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Large-scale functional reorganization in adult monkey cortex after peripheral nerve injury

(somatosensory cortex/median nerve/ulnar nerve/cortical plasticity)

PRESTON E. GARRAGHTY* AND JON H. KAAS

Department of Psychology, Vanderbilt University, Nashville, TN 37240

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ABSTRACT **In adult monkeys, peripheral nerve injuries induce dramatic examples of neural plasticity in somatosensory cortex. It has been suggested that a cortical distance limit exists and that the amount of plasticity that is possible after injury is constrained by this limit. We have investigated this possibility by depriving a relatively large expanse of cortex by transecting and ligating both the median and the ulnar nerves to the hand. Electrophysiological recording in cortical areas 3b and 1 in three adult squirrel monkeys no less than 2 months after nerve transection has revealed that cutaneous responsiveness is regained throughout the deprived cortex and that a roughly normal topographic order is reestablished for the reorganized cortex.**

The somatosensory system provides an excellent model for studying plasticity in the mature brain. In adult monkeys, for example, depriving parts of cortical areas 3b and 1 of their normal activating inputs by cutting and ligating a peripheral nerve to the hand initially eliminates responsiveness to cutaneous stimulation within the deprived cortex (1, 2). Over a period of weeks to months, however, responsiveness is regained but to nearby skin surfaces with intact innervation (2, 3). Similar topographic reorganizations in the cortical representations are seen after a variety of different peripheral injuries in monkeys (4). Descriptions and hypotheses (4, 5) have generally stressed the role of cortical selection of "degenerate" inputs (6). That is, it is assumed that the cortex has available to it a wider range of inputs than are actively expressed under normal conditions and that the normally silent inputs can gain potency when the dominant inputs are removed or silenced (4). This is an attractive hypothesis, and it receives indirect support from the observation that thalamocortical axonal arbors are large with respect to the grain of the cortical map (7), implying that effectiveness in driving postsynaptic activity is not distributed homogeneously throughout the arbors (8, 9). It is possible that these normally ineffective inputs are expressed in the enlarged cortical receptive fields found when the activity of γ-aminobutyric acid is antagonized (10–13). Given these considerations, it is possible that the amount of reorganization in the cortex after a peripheral injury is constrained by static anatomical features of thalamocortical arbors. Indeed, a cortical distance limit of 1.5–2 mm has been suggested based on the assumption that the potentiation of subliminal synapses on the fringes of thalamocortical arbors provides the main mechanism for cortical reorganization (1–4, 14). In the present experiments, we have subjected this hypothesis to further test by depriving an expanse of cortex 3–3.5 mm in breadth. Reactivation of this expanse of cortex would seem to require mechanisms in addition to alterations in the effectiveness of existing thalamocortical connections.

METHODS

To accomplish the deprivation, three squirrel monkeys underwent transection and ligation of the median and ulnar nerves to the hand 2–5 months before the terminal recording experiments. For this, and the terminal recording experiments, the monkeys were anesthetized with a mixture of ketamine hydrochloride (30 mg per kg of body weight) and xylazine (4 mg per kg of body weight). Under aseptic conditions, an incision was made in the ventral forearm, and the nerves were located, separated from surrounding tissue by blunt dissection, and transected 50–70 mm from the distal tip of the third digit. The epineural sheath was slid up the proximal stump and the nerves were transected again 1–1.5 cm above the initial cut. The empty epineural sheath was then reextended, folded back on itself, and ligated, establishing a dead end at the proximal stump (in all monkeys, this procedure prevented the regeneration of the nerves back into the hand). The incisions were then sutured and the monkeys were allowed to recover. Recovery from this procedure was uneventful in all of the monkeys, and they resumed using the partially deafferented hand within 2 weeks.

