Reorganization of Retinotopic Cortical Maps in Adult Mammals After Lesions of the Retina

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unusual level of biological regulation with multiple fates and hence multiple functions encoded within a single species of mRNA, and (iii) new variables and caveats to be considered in the prediction of protein structure from primary sequence.

**REFERENCES AND NOTES**


10. C. S. Yost et al., Cell 34, 759 (1983).


15. K. Basler et al., Cell 46, 417 (1986).


31. The SP6 expression plasmids were constructed as follows. Plasmid pSPHaPrP: PrP cDNA from Syrian hamster was cloned into SP6 (19). Plasmid pSPHSV G: pSPSVG was cut with Hind III and Bgl II, gel-purified and ligated with T4 DNA ligase into vector pSP64T (that had been opened with Hind III and treated with calf intestinal phosphatase). Plasmid pSP6V Gk: a Kpn I site and an Xba I site were added by cutting a peripheral nerve, the cortical representation reorganizes over a period of hours to weeks so that neurons in the deprived zone of cortex acquire new receptive fields on other parts of the hand. Such adult plasticity implies that previously existing connections in the brain are capable of changing in synaptic effectiveness so that new receptive fields and new representation-al organizations can emerge in cortex. Such changes could be important in normal adjustments of the nervous system, as well as in compensations for peripheral and central damage to the nervous system. Because the potential for such reorganization would seem to exist in other sensory fields, we investigated the possibility of adult plasticity in visual cortex with an experimental approach that has been used successfully for the somatosensory system.

32. To ensure translation was completely blocked, a mock control was done in parallel without transcript during the initial 30-min translation. The sample was then split and one portion was treated with GTA and emetine and the other with HLO and compensating salts. Transcript was then added and reactions were allowed to incubate the remaining 40 min. The sample that was treated with GTA and synthesis inhibitors did not synthesize product, whereas the sample that received mock inhibitors did (21).

33. A decrease in the number of chains after proteolysis of posttranslational translation reaction was reproductively observed. This phenomenon is observed with other proteins translated after translation (21).

34. We thank J. Rose for the VSV G cDNA and J. Forbes and members of the Lingappa lab for useful comments. Special thanks to C. Wilson and members of the departments of neurosurgery and neurology for help at a critical phase of this work. This work was supported by NIH grants AG02132 and NS14069 to V.R.L., R.M.M., and S.B.P.

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**Reorganization of Retinotopic Cortical Maps in Adult Mammals After Lesions of the Retina**

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The organization of the visual cortex has been considered to be highly stable in adult mammals. However, 5° to 10° lesions of the retina in the contralateral eye markedly altered the systematic representations of the retina in primary and secondary visual cortex when matched inputs from the ipsilateral eye were also removed. Cortical neurons that normally have receptive fields in the lesioned region of the retina acquired new receptive fields in portions of the retina surrounding the lesions. The capacity for such changes may be important for normal adjustments of sensory systems to environmental contingencies and for recoveries from brain damage.

**A RE THE MAPS OF VISUAL SPACE IN VISUAL CORTEX capable of reorganization in adult mammals? As in other mammals, the visual cortex of cats contains several retinotopic representations of the visual field, including those in areas 17 and 18 (1). Such systematic representations of peripheral receptor arrays also characterize somatosensory and auditory cortex (2). Under normal circumstances, these maps develop in a highly consistent manner in individuals of the same species. However, developmental of these topological maps can be altered by abnormal sensory inputs, including those produced by sensory deprivation and damage to the peripheral sensory input (3, 4). Thus, the nature of the input from the receptor sheet partly determines the ultimate organization of developing sensory maps. In the visual system, sensory manipulations such as monocular deprivation, induced strabismus, and unilateral de-focusing of the image can alter cortical organization (3). However, these manipulations affect cortical organization mainly or only within a critical developmental period extending a few months postnatally in cats or several years in humans (3). Thus, evidence supports the view that the organization of visual cortex remains highly stable after initial development, and there has been little reason to suppose that basic features of retinotopic maps can change in adults.

In contrast to the visual system, recent experiments on somatosensory cortex indicate that the organization of sensory maps can be modified even in adults (4, 5). For example, if part of the normal representation of the hand in primary somatosensory cortex is deprived of its normal source of activation by cutting a peripheral nerve, the cortical representation reorganizes over a period of hours to weeks so that neurons in the deprived zone of cortex acquire new receptive fields on other parts of the hand. Such adult plasticity implies that previously existing connections in the brain are capable of changing in synaptic effectiveness so that new receptive fields and new representation-al organizations can emerge in cortex. Such changes could be important in normal adjustments of the brain to alterations in the sensory environment, as well as in compensations for peripheral and central damage to the nervous system. Because the potential for such reorganization would seem to exist in other sensory fields, we investigated the possibility of adult plasticity in visual cortex with an experimental approach that has been used successfully for the somatosensory system.

