The representations of the surfaces of the hand in the primary somatosensory cortical field, area 3b, were reconstructed in detail in seven owl monkeys and two squirrel monkeys trained to pick up food pellets from five wells of different sizes. From an early clumsy performance in which several to many retrieval attempts were required for each successful pellet retrieval, the monkeys exhibited a gradual improvement in digital dexterity as shown by significant decreases in mean numbers of grasp attempts/successful retrieval and corresponding standard deviations (e.g., 5.8 ± 4.5 and 4.8 ± 3.1 respectively, for the smallest well) between the first and last training sessions. All monkeys commonly used alternative, specific retrieval strategies involving various combinations of digits for significant time epochs before developing a highly successful strategy, which, once achieved, was rapidly stereotyped. For example, the numbers of digit combinations used during the first five versus the last five training sessions decreased from 3.3 ± 0.7 to 1.8 ± 0.6 for the smallest well. In both owl and squirrel monkeys, as the behavior came to be stereotyped, monkeys reliably engaged limited surfaces of the glabrous tips of two digits (in eight monkeys), or of three digits (in one monkey) in the palpation and manipulation of these small pellets for their location, capture, and transportation to the mouth. In cortical area 3b, the magnification of representation of these differentially engaged glabrous fingertip surfaces was nearly 2× larger than for the corresponding surfaces of other hand digits, or for the contralateral cortical representations of the same digit surfaces on the opposite hand. In parallel, cutaneous receptive field for area 3b neurons representing crucial digital tip surfaces were less than half as large as those representing the corresponding surfaces of control digits. Receptive field overlaps were smaller on the trained fingertips than on control fingers. Moreover, the proportion of small overlaps was greater for the trained digits (76 ± 7%) than for the other digits of the same hand (49 ± 5%). There was still a simple, single — but apparently topologically expanded — representation of these differentially engaged skin surfaces in these monkeys. Thus, with very limited manual exercise over a total period of a few hours of practice at a skill played out in brief daily sessions over several weeks, the representations of skin surfaces providing information crucial for successfully performing a small-object retrieval behavior appeared to be substantially remodeled in the most ‘primary’ of the SI somatosensory cortical fields, cortical area 3b. By that remodeling, behaviorally important skin surfaces were represented in a much finer representational grain than normal. Some implications of these findings for motor skill acquisition are discussed.

Introduction

In earlier studies, we have shown that the details of the cortical representations of the hand surfaces in adult monkeys are modified by behavioral training in which restricted sectors of the hand are engaged by a behavioral task (Jenkins et al., 1990, 1993; Recanzone et al., 1992a-d; Wang et al., 1994, 1995). Behavioral training resulted in changes in cortical area 3b territories of representations of specific behaviorally important stimuli, and of the representations of the specific surfaces of the hand that were selectively engaged by the behaviors that the monkeys performed in these studies. Taken with experiments conducted using classical and operant conditioning procedures in other cortical areas and in other species (e.g., Woody and Engel, 1972; Disterhoft and Stuart, 1976; Diamond and Weinberger, 1986; Weinberger et al., 1993; Woody et al., 1991; Ahissar et al., 1992; Aou et al., 1992; Recanzone et al., 1993), these studies suggest that even primary cortical sensory areas are remodeled by our experiences, and suggest that experience-induced changes in selective neural responses and their distributed representations contribute to learning and skill acquisition (for reviews, see Woody, 1986; Merzenich et al., 1990a,b; Merzenich and Sameshima, 1993; Weinberger, 1993; Merzenich and Jenkins, 1994; Merzenich and DeCharms, 1995).

In related experiments, we have reconstructed the changes in the movement representation in cortical area 4 that result from and presumably manifest that cortical area’s contributions to the development of manual dexterity in a particular small-object retrieval task (Milliken et al., 1992; Nudo et al., 1996). That task involved the training of a monkey to pick up 3.6 mm diameter 45 mg. rough-surfaced food pellets from small wells on a modified ‘Kübler Board’ (Kübler, 1961; Lawrence and Kuipers, 1968). We found that when New World squirrel monkeys were challenged to retrieve food pellets from small food wells that required that they differentially introduce fewer than four fingers into them, their initial retrieval success was limited because of the requisite differential movement of the fingers and because fine manipulative movements required for grasping a pellet as it was drawn out of a well were initially difficult for the monkey to achieve. However, these monkeys’ performances improved continuously with practice. After 10–35 days of limited daily practice (50 or 100 pellet retrievals/day), monkeys successfully captured and successfully carried these small round pellets to the mouth on nearly every retrieval attempt. At that point, monkeys were dexterous, and performed this small object retrieval task in a stereotypic way with rapid and fluid movement sequences.