For the terminal recording experiments, the monkeys were again anesthetized and placed in a stereotaxic frame, and the somatosensory cortex (15) contralateral to the peripheral deafferentation was exposed. A photograph of the relevant cortex was made so that electrode penetrations could be sited on an enlarged print with respect to the surface vasculature. Electrophysiological mapping in the cortex was largely confined to the region of areas 3b and 1 where the hand is normally represented. This region was identified by extending recordings both rostrally and caudally into areas 3a and 2, respectively, where neurons are generally responsive only to noncutaneous stimulation, and by extending recordings medially and laterally into representations of the forearm and face, respectively (15). All recordings were made with low-impedance (1.0–1.5 MΩ at kHz) tungsten electrodes and were generally from clusters of units. Peripheral stimulation was accomplished with fine probes, camel hair brushes, palpation, and manipulation of joints. No noxious stimuli were used. At the conclusion of the recording experiments, the monkeys were given a lethal dose of sodium pentobarbital and perfused intracardially with 0.9% saline followed by fixative.

RESULTS

Several findings regarding the cortical data should be emphasized. First, our cortical recording revealed that, in each of the squirrel monkeys used in these experiments, the entire dorsal surface of the hand remained innervated after transection of the median and ulnar nerves, whereas the entire volar

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*To whom reprint requests should be addressed at: Department of Psychology, 301 Wilson Hall, Vanderbilt University, Nashville, TN 37240.

surface of the hand was consistently deafferented. These conclusions are based on the fact that the entire dorsal surface of the hand and digits was represented in the cortex of each of the squirrel monkeys, while we recorded no neurons with receptive fields on the glabrous surface in any animal. Although the innervation zones of the different nerves in the hand were not previously known for squirrel monkeys, denervation experiments in owl monkeys suggested that the median nerve innervates the radial glabrous digits and pads; the ulnar nerve, the ulnar side of both the volar and dorsal surface; and the radial nerve, the radial side of the dorsal hand and digits (3). Since the entire dorsal surface of the hand was represented in the cortex of the squirrel monkeys in the present experiments, our results suggest that an overlap zone of innervation by both the ulnar and radial nerves may exist for the ulnar side of the dorsal hand.

Second, even with a deprivation of this magnitude, we found no evidence of unresponsive cortex in any of the monkeys. Responses to peripheral stimulation were recorded across the entire breadth of the cortex formerly representing the palm and glabrous digits. The new receptive fields were in all cases on the dorsal surface of the hand and/or digits. Finally, this reorganized hand map in the cortex was roughly topographic. In areas 3b and 1 of normal squirrel monkeys, the ulnar hand and digits are represented medial to the radial hand and digits (ref. 15; see Fig. 1). In the reorganized map after deafferentation of the volar surface of the hand, we detected a strong tendency for a similar topography for neurons with new receptive fields on the dorsal surface of the hand. Fig. 2 illustrates this point with receptive field sequences 1–5 and 15–19. For example, sites 1 and 2 had receptive fields on the radial dorsal hand and dorsal digit 1, respectively, and with the intervening progression, site 5 had a receptive field on dorsal digits 4 and 5. Thus the medial-to-lateral topography that is appropriate for the normal representation of the volar hand was approximated in the new representation of the dorsal hand. The normal rostral-to-caudal organization was only crudely reestablished if at all. In normal monkeys, areas 3b and 1 both contain a complete and separate representation of the hand (15). The representations are rough mirror images of each other with the distal portions of the hand represented rostrally in area 3b and caudally in area 1 and with the proximal portions of the hand along the common border of the two areas. There was a slight tendency for such a rostral-to-caudal topography in the reorganized cortex, as illustrated by receptive field sequences A and B, but this tendency was much less compelling than the reestablished mediolateral organization.