Parts of areas 17 and 18 of the visual cortex were deprived of a normal source of activation by placing lesions 5° to 10° in diameter just above the area centralis in the retina of one eye of adult cats (6). By itself this procedure produced no notable change in retinotopic organization when tested in one cat. Most cortical neurons are binocu-larly activated and thus have two retinotopi-
suprasylvian sulcus. The normal organizations of wall. The receptive fields for the lettered record-
sizes. Thus, in the explored region of cortex,
aE, anterior ectosylvian sulcus; LS, lateral sul-
altered cortex in areas 17 and 18, neurons
had receptive fields of normal locations and
outside the zone of cortex were totally
deprived of normal sources of visual activa-
tion by placing a lesion in one eye and
removing the other eye, dramatic changes in
the retinotopic organization of areas 17 and
18 were produced. Neurons in the deprived
zone of cortex acquired new receptive fields
representing inputs from retinal locations around the margins of the lesion.

To allow time for cortical reorganization
to occur, most of our recordings were made
2 to 6 months after the retinal lesion and
the enucleation of the other eye. In each experi-
ment, microelectrode recordings were made
from neurons in an array of closely spaced
electrode penetrations within and around
the deprived cortex (8). Outside the zone of
altered cortex in areas 17 and 18, neurons had receptive fields of normal locations and
sizes. Thus, in the explored region of cortex,
rows of recording sites extending mediola-
terally from area 17 to area 18 produced rows of receptive fields systematically dis-
placed from the last, forming a progression
within the contralateral lower visual quad-
rant toward the zero vertical meridian as the
border of areas 17 and 18 was reached, and
back again for sites in area 18. Within the
zone of altered cortex, neurons were activat-
ed by visual stimuli and had receptive fields of
normal sizes. However, the receptive fields of these neurons were displaced from the
region of the retinal lesion to adjacent parts of the retina (Fig. 1). Thus, for mediali-
lateral rows of recording sites into the re-
gion of deprived cortex, receptive fields
progressed from locations just temporal to the
scotoma or “blind spot” produced by the
lesion to the margin of the scotoma. Then,
the progression of receptive fields ceased as
the deprived cortex was reached. Receptive
fields remained on the temporal side of the
scotoma for several successive recording
sites over 2 mm of cortex. Next, receptive
fields jumped to the opposite side of the
scotoma and remained stationary for several
recording sites; they then resumed their
normal progression for recording sites out-
side the deprived zone. In addition, some
recording sites (Fig. 1, sites d/e in row 4)
had two receptive fields, one on each side of the
scotoma. The responsiveness of neurons
with new receptive fields was not notably
abnormal (9). Both area 17 and area 18 were
altered in this way, and comparable results
were obtained in four cats with retinal le-
sions of 5° to 10°.

An example of how progressions of recep-
tive fields for rows of recording sites differed
in normal and reorganized cortex is shown in
Fig. 2. In normal cortex, receptive field
centers shift systematically as recording sites
progress across the retinotopic representa-
tion in area 17. In contrast, receptive fields
for recording sites over a considerable tan-
gential distance in cortex can have nearly the
same receptive field center in reorganized
cortex.

In two other cats, larger retinal lesions of
10° to 15° in diameter produced a larger zone
of deprived cortex. In these cases, neurons near the margin of the deprived
zone of cortex had displaced receptive fields,
but neurons in a 2- to 3-mm-wide center of
the deprived visual zone of cortex were
unresponsive to visual stimuli. Thus, large
zones of deprived cortex may not completely
reorganize.

The present results (Fig. 1) indicate that
portions of retinotopic cortical maps as large
as 4 to 8 mm and encompassing 5° or more
of the visual field can reorganize such that
neurons within this cortex acquire receptive
fields in new locations. Reorganization over
such distances could result from changes in
the effectiveness of synapses within the arbors of thalamocortical axons of previously existing inputs (10). Comparable results have been obtained by Heinen and Skavenski (11) from part of area 17 of one monkey. Cortex with neurons initially unresponsive to visual stimuli after bilateral lesions of the focusa later contained neurons responsive to visual stimuli. Results from visual cortex are similar to those obtained from somatosensory cortex of monkeys; removing the inputs from part of the hand produces a zone of altered cortex where neurons achieve new receptive fields of normal sizes in other parts of the hand (4, 5). Furthermore, removing inputs from more than half of the hand produces a larger zone of deprived cortex where complete reactivation does not occur (12).

These results are important for at least two reasons. First, in certain ocular diseases in humans, lesions are commonly found in the retinas of both eyes, and retinotopic reorganization of visual cortex could result when lesions