In examining the motor cortex representations of evoked movements, same-subject intracortical microstimulation pre-training versus post-training mapping studies have shown that specific movements that mark this practice behavior were represented over larger cortical territories than was the case before this limited training period was begun (Milliken et al., 1992; Nudo et al., 1995). Moreover, movements that occurred in this behavior came to be evoked together, with high probability. Thus, movement maps of the motor cortex are remodeled by the relatively few hours that these monkeys had practiced this small-object retrieval behavior, consistent with the
view that movement representations in cortical area 4 are dynamic, as posited classically by Sherrington and colleagues (Graham Brown and Sherrington, 1912; Leyton and Sherrington, 1917), by Lashley (1923) and by more recent associative conditioning studies (e.g. Woody and Engel, 1972; Woody, 1986; Iriki et al., 1991; Woody et al., 1991; Aou et al., 1992; Keller et al., 1992; Sanes et al., 1992; Hess and Donoghue, 1994; Kimura et al., 1994). Our objective in the present experimental series was to document the plasticity of the cortical representations of different skin surfaces engaged in the progressive development of this simple motor skill acquisition, as a part of determining how changes in the representations of these engaged skin surfaces in cortical areas 3b, 3a, 1, 2 and SII might contribute to progressive improvements in digital dexterity. This approach provides us with a model of how cortical plasticity arising in parallel and in serial relationships linking a number of cortical areas can contribute to specific aspects of motor skill development. In this report, the focus is on a description of differences in the representations of the hand surfaces in area 3b, contrasting its representation of the specific skin surfaces that each monkey had heavily engaged in this behavior with the representations of other hand surfaces, and with the representations of corresponding hand surfaces of the contralateral, less-exercised hand.

Significant differences in cortical territories of representation, in cortical magnification (area of representation/skin surface area), in receptive field sizes and in some aspects of local representational topography were recorded for these specific skin surfaces that were directly engaged by monkeys successfully performing this small-object retrieval task under difficult task conditions. These substantial changes in cortical field 3b, again, were recorded with training that was limited to a total period of a few hours extending across a small number of brief daily ‘practice’ sessions.

Materials and Methods

Behavioral Training

Experiments were conducted in seven owl monkeys (Aotus nancymai) and in two squirrel monkeys (Saimiri sciureus). All were judged by their histories and dentition to be young adults. Monkeys were trained to retrieve 3.6 mm diameter banana-flavored pellets from a modified Klüver Board. This device consisted of a rectangular Plexiglas board containing five food wells of different sizes. It was modified to match the finger dimensions of these small primates. The wells gradually varied in diameter (9, 11, 13, 19, and 25 mm for owl monkeys; 8.5, 9.5, 13, 19, and 25 mm for squirrel monkeys) and depth (6, 7, 9, 15 and 20 mm for owl monkeys; 6, 7, 9, 11 and 13 mm for squirrel monkeys). The Klüver Board was attached to the front of the monkey’s home cage. The animal had to reach down through an opening in the front of the cage to recover the pellets. Monkeys were permitted to use either hand to perform this retrieval task.

Typically, each experimental session consisted of 100 trials: the monkey was presented with 100 pellets delivered randomly to one of the five food wells (20 trials/well), and allowed to retrieve it. Monkeys were food deprived for 20 h prior to each testing session. They were fed ad libitum at the end of each session. Retrieval in the larger wells was relatively more successful and more consistently rewarded in early small-object retrieval trials. The training procedure included three sessions per week over a total of 23–42 practice sessions.

The Klüver Board was reversed every five or six sessions to assure that the animal’s performance was not dependent on board orientation. Each trial was videotaped for subsequent analysis. Movement strategies and sequences were reconstructed from frame-by-frame analyses. For every trial, the number of attempts/successful retrieval, the specific digit surfaces employed by the monkey in retrieval attempts, the failure modes of the monkey and other specific aspects of the retrieval movement were documented.

Training was continued until the monkey was able to retrieve pellets from all wells on almost every retrieval attempt. At that point, a highly detailed electrophysiological response ‘map’ of somatosensory cortical fields 3b and 1 representing the contralateral hand, and the region of 3a bordering on 3b was derived.

Electrophysiological Mapping Procedures

To define the representational status of the somatosensory cortex in trained monkeys, cortical areas 3b and 1 were mapped with high sampling densities using methods described in earlier reports. Brieﬁly, monkeys were pre-anesthetized with 2% halothane in a nitrous oxide/oxygen (75:25) mixture, and a venous cannulae was introduced into the femoral vein. Animals were then weaned from the halothane–nitrous mixture and administered an anesthetic dose of sodium pentobarbital (15–50 mg/kg) to maintain and stabilize an areflexic level of anesthesia. Monkeys were subsequently maintained at an areflexic level by supplemental i.v. administration of dilute pentobarbital. The monkey’s temperature was recorded and maintained at 37.5°C. Heart rate, respiration rate and depth and skin turgidity were monitored. Lactated Ringer’s solution was continuously infused at a variable rate (averaging ~6 cm³/h), to maintain body hydration.

A wide craniotomy of the anterolateral parietal bone exposed the hand zone of SI cortical cortex. The dura mater was removed by dissection and the cortex bathed in a thin layer of viscous (15% centistoke) silicon oil. A highly magnified video image of the cortical surface was captured on a Macintosh computer using NIH Image software and a high-resolution Cohu CCD camera. Before surgery was initiated, magnified video images of both surfaces of the hand had been recorded using the same procedure.

Using the brain surface vasculature for locational reference, 189–295 (average 257) parallel microelectrode penetrations were introduced into the hand zones of the SI cortical fields on a grain of 50–60 samples/mm². Sampling microelectrode penetration sites were marked with respect to brain surface locations using a data acquisition program designed speciﬁcally for conducting these experiments and for managing subsequent data analyses (MAP, Peterson and Merzenich, 1995). Parylene-insulated tungsten microelectrodes (Microprobe) with impedances of 1–1.5 mΩ (1 kHz) were used for multiple unit recording. All penetrations were parallel to one another. As a rule, neuronal response samples were derived 700–800 µm deep to the cortical surface, which in these species corresponds with deep layer 3–layer 4 in cortical area 3b.