Two other aspects of the present data are worthy of mention because of their difference with respect to data obtained in monkeys after smaller deprivations. First, cutaneous receptive field sizes for neuronal clusters were not very small, as would be expected if normal magnification functions were retained (ref. 7; cf. figures 5–7 in ref. 3). That is, even though a given skin surface (the dorsal hand and digits) was represented over a much larger expanse of cortex than normal, receptive fields were as large or larger than normal, and not smaller as would be expected if normal map grain had been retained. Finally, while cutaneous receptive

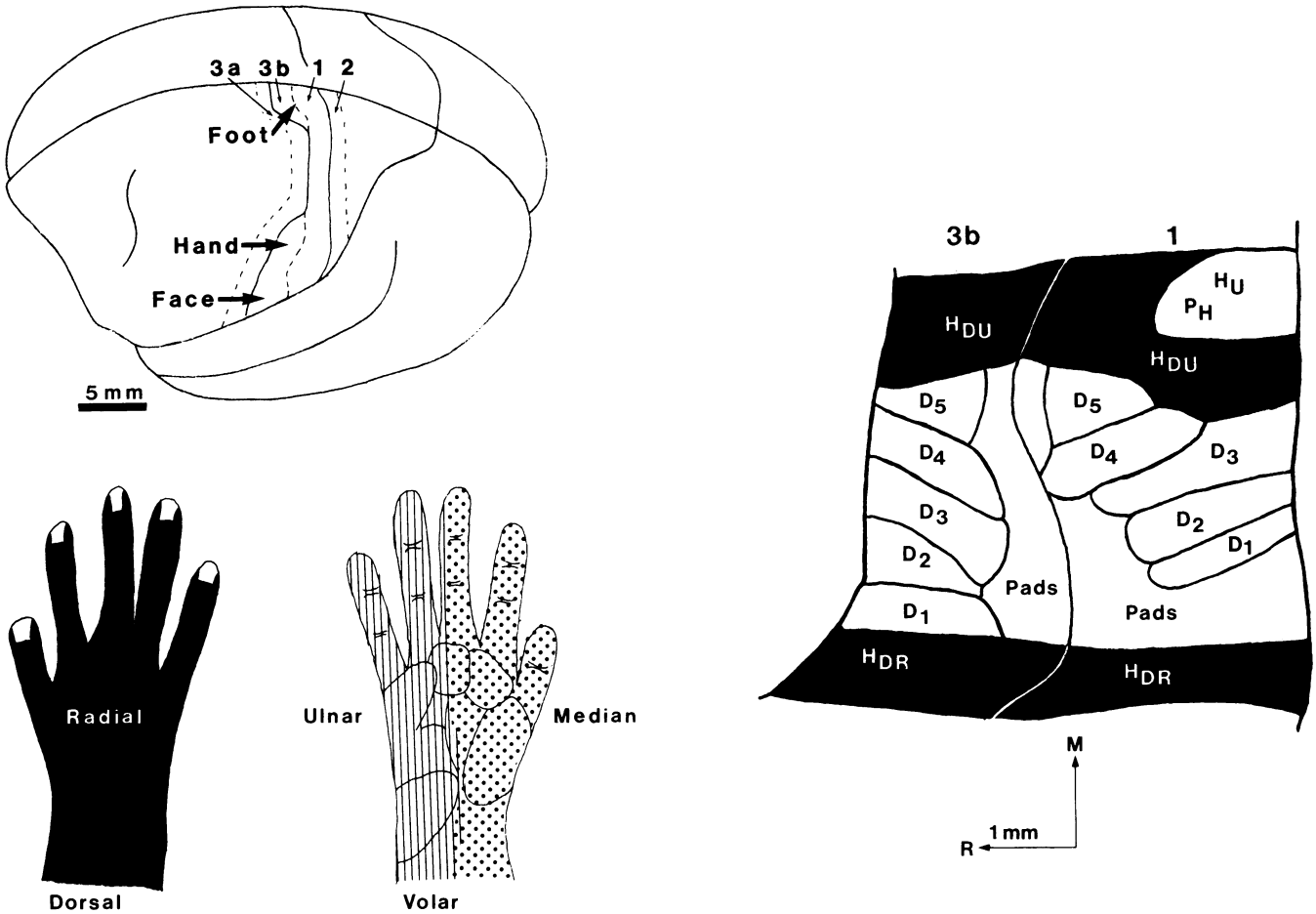

FIG. 1. (*Upper Left*) Dorsolateral view of squirrel monkey brain and location of the somatosensory cortex. (*Lower Left*) Innervation territories of the nerves to the hand. (*Right*) Organization of the hand maps in normal areas 3b and 1. Hairy surfaces are shown in black. Glabrous surfaces are white. H_{DR}, dorsal radial hand; H_{DU}, dorsal ulnar hand; H_U, ulnar hand; P_H, hypothenar pad; D_1–D_5, digits 1–5.

