaas 1986) as well as by physiologically measuring spreads of functional inputs or thalamocortical arbors (Juliano and Whitsel 1987; Snow et al. 1988; Zarzecki and Wiggin 1982), thereby indicating that the appropriate anatomic divergence for these horizontal changes are preexisting.

Correlation of psychophysical performance

Several changes noted in the representation of the stimulated skin were evaluated to determine whether they were correlated with the psychophysically measured performance in the tactile discrimination task (Recanzone et al. 1992a). The increase of receptive-field sizes observed in some monkeys could not by itself account for practice-based changes in behavioral performance. Receptive-field sizes increased in the one animal that had only limited improvements in performance (*E4*). Moreover, in a second animal that exhibited marked discrimination performance gains with training (*E5*), there was not a significant increase in receptive-field sizes. Not surprisingly, then, there was no significant correlation of the mean receptive-field size with the behavioral threshold.

A second possibility is that changes in the areas of representation of the different skin surfaces could account for performance gains. It was clear that the area of representation of the entire digit could not account for the difference in behavioral performance (correlation coefficient, 0.045). The analysis with respect to the area of representation of the

stimulated skin did show a better correlation coefficient (0.749). This relatively low value is not a very satisfactory explanation of the improvement in performance, yet it does show that the area of representation of the engaged skin roughly paralleled frequency discrimination abilities.

An alternative possibility is that the improvements in behavioral performance with training resulted from an enhancement of the neural representation of the stimulus either in a different cortical area, or coded as a second parameter, for example, by the temporal response properties of cortical neurons. This second parameter could have come to be represented over a larger area either in area 3b, or in another cortical area that is interconnected with area 3b. These possibilities are tested in the following two reports of this series (Recanzone et al. 1992b,c).

Results from animal E4

One animal in this study, *monkey E4*, did not show a progressive improvement in performance throughout the training period, in contrast to all other monkeys in which discriminative performances progressively improved. This single exceptional case provided a unique control case for the effects of stimulation and attention. This animal clearly attended to tactile stimuli, because the performance at S2 frequencies >28 Hz was similar to that of other animals. However, it never reliably discriminated S2 frequencies <25 Hz (Recanzone et al. 1992a). There were significantly enlarged receptive fields over the stimulated digit that were comparable with those in three well-trained monkeys with large receptive fields. On the other hand, the absolute area representing the stimulated skin was on the order of other control digits from the same and different animals, and a cutaneous representation did not emerge in area 3a. The previous report raised the possibility that this one animal may have used subjective intensity cues to discriminate tactile stimulus frequency differences. If this animal was using a different strategy to perform the tactile discrimination task, one might expect an entirely different consequence for cortical functional remodeling. Unfortunately, the data collected in this study cannot resolve whether or not this animal was using different stimulus cues to perform the behavioral task.

Effects of passive stimulation

Experiments addressing cortical topographic reorganization after a variety of manipulations have not directly addressed the possible gating influences of selectively attending to tactile stimulation. Attention to a stimulus has been hypothesized to be a requirement for generating the changes in synaptic efficacy that may underlie cortical reorganization (see Merzenich 1987; Merzenich et al. 1987, 1988, 1990; Singer 1990). Attention can strongly affect the responses of neurons in a variety of cortical areas (Bushnell et al. 1981; Mountcastle et al. 1981, 1987; Richmond and Sato 1987; Robinson et al. 1978; Sato 1988; Spitzer et al. 1988, Spitzer and Richmond 1991). Human observers noted that the tactile discrimination task used in this current study demanded their complete attention to perform it successfully, implying that the monkeys devoted similarly focused attention to these tactile flutter-vibration stimuli. By directly comparing the results from the cortical representational maps of passively stimulated hands with those of hands used in the behavioral task of trained monkeys, as well as with those of the contralateral, unstimulated and untrained hands, the specific effects of passive stimulation have been measured in this study.

Interestingly, representations of passively stimulated hands, like those of behaviorally trained hands, appeared to be somewhat more topographically complex than those of control hand representations. Topographic irregularities and anomalies were noted in all passive-stimulation hemispheres. These irregularities were less marked than those seen in trained hemispheres and were not necessarily associated with the stimulation site. It should be remembered that these animals were also engaged in a tactile task in the sense that they were required to make the same controlled hand placements as tactile discrimination animals. Changes in topographic complexity throughout their hand representations may therefore be due to the tactile stimulation resulting from the hand-placing part of the behavioral task.

The limited data derived from these representations also suggest that there was a small increase in the representation of the stimulated skin in these passively stimulated monkeys. This was evident, for example, when comparing the areas of representation of these skin surfaces between the passively stimulated and naive hemispheres in one well-studied monkey. Unfortunately, the sample size is too small to be certain of these effects or their origins.

Another clear difference between the passively stimulated and the trained monkeys was in the sizes of receptive fields. Statistical treatment showed that receptive-field sizes were not different on passively stimulated fingers when compared with other mapped fingers in the same hemisphere. However, receptive-field sizes on stimulated and adjacent digits were statistically significantly larger than those recorded on the homologous digits in the contralateral hemisphere in the one case in which both hemispheres were investigated.

Thus these limited alterations in cortical representation of passively stimulated hands were much less marked than those seen in experimental hemispheres. This result indicates that stimulation alone is far less efficient in driving cortical reorganizations when compared with actively discriminating the stimulus. These results provide further evidence that the normally expressed functional organization of the cerebral cortex is modifiable by use in the adult animal and is probably a continuous process that occurs throughout life.

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