Four investigators participated in defining cutaneous receptive fields of sampled neurons in these cases; only one of them had knowledge of the monkey’s pellet retrieval performance history or behavioral progression. Receptive fields were defined by exploring the skin surface of the monkey at each sampled site using just-visible skin indentation, hair deflection effective with fine opaque glass probes, thereby determining the skin area over which neurons recorded in each sample penetration were reliably excited. These ‘minimum receptive fields’ were drawn onto the stored computer images of the hand surfaces that were recorded for each monkey, using a mouse cursor.

Representational maps were constructed by drawing boundaries enclosing cortical sites at which receptive fields were centered on the same skin region (Canvas software, Deneba). When receptive fields overlapped the boundaries of different skin surfaces, the cortical representational boundary was drawn to reflect the proportional skin surface representations reflected by these boundary fields. Given the sampling densities employed in these experiments, there were usually many sampling penetrations introduced into the zones of representations of even small hand surface regions, e.g. representing individual digit phalanges. Thus, for each such area, there were usually many estimates of the locations of the border positions bounding these representational zones, and estimates of their representational territories are therefore accurate (see Stryker et al., 1987). For example, with the definition of cortical areas from a patch of cortex including 10 samples representing a given skin surface like a fingertip, errors for estimating representational territory would be <10%. All of the important conclusions of this study were drawn from sampling that provided this level of measurement.
precision for directly compared areal categories that are here determined to be statistically significant.

The significances of differences between experimental and control data were analyzed using ANOVA and Fisher PLSD tests, Wilcoxon matched pairs and chi-square tests. Control groups included (i) the cortical representations of the corresponding surfaces of non-engaged digits on the same and opposite, untrained hand; and (ii) the representations of the corresponding surfaces on the contralateral hand.

Results

Improvement at Pellet Retrieval with Practice

Typically, the monkeys grasped the cage bars with one hand while reaching for the pellets with the other hand. For each trial, the animals looked through the front panel of the Klüver Board to locate the well in which the pellet was deposited by the experimenter. Once the well was reached, the monkeys tried to dislodge the pellet. Owl monkeys rarely looked at their hand while attempting to retrieve the pellets; squirrel monkeys usually did so, although the animals could not see the pellets while palpating and manipulating them. Successful retrieval from the large wells (1 and 2) was generally achieved by a scooping movement of the fingers after reaching the appropriate well. Initially, successive flexions and extensions of one or several digits were needed to retrieve the pellets from the small wells (3–5). As a general rule, the number of reaching movements (R) was much less than the number of grasping movements (G). For example, the R/G ratio calculated in the whole population of monkeys over the first five training sessions for retrievals from wells 4 and 5 averaged 0.3 ± 0.1. In most trials, the retrieved pellet was held either between the flexed digits and the palm (large wells) or between the digit tips or between the middle and the distal phalanges of the grasping fingers (small wells).

Seven animals (five owl monkeys, two squirrel monkeys), exhibited a clear preference for the left hand from the beginning of training, although they also used the right hand at that stage when attempts with the left hand were not successful. Initial hand preferences strengthened to an absolute preference after two or three testing sessions. Changing the Klüver Board orientation did not alter this hand preference. Two owl monkeys were initially virtually ambidextrous and used both hands alternatively through successive trials. They remained ambidextrous throughout most or all of the training period, but both preferred to use the left hand to retrieve pellets from the two largest wells and the right hand to retrieve pellets from the three smallest wells, independent of Klüver Board orientation, again indicating clear distinctions and clear preferences in hand use. In one of these monkeys, an absolute hand preference eventually developed.

The data recorded from the two ambidextrous monkeys (OM2145, OMT233) included in the ‘experimental’ data cases are from the area 3b representation of the hand performing the more difficult small-food-well retrievals. Exclusion of these monkeys from this series had no significant effect on any of its main outcomes or conclusions.

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The owl monkey and squirrel monkey cases shown in Figures 1 and 2 illustrate some aspects of the development of digital dexterity for monkeys performing this simple small-object retrieval task. A representative owl monkey (OM2183), whose food retrieval behavior over time is summarized in Figures 1 and
2, initially retrieved a pellet from the three larger wells on every third or fourth attempt on average. Relatively few food retrieval attempts were unsuccessful after about the 10th day of practice — for the largest well, after about the 4th day. Pellet retrieval from the two smallest wells (Fig. 1, left) required more differentiated and more precisely controlled limb, hand and especially digit movements. Initial performance was invariably relatively poor; in this typical case, the monkey successfully retrieved a pellet on about every 10th attempt. Note that the monkey was being delivered the same number of food pellets (20) into each food well every training day. Thus, this monkey initially made about twice as many attempts to retrieve pellets from the smallest two wells as it made at pellet retrieval at the three largest wells. As the monkey practiced this small-object retrieval behavior: (i) it took fewer attempts/session to retrieve food pellets as training progressed day by day (Fig. 1A, left); and (ii) the variance in the number of attempts/successful retrieval fell (Fig. 1B, left) in parallel. As this simple motor skill was perfected and movements became more stereotyped, the time that these monkeys spent at this behavior also declined progressively from ∼60 min for the initial training sessions to ∼30 min for the final ones. Note that these general observations are representative of those obtained from all seven owl monkeys and two squirrel monkeys studied in this series. The mean numbers of grasps attempts per successful retrieval recorded over the first three training sessions for wells

![Figure 2](image_url)

**Figure 2.** Summary of the small-object retrieval behavior of a representative owl monkey (OM2183) and squirrel monkey (SM634). (A) Success and failure modes as percentages of total number of trials for retrieval attempts at well 5 summarized for the daily training sessions. Results for well 4 were similar. (B) Frequencies of the different combinations of fingers used, for each daily session, for 20 trials of pellet retrievals from the smallest food well (well 5). Results for well 4 were similar.