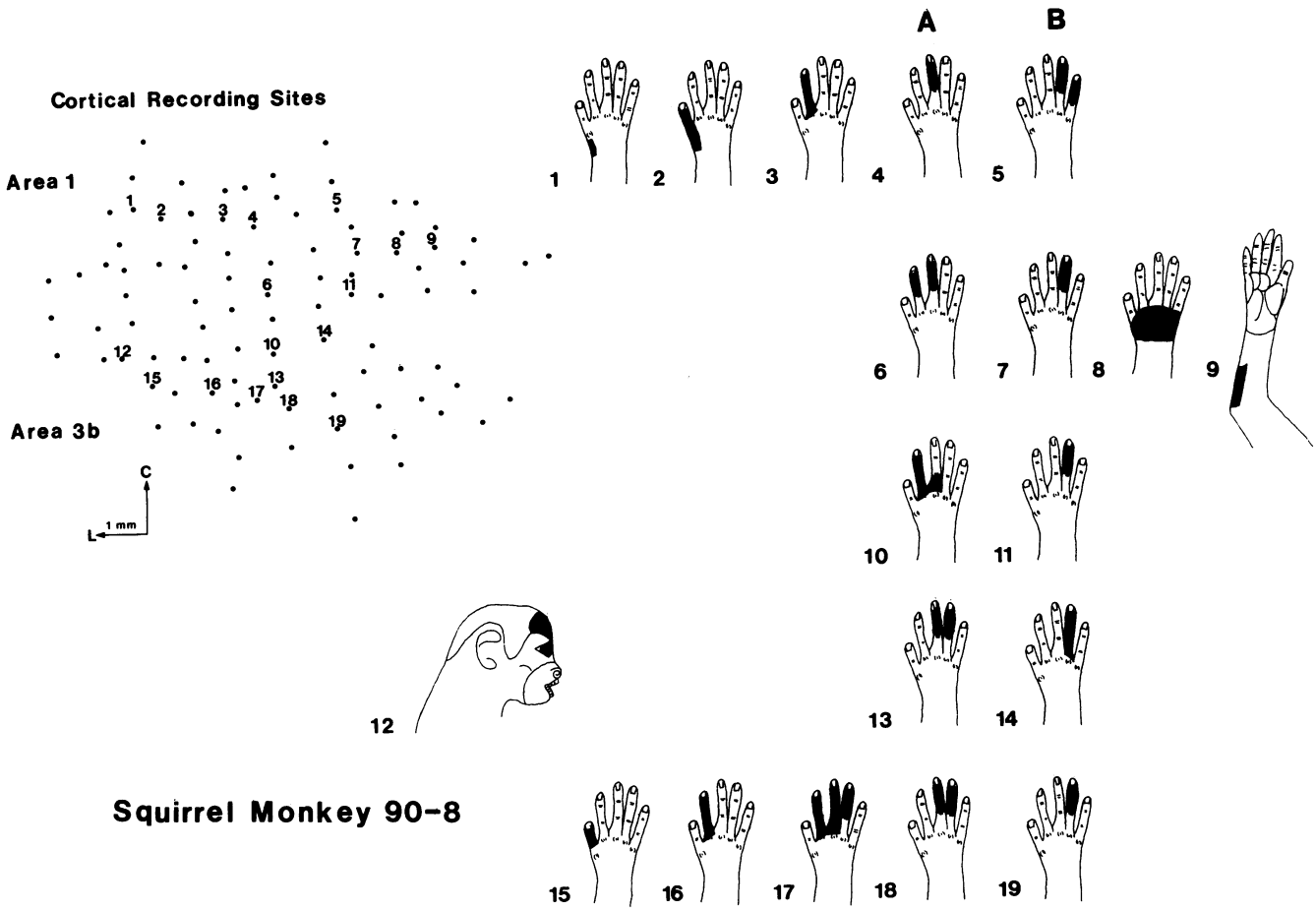

FIG. 2. Mapping data from cortical areas 3b and 1 in a squirrel monkey after both median and ulnar nerves were cut and ligated. Numbered recording sites and their associated receptive fields illustrate two organizational features resembling normal maps. First, as in normal cortex, progressions from radial to ulnar digits occur as recording sites move progressively medial (sites 1–5 for area 1 and sites 15–19 for area 3b). Second, there is a far less reliable tendency for progressions from distal to proximal to distal hand receptive fields from caudal in area 1, across the 3b/1 border, to rostral in area 3b (sites in columns A and B). The 3b/1 border was not identified with precision in this animal because (*i*) the receptive fields on the dorsal hand and digits were large, and obvious reversals were not generally evident, and (*ii*) the brain was cut in the coronal plane, parallel to the cytoarchitectonic subdivisions. While cutaneous receptive fields were found throughout areas 3b and 1, many recording sites were also activated by palpation or manipulation of the hand and/or digits.

fields could be defined at each cortical recording site in the hand regions of areas 3b and 1, there appeared to be some convergence between cutaneous and deep inputs. That is, in addition to the cutaneous receptive field, vigorous responses frequently could also be evoked by manipulation or palpation of the hand and/or digits, a finding not reported for normal cortex (15). Whereas the resulting neural activity could have resulted from inadvertent stimulation of cutaneous receptive fields, our observations suggested activation via noncutaneous afferents. Because recordings were of multiunit activity, we cannot assert that this convergence occurred within single neurons, but noncutaneous activation is relatively rare in normal area 1 and is almost never found in normal area 3b.

DISCUSSION