<table>
<thead>
<tr>
<th>Well 4 training sessions</th>
<th>Well 5 training sessions</th>
</tr>
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<tbody>
<tr>
<td>First</td>
<td>Last</td>
</tr>
<tr>
<td>OM1357</td>
<td>3.9 ± 3.1</td>
</tr>
<tr>
<td>OM2145</td>
<td>10.6 ± 8.2</td>
</tr>
<tr>
<td>OM2147</td>
<td>3.1 ± 2.1</td>
</tr>
<tr>
<td>OM2149</td>
<td>11.1 ± 8.1</td>
</tr>
<tr>
<td>OM2183</td>
<td>7.5 ± 5.8</td>
</tr>
<tr>
<td>OM2258</td>
<td>4.4 ± 3.8</td>
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<tr>
<td>OM233</td>
<td>9.9 ± 7.1</td>
</tr>
<tr>
<td>SM559</td>
<td>3.2 ± 2.3</td>
</tr>
<tr>
<td>SM634</td>
<td>4.1 ± 3.0</td>
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Data are mean ± SD. Results are expressed as the mean numbers of grasp attempts ± successful retrieval averaged over the first three and last three training sessions for wells 4 and 5. SDs were averaged using the same procedure. Differences between the first and last sessions were statistically significant for both mean and sd parameters (Wilcoxon matched pairs test; \( P < 0.008 \)).
4 and 5 were averaged for each monkey. This average performance was compared to the corresponding value calculated for the last three training sessions (Table 1). The same comparisons were made for the standard deviations (SDs). The analysis showed statistically significant differences (Wilcoxon matched pairs test; \( P < 0.008 \) for the comparisons of mean and SD values).

On average, the mean numbers of grasp/retrieval decreased by 4.5 ± 3.3 and 5.8 ± 4.5, and the SDs decreased by 3.9 ± 2.5 and 4.8 ± 3.1 for wells 4 and 5 respectively.

When these New World monkeys attempted to remove these small spherical objects from a shallow well, they directly palpated the pellet with the digits extended, and drew it to the side of the well prior to the rapid withdrawal that removed the digits and pellet from the well. A significant percentage of the pellets were ‘ejected’ from the well, some of which were lost from the apparatus (Fig. 2A). Others were dropped and lost after initial capture (the ‘fumbled’ pellets) before they could be brought to the mouth. Owl monkeys, especially, made rapid, repeated extensions and flexions of the fingers down into the well, then a digit withdrawal that brought the pellet to the top of the well where it could be grasped between two adjacent fingers, or captured near the distal/middle interphalangeal joint by rapidly flexing the digit tips.

As the animal practiced the behavior, the strategy the monkey used to retrieve the pellets from the smallest wells stabilized progressively, usually after the monkey attempted to use several different capture/retrieval strategies (Fig. 2B). In the representative owl monkey case illustrated in Figure 2, the monkey initially used digit 3, or digits 2 and 3, or digits 3 and 4, or digits 2, 3 and 4 in individual pellet retrieval trials. In this case, for example, the most common strategy for retrieving pellets from the smallest well initially involved the use of digit 3 alone. The monkey then shifted to a combined use of digit 3 with digit 4. At the same time, its most common strategy for retrieving pellets from the next larger well (well 4; not illustrated) was also to use digits 3 and 4 in combination, a strategy that became more predominant over the first several days of practice.

Over a subsequent period, the monkey returned to a predominant use of digit 3 alone on the smallest well, and began also to employ that strategy predominantly for pellet retrieval from food well 4. As that strategy became progressively more predominant, the animal’s successful retrieval of pellets declined. Up to \( >40\% \) of pellets withdrawn from the well were ‘ejected’ by this single-digit manipulation, and a larger number of pellets were dropped because of the inadequacies of a single-digit grasp for bringing them to the mouth (Fig. 2A). On the 12th day, the monkey sharply increased its use of digit 2 in combination with digit 3 for retrieval, first on the next-to-hardest well, then a day later.
later, on the most difficult well (Fig. 2B). Interestingly, the animal’s retrieval success was not immediately greatly improved by the use of this alternative strategy (Fig. 2A), but after several days of practice its success rate began to improve for retrieval on both small wells. In parallel with that improvement, the animal adopted a progressively more exclusive use of this digit 2–3 strategy. It employed this strategy in all trials for well 4 retrievals by the 20th day, and for well 5 retrievals by the 22nd day. Thus, a stereotyped movement behavior evolved to accomplish retrieval under the most difficult task conditions presented by the smallest wells. To quantify the changes in digit combinations, the numbers of combinations used during the first five versus the last five training sessions were calculated for wells 4 and 5, for each monkey. On the average, these numbers decreased from 3.4 ± 0.2 to 1.9 ± 0.5 for well 4 and from 3.3 ± 0.7 to 1.8 ± 0.6 for well 5 (chi-square test; \( P < 0.008 \) and \( P < 0.01 \) respectively).

The parallel performances on the three largest wells are not illustrated. At the beginning of training, the monkeys tended to use all digits except digit 1 to dislodge pellets from the two largest wells, whereas they most often used a combination of the three long digits – 2, 3 and 4 – to retrieve pellets from the medium size well (3). As monkeys improved in their retrieval from the smaller wells, they appeared to contact and manipulate pellets for larger wells predominantly with the same fingers that were used stereotypically in the smaller-well task. However, they still continued to introduce combinations of 3 or 4 or 5 fingers together into large wells throughout the small-object retrieval behavioral training period.

A similar gradual evolution of hand dexterity behavior was recorded in every trained monkey. That is, through a period of movement progressions using different digit combinations and different approaches to the wells, all monkeys predominantly employed two or more alternative pellet retrieval strategies during different training epochs before ultimately settling on a specific, ultimately highly successful strategy for retrieving pellets under the difficult conditions presented by the smallest food wells.

In both owl and squirrel monkeys, the distal segment of the fingers employed in pellet retrieval under difficult task conditions were strongly differentially involved in it. Frame-by-frame video reconstructions revealed that the monkeys (i) first palpated the pellets with specific digit tips; (ii) brought only those digit tips onto the surfaces of a small well; (iii) brought the pellet to the top of the well with it pressed against the side of the well by those glabrous digit tip surfaces; (iv) grasped the pellet for retrieval within or just above the top of the well, either by pinching it between the tips of those two specific adjacent digit tips, or by capturing it by a rapid flexion of the distal-middle interphalangeal joint; and (iv) delivered the pellet to the mouth from off the same digit tip (and sometimes distal proximal finger segment) surfaces. As a point of reference, note that the pellets were about one-half to one-third the width and about one-quarter to one-fifth the length of the glabrous skin overlying the distal segments of digit 2 or 3 or 4 in these adult monkeys.

It might also be noted that fingernails were also brought into contact with these wells in many, if not all, retrieval attempts. Afferents innervating the nail beds and the hairs and glabrous skin just proximal to the nails were also potentially excited in the instances in which these monkeys captured these food pellets with a two-digit pinch grasp. However, pellets were manipulated by and carried predominantly on the volar glabrous digit tip surfaces.

Thus, with practice, an initially clumsy, highly variable movement sequence progressively developed into a fluid, rapid, stereotyped movement sequence. The central questions asked in this study were: (i) What representational changes for these differentially engaged skin surfaces are induced by this behavioral training in the primary somatosensory cortical field, area 3b? (ii) How do those changes relate to the progressive improvements in digital dexterity attributed to practice in these adult monkeys?

**Cortical Representations of the Behaviorally Engaged Glabrous Digit Surfaces in Trained Monkeys**

After a period of training in which each monkey developed a successful, relatively stereotyped strategy for removing food pellets, the representation of the fingers of the engaged hand in cortical area 3b was mapped in detail. A representative example of a trained hand representation is shown in Figure 3. Note that as in this example these ‘maps’ also included a reconstruction of the representation of the hand in cortical area 1 in seven out of nine monkeys. Equally detailed control maps were also derived for the representation of the opposite hand in six monkeys in this series.

From examination of the maps of the hands in these nine cases, it was evident that the tips of the digits that the animal used in a stereotypic manner to palpate and grasp pellets in the final days of training were commonly represented over larger cortical areas than were the tips of other digits of the same hand. No equivalently disproportionate representation of these digits was recorded in the representation of the second, little- or not-trained hand reconstructed in area 3b in contralateral hemispheres. This finding is illustrated, first, by cartoon maps that show the zones of representations of the digit tips in six of these nine experimental hemispheres (Fig. 4A). There, cortical zones representing the glabrous digit tips predominantly used for pellet retrieval under difficult task conditions are marked by asterisks. Cortical regions in which neurons responded selectively to dorsal digit surfaces are shaded. Note that the zones of representations of some of these differentially behaviorally engaged glabrous fingertips appear to be wider in the mediolateral dimension than the zones of representation of non-engaged digits. In other monkeys, they appear to be elongated primarily in the rostrocaudal representational dimension. To compare the representations of the distal digit surfaces of different fingers, data were normalized with reference to skin surface area, i.e. using a ‘representational magnification’ (cortical area/skin surface area) measure. The magnifications of representation of the glabrous digit tip segments used for pellet retrieval were nearly 2× larger than the magnification in zones of representation of the other finger tips [\( F(1,13) = 6.93, \ P < 0.001 \)] (see Fig. 4B). The magnifications of representation of these digits were also twice as large as the representations of the tips of the same digits of the opposite hand, reconstructed from maps derived in the contralateral hemisphere (\( P < 0.01 \)). The ipsilateral hemisphere controls present the potential complication that monkeys commonly employed one or two additional digits in retrieval attempts not many days before these maps were derived. The contralateral hemisphere controls present the potential complication that two of these monkeys had some earlier practice using the contralateral hand before the hand preference became exclusive. Both of these factors might be expected to result in an understatement of the representational differences in area 3b attributable to this behavior.
Changes in Cortical Receptive Fields Representing Behaviorally Engaged Digital Surfaces

Major differences in cortical receptive fields were recorded for the digit tips — and to a lesser and much more variable extent for the middle finger segment surfaces — of the fingers that were almost exclusively engaged in the final days of pellet retrieval behavior. Typical examples of receptive fields from engaged and control fingers are illustrated for representative owl and squirrel monkey cases in Figure 5A. Note that in that illustration, receptive fields are separated from one another artificially, so that their extents can be visualized. If they were shown in true relationship to one another, many would overlap. Differences in receptive field sizes between these fingertips and the other fingertips on the same hand were significant in all cases, as in these two illustrated examples (Fig. 5B).