The present results differ substantially from previous reports involving monkeys with smaller deprivations. The most relevant of the earlier studies involved monkeys that had undergone transection and ligation of just the median nerve (4) or single or double digit amputations (16). The major differences between the present and previous reports involve (*i*) the extent of reorganization, (*ii*) the sizes of receptive fields, and (*iii*) cross-modality convergence.

Large-Scale Reorganization. It has been reported that regions of area 3b remain unresponsive to cutaneous stimulation in owl monkeys after two digits of the hand are amputated (16). This result was interpreted as supporting the hypothesis that a cortical distance limit exists and that the "silent" cortex was in areas that exceeded this limit. In the present experiments, with larger deprivations, we found cutaneously responsive neurons at all of our recording sites in areas 3b and 1. Several explanations for this difference exist. First, it is possible that the reorganized maps in our monkeys reflect more than one distance limit. That is, if islands of dorsal hand representations are scattered throughout the representation of the volar hand, the distance between any two patches of dorsum representation could be smaller than the hypothetical distance limit. No such islands were reported in the original mapping papers in squirrel monkeys (15) or owl monkeys (17), but subsequent papers have illustrated occasional intercalations in these species (2, 16) and in macaques (18).

Second, the distance limit may be different for different types of reactivation. We have recently observed that deafferentation of the entire arm in monkeys by rhizotomy of the appropriate dorsal roots is followed by reorganization in which parts of the face gain representation in the deprived cortex (19). This may be a markedly different deprivation from peripheral nerve transection, however, because many, if not most, dorsal root ganglion cells (and their central processes) survive section of their peripheral processes (see ref. 20 for review).