Receptive Field Size versus Cortical Magnification

Our data show that receptive field sizes changed, on average, to a slightly greater extent than did cortical magnification. At the same time, differences were nearly corresponding and tended to be correlated, as is illustrated by example in Figure 6A. In individual monkey cases, the cortical magnification for digit tips, including the larger zones representing the tips of the behaviorally engaged digits, had, on average, roughly inversely proportional changes in receptive field sizes. When the pop-
Changes in Local Cortical Representational Topography

Analysis of receptive field overlaps versus distance across the skin provided us with some insight into the behaviorally induced changes in topography and in spatial resolution of cortical maps. Figure 7 shows the percentage overlap for nearly all overlapping receptive fields plotted as a function of the distance between the centers of corresponding receptive fields for four representative cases. Receptive field pairs for which field sizes differed by >45% were excluded from this analysis because they provided distorted small and large percentages, depending upon which receptive field was used as the reference for overlap. All other pairs of receptive fields are shown for each set of digit tips in each case, including all fields that did not overlap. Note that for any given skin distance: (i) overlaps were smaller for fields on trained fingertips than for control fingers; and (ii) for trained fingertip representations, a larger proportion of recorded receptive fields did not overlap, even for short distances between sample sites. The overlaps recorded for the 0–4 mm range of skin distances between receptive field centers were assigned to two categories according to whether they were lower (small overlaps) or higher (large overlaps) than 50%. The total numbers of overlaps falling into each category were averaged over the population of nine monkeys. The proportion of small overlaps was greater for the trained digits (76 ± 7% versus 24 ± 7%), while small and large overlaps were equally encountered for the other digits of the same hand (49 ± 5.4% and 51 ± 5.4%, respectively) (chi-square test; \( P < 0.00001 \)). This greater proportion of smaller overlaps within the representation of the trained skin surfaces is accounted for by the decrease in receptive field size, and not by a sampling bias (e.g. lower density mapping resulting in longer skin distances). These data reveal that trained skin surfaces came to be represented in a finer topographic grain, and with more highly ordered shifts in receptive field centers versus distance than before training.

Whatever the change in receptive field sizes, the territories of representation of the behaviorally engaged digits expanded almost twofold. How were the surfaces of the digits represented topologically across this expanded zone? The representational topology was reconstructed in these experiments by defining the skin sites marking the centers of receptive fields on experimental and control fingertips, and then plotting their locations on the finger axes as a function of distances across the cortical axes. A representative case illustrating this analysis is shown in Figure 8. These reconstructions showed that for either the rostrocaudal or mediolateral dimension along the finger tip representations, the centers of receptive fields shifted continuously across the experimental fingertips. As a rule, this organization was indistinguishable in topographical order and precision from that of area 3b representations of control digits. Thus, for a progression of response samples shifted across the cortical area in the \( x \) or the \( y \) direction, the average locations of the centers of receptive fields shifted roughly continuously, for both trained and control fingertips. Although the distances across expanded representations were greater, on average, in trained monkeys, receptive fields shifted continuously across them, with the tip and base and ulnar and radial margins of the fingertip represented along the four boundaries of the digit tip representational zones in any ‘normal’ digit tip representation. This is consistent with a behaviorally driven, topologically ordered expansion of the representation of behaviorally engaged finger surfaces.

Discussion

How do these Cortical Changes Relate to the Evolution of this Simple, Practiced Motor Skill?

These studies further demonstrate experience-driven cortical plasticity paralleling motor skill acquisition. Specifically, they show that as a monkey practices a given, specific strategy for small-object retrieval, that behavior results in task-specific changes in one of the cortical representations of sensory inputs that contribute to this progressively refined movement ability. Here, some simple aspects of this learning-induced representational plasticity for sensory feedback information in a single somatosensory cortical area, area 3b, have been documented. With these cortical representational changes, the specific finger surfaces that have been engaged in the manipulation and grasping of these small spherical objects have come to be represented with about a 2× greater spatial resolution than was the case just a few days and a few hundred practice events earlier.

Other studies have shown that along with these apparent behaviorally driven changes in cortical area 3b, for monkeys trained in this small-object retrieval task, parallel, movement task-specific changes evolve in the distributed movement repres-
entations of cortical area 4 (Nudo et al., 1996; also see Grafton et al., 1992; Pascual-Leone et al., 1994; Schlaug et al., 1994; Karni et al., 1995). Studies with other sensory input-guided movement behaviors as well as maps derived in cortical areas 3a and 1 in this and in other experimental series indicate that representational changes are also generated for the specific aspects of behaviorally guiding sensory inputs and by contingent aspects of the behavioral task in premotor cortex (e.g. Mitz et al., 1991; Germain and Lamarre, 1993; Seitz et al., 1994), in supplementary motor cortex (e.g. Aizawa et al., 1991; Matsuzaka et al., 1992; Tanji, 1994), and in other somatosensory or auditory or visual cortical areas that are engaged by the behavior (e.g. area 1: Merzenich et al., 1990a; area 3a: Recanzone et al., 1992c; area AE: Recanzone et al., 1993). As a monkey begins to apply a specific strategy for retrieving small objects, changes in many cortical areas apparently arise in parallel, with changes in each cortical area presumably contributing to the parallel improvements of different sensory, perceptual, sensory feedback-guiding and motor control aspects of the overall skill. It is hypothesized that these manifold representational changes in sensorimotor areas collectively comprise the cortical contribution to motor skill acquisition.

It might be noted that the SI field studied in these current experiments, cortical area 3b, has only relatively modest direct projections to area 4 in this species (Stepniewska et al., 1994; see also Jones et al., 1978; Ghosh et al., 1987; Krubitzer and Kaas, 1990). This direct 3b-to-4 projection may be even sparser, or absent, in other primates including humans (Jones et al., 1978; Künzle, 1978; Jones, 1983). At the same time, area 3b does project topographically to four principal anterior and ventral parietal cortical fields that have major, topographically ordered projections to area 4 in the owl monkey (areas 3a, 1, 2 and SII) (Jones et al., 1978; Künzle, 1978; Cusick et al., 1985; Pons and Kaas, 1986; Ghosh et al., 1987; Huerta and Pons, 1990; Krubitzer and Kaas, 1990, 1993). Moreover, it has strong, orderly projections to at least three other functional regions that provide strong, direct projections into area 4: the supplementary motor cortex (Jones, 1983; Stepniewska et al., 1994); a strip of cortex that appears to encompass a part of classical area 6 bordering area 4 (see Stepniewska et al., 1994); and the subcortical putamen (Flaherty and Graybiel, 1993). The substantial changes in the area 3b representation of digit tips consequent from this behavioral training that we have recorded in these experiments would be expected to substantially influence the shaping of learning-induced changes recorded in other experiments (e.g. Merzenich et al., 1990a; Aizawa et al., 1991; Mitz et al., 1991; Aosaki et al., 1994; Graybiel et al., 1994) in these major area 3b projection targets that feed cortical area 4.

Figure 7. Receptive field overlaps plotted as a function of the distance between receptive field centers on the skin, for all combinations within the digit tip representation zones for directly engaged and control digit tips, for four representative monkeys. Receptive fields that differed in size by >45% were not included in this sample, as they resulted in an artificial inflation of the numbers of receptive fields with very high or very low percentage overlaps. The solid, thin lines on the graphs drawn from 100 to 4 are shown to facilitate comparison.
The critical importance of SI somatosensory cortex inputs for motor skill learning has been reaffirmed by recent studies of Pavlides et al. (1993), who have shown that tactually guided motor skill learning in macaque monkeys requires an intact SI cortex. Hikosaka et al. (1984) have shown that the digital manipulation and grasping of small objects is grossly degraded by temporary anesthesia of restricted sectors of cortical area 2. We have recently recorded similar effects following the induction of microlesions in monkeys that had been trained at the same small-object retrieval task used in this current study (Xerri et al., 1998). In that experiment, cortical microlesions followed derivation of detailed hand representation maps in trained owl monkeys. Those microlesions were designed to selectively destroy the area 3b representations of the fingertips that each monkey had used to palpate and manipulate pellets in this behavior. The performance of these monkeys at pellet retrieval was dramatically degraded. Indeed, monkeys behaved as if these digital surfaces were insensate; they commonly adopted a behavioral strategy in which they peeked into their partially opened hand on each behavioral trial to determine whether they had successfully grasped a pellet (they usually had not) before they brought the hand up to the mouth. Monkeys recovered from this striking functional deficit only after several further weeks of behavioral training (Xerri et al., 1998).

While many studies support the view that SI somatosensory cortex inputs contribute to motor skill learning, it has been reported that the transmission of cutaneous signals to SI is diminished during movement (Chapin and Woodward, 1981; Chapman et al., 1988; Jiang et al., 1990, 1991). This gating influence seems to be modulated in a context-dependent manner (Chapin and Woodward, 1982). Chapman and Ageranioti-Bléanger (1991) have recorded single units in areas 3b and 1 in monkeys performing a tactile discrimination during scanning movements over a groove. Cortical neurons that displayed cutaneous receptive fields not in contact with the discriminated surfaces were more likely to exhibit decreased discharge than were those with cutaneous fields in contact with the surfaces. It is therefore reasonable to assume that movement-related gating that probably occurred during our digital dexterity task tended to increase the ‘contrast’ between cutaneous inputs from the distal phalanges of the digits more heavily stimulated during this behavioral task and the inputs from other skin surfaces less involved in this task. It is worth mentioning that the ability to discriminate suprathreshold stimuli is not affected by movement in spite of the occurrence of movement-related gating (Post et al., 1994), suggesting that relative intensity of suprathreshold cutaneous stimuli is preserved during movement.

A growing body of evidence shows that the induction of these cortical changes is critically dependent upon the behavioral state of the animal (Ahissar et al., 1992; Recanzone et al., 1992b-d;
et al. (1993; Weinberger, 1993). It is interesting to note, in this respect, that changes in area 3b only reflected digit surface engagement that was required for object retrieval under difficult task conditions, i.e. for wells 4 and 5. No changes were recorded for other digital or palmar surfaces that contacted the pellet or well only under easy retrieval conditions, especially in wells 1 and 2. Similar task-difficulty-specific changes have been recorded in the same behavior in cortical area 4 (Nudo et al., 1996).