The map that emerges in the deprived cortex after transection and ligation of the median and ulnar nerves is remarkably similar across subjects. Not only is relatively normal topography retained in the reorganized map, but the representations of the various dorsal digits move different distances across the cortical surface as the reorganized map emerges, as if the dorsal surface of the various digits had preferential access to the territory formerly representing their respective glabrous surfaces (see ref. 21). If such a preference truly exists, incomplete reorganization could follow multiple digit amputation because both the dominant glabrous and the normally latent inputs from the hairy hand have been removed. Thus, the new map emerging after deafferentation of the entire volar hand could result from the expression of a preferred, but normally latent, set of inputs. Another possibility is that our recording densities were too sparse to detect silent cortex. Merzenich and colleagues (2, 3, 16) have generally sampled cortex with many more electrode penetrations, raising the possibility that our lower sampling density caused us to miss unresponsive cortex. It would seem, however, that at least one penetration in one of our three animals would have chanced upon such a silent region. Alternatively, the higher densities used in other experiments could have produced local cortical damage on occasion, transiently silencing neighboring cortex. This possibility also seems unlikely, however, because silent zones are rarely observed in normal monkeys mapped with comparable high penetration densities (e.g., see ref. 21).

Receptive Field Size. Another feature of the data of Merzenich and colleagues (2, 3, 16) that differs markedly from the present results is the issue of receptive field size. They report that multiunit receptive fields are notably smaller in reorganized cortex after either median nerve cut or digit amputation(s), generally restricted to small parts of single phalanges. Their interpretation of those results was that because a given skin region was now represented over a larger area of cortex, individual receptive fields became smaller so that map grain was retained. That is, in the normal representation of the hand in cortex, neurons with completely nonoverlapping receptive fields are separated by 600–700 μm (7). Merzenich and colleagues find a similar grain after median nerve cut or digit amputation. Receptive fields in the monkeys in the present experiments were as large as or larger than previously reported receptive fields on the dorsal surface of the hand for neurons in area 3b of owl and squirrel monkeys (7, 21), generally involving multiple phalanges and/or digits (see Fig. 2). Cortical receptive fields as large or larger than normal are also found in raccoons after chronic digit amputation (22), in cats after acute epidural block (23), and in flying foxes immediately after digit amputation (24).

What Are the Sources of Reactivation in Deprived Cortex? Even though an extensive zone of cortex has been reactivated, it still seems possible to interpret the results as a consequence of the potentiation of previously existing pathways, rather than an extensive growth of new connections. While the extent of reorganized cortex found in the present experiments is larger than any previously reported after peripheral nerve transections, thalamocortical axonal arbors may still be large enough to support the reorganization. Data from intracellular fills have shown that single axons can span as much as 3.5 mm of cortex in macaque monkeys (9). Unfortunately, comparable data do not exist for squirrel monkeys, in which axonal arbors might be expected to be smaller given their smaller brains. It is the case, however, that immunostaining for γ-aminobutyric acid is reduced in the deprived cortical regions of our partially deafferented squirrel monkeys (25), as would be expected if a decrease in cortical inhibition permitted the expression of normally subliminal inputs.

Another possibility relates to our observation that many of the recording sites appeared to receive both cutaneous and noncutaneous inputs. Similar "convergence" has been reported onto single neurons in cat somatosensory cortex after acute epidural block (23). With multiple digit amputation, Merzenich *et al.* (16) also note that the silent zones in their maps could be activated by noncutaneous stimulation. The activation of neurons by afferents apparently from deep tissues, or at least by receptors that code intensity, could be simply a result of the potentiation of inputs from area 3a, which is activated by muscle spindle afferents relayed from the thalamus, or area 2, which also receives inputs relayed from deep receptors (see ref. 26). However, while feedback connections from area 2 to area 3b have been demonstrated (e.g., see ref. 27), descending inputs of that type are considered to be modulatory and not a source of activation. Feedforward inputs from areas 3a and 2 to area 3b have not been demonstrated (see ref. 27). The possible roles of areas 3a and 2 in the reactivation of areas 3b and 1 after peripheral deafferentation can, however, be addressed with ablation experiments by recording from areas 3b and 1 before and after sequential or simultaneous ablations of areas 3a and 2 (cf. ref. 28). Another source of activation by apparently deep receptors is via direct projections from the ventroposterior complex of the thalamus (VP). The spinothalamic tract apparently activates a small population of neurons within the VP (29), and the VP is the main source of inputs to area 3b (e.g., see ref. 26). In addition, the ventroposterior superior nucleus, which relays deep inputs to the cortex (30), may provide a very sparse projection to area 3b and possibly to area 1 (31).

The reactivation of area 3b by cutaneous receptors undoubtedly depends largely or completely on inputs relayed from the VP. Recordings from the hand subnucleus of the VP in the same monkeys for which cortical data are reported here revealed neurons throughout to be responsive to inputs from the dorsal surface of the hand (25). Normally, inputs from the volar surface of the hand dominate the subnucleus (30). Because VP is the normal source of activation for area 3b, it is possible that a reorganized VP accounts for the changes in area 3b. We are uncertain what accounts for the VP reorganization. Normally, the dominant activation of VP is from the dorsal column and trigeminal systems (e.g., see refs. 32–34), but VP also receives substantial inputs relayed by the spinothalamic and lateral cervical tracts (e.g., see ref. 33), and inputs from different ascending systems can converge onto single VP neurons in cats (35) and monkeys (36). The response properties of neurons in these systems include responsiveness to cutaneous, noxious, and deep stimulation (see ref. 37 for review), response properties comparable to those we have found in deprived areas 3b and 1 of monkeys with partially deafferented hands. Furthermore, somatotopically correct evoked potentials can be recorded in somatosensory cortex when the dorsal columns are lesioned (38), demonstrating the availability of non-dorsal column inputs in the cortex. The hypothesis that alternative inputs can be uncovered when dominant inputs are eliminated is not novel. For example, Rhoades *et al.* (39) lesioned the trigeminal nucleus principalis in rats and found that initially very few neurons in the thalamus were responsive to peripheral stimulation. Within a month, however, responsiveness reemerged, but the new activity was characteristic of the normally unexpressed input from the spinal trigeminal nucleus interpolaris (SpVi) and could be abolished by ablation of SpVi. If a comparable state of affairs exists in monkeys with partially deafferented hands, lesions of the dorsal column system should have little or no effect on the reorganized cortical map. Lesions of the spinothalamic and/or lateral cervical tracts, on the other hand, should silence the new responses. This hypothesis can be easily tested and raises the

possibility that, at least with larger deprivations, enhancement in the relative strength of inputs conveyed over alternative ascending systems can account for much or all of the recovery evident at the level of the cortex.

Finally, it is possible that a reorganization occurs in the cuneate nucleus of the brainstem. Previous studies of the termination patterns of inputs from the hand to the cuneate nucleus have shown that the cell clusters that receive dense inputs from afferents from the glabrous skin of each digit also receive much sparser inputs from afferents related to the dorsal skin of the same digits (41). Thus, local potentiation of these sparse inputs could result in a somatotopically organized relay of inputs from the dorsal hand that would correspond to that observed in the new map of the dorsal digits in the cortex of monkeys with partially deafferented hands. In this view, the cuneate nucleus has both a normal map of the hand, dominated by a representation of the glabrous skin, and an embedded and superimposed latent map of the dorsal skin that is expressed after deactivation of the dominant inputs. This hypothesis can be rather easily tested by recording from the cuneate nucleus after section of the median and ulnar nerves. Previous studies of plasticity in the dorsal column nuclei after peripheral damage are limited, but they suggest that some plasticity, perhaps of a lesser extent, is possible (40). Alternatively, if the new map in deprived cortex is due to the expression of inputs relayed over non-dorsal column systems, the cuneate nucleus could fail to reorganize after peripheral nerve injury because it receives no inputs relayed by the spinothalamic or lateral cervical tracts.

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