**Some Precautions**

In these studies, each monkey was allowed to use a preferred hand in this behavior. It might be expected that this could result in the monkey employing digital surfaces that are initially optimally favorable for successful pellet retrieval, which might bias mapping results. However, there did not appear to be any strong predisposition for these monkeys to use any highly specific small-object retrieval strategy. Every owl monkey attempted to use digital manipulation and grasping strategies during the earlier stages of training that involved different fingers and different digit surfaces than were seen in the initial training phase, and most monkeys began by using a predominating strategy that differed from the final, stereotyped one. In final maps in all of these cases, changes were highly selective in every case for those skin surfaces used by these monkeys during the final days of small-well training. Secondly, hand surface representations have now been constructed in detail in >50 untrained adult owl and squirrel monkeys (e.g. Merzenich et al., 1987). The marked, digit tip-specific representational remodeling recorded in this current experimental population is unprecedented in this large ‘naïve’ monkey group. Moreover, interhemispheric differences in area 3b hand maps of this magnitude have never been recorded in untrained monkeys.

Finally, the boundaries between cortical area 3b and area 3a were defined in this experimental series on functional bases. Our main criteria for defining this boundary were: (i) a transition from predominantly cutaneous inputs (in area 3b) to predominantly deep receptor inputs (in area 3a); and (ii) the line of representation of the extreme, rostral glabrous digit tip skin just under the nail bed in continuous receptive field progression with the representation of the glabrous fingertip surfaces within the cortical area 3b hand zone. This boundary has been defined anatomically and functionally in a large number of ‘naïve’ and behaviorally trained monkeys (e.g. Merzenich et al., 1987; Jenkins et al., 1990; Recanzone et al., 1992a–d; Wang et al., 1995), in which a close correspondence of cytoarchitecturally and functionally defined boundaries have been reconstructed. Some expansion of the representation of the digit tips into area 3a was suggested in the current maps by the emergence of off-focus responses creating discontinuities in digit representation in derived cortical maps in several of the experiments in this series (OM2145, OM11357, OM2258; see Fig. 44). However, in other maps, a significant expansion into area 3a appeared to be very unlikely (e.g. OM2149, OM2253; see Fig. 44). Most importantly, in all maps, the extreme glabrous digit tip skin was represented by the distal-most receptive fields in the experimental digit tip zones outlined in Figure 44. They clearly appeared to be part of a single, complete, continuous representation of the area 3b hand representation. At the same time, it should be noted that a small part of the topologically expanded representation of digit tips recorded in this series could involve a limited representational encroachment of the area 3b hand representation into cortical area 3a (see Jenkins et al., 1990).

**Cortical ‘Hypercolumn’ and ‘segregates’**

In the normal body surface representation, it has been historically argued that, on average, the magnification of representation of any given body surface (cortical representation/skin surface area) is inversely related to the mean receptive field size defined in that region (Sur et al., 1980; also see Hubel and Wiesel, 1974). That is another way of saying that (i) receptive field overlaps should change as a constant function of cortical distance all across the cortical area 3b representation of the skin; and (ii) a hypothetical ‘hypercolumn’ of cortical neurons of constant dimension (and hence a relatively constant number of neuronal elements) represents the skin surfaces included in any average receptive field. Our data indicate roughly parallel changes in cortical magnification and receptive field size that were consistent with the rough maintenance of a ‘hypercolumn rule’ through cortical remodeling, as shown in earlier cortical plasticity experiments (Merzenich et al., 1983, 1984; Jenkins et al., 1990).

The possible existence of a dimensionally fixed cortical processing unit gained further support from the fundamental cortical mapping studies of Favorov and colleagues, who studied the overlaps of receptive fields of neurons in local regions of the somatosensory cortical areas (Favorov and Diamond, 1990; Tommerdahl et al., 1993). They described a hypothetical basic processing unit, a tile in a mosaical representation of the skin, very similar to a visual cortex hypercolumn, that they termed a ‘segregate’. Receptive fields within this fundamental unit hypothetically represent all elementary aspects of inputs for their basic processing. Collectively, a population of mutually overlapping receptive fields comprises the compound receptive field of the mosaic element. This compound receptive field is discontinuously related to those of adjacent ‘segregates’.

This current study is consistent with these views. Changes in cortical magnification are correlated with changes in receptive field sizes, a prediction of a ‘hypercolumn’ rule. Moreover, consistent with the existence of ‘segregates’, for the representation of any given fingertip zone, closely adjacent receptive field samples could be identified that completely overlapped with one another. At the same time, these data also show that the inputs that are predominantly expressed in segregates or hypercolumns are clearly subject to plastic change. These findings indicate that these hypothetical constructs are dynamically and functionally refined, and are not invariant, strictly anatomically based processing units.

It should be noted that several clear exceptions to a strict hypercolumn rule have been recorded (e.g. Merzenich et al., 1991a; Recanzone et al., 1992b,d; Wang et al., 1995). The capacity to generate rapid and powerful changes in the effectivenesses of horizontal connections in cortical networks indicate that the horizontal extent of neurons representing a given receptive field or a given point on the sensory epithelium is subject to modification by the operation of cortical plasticity mechanisms in learning (e.g. Recanzone et al., 1991; Aihisa et al., 1993; Darian-Smith and Gilbert, 1995). Thus, while dynamic systems may commonly behave as if they are maintaining hypercolumns of fixed cortical dimension as in the current experiment, there are special circumstances under which measured hypercolumns shrink over time (as in the nursing rat: Xerri et al., 1994), or expand to up to <100× their usual size (as in a monkey trained with stimuli that simultaneously engage large skin surfaces: Merzenich et al., 1991; Wang et al., 1995). While ‘hypercolumns’ and ‘segregates’ might be used as descriptors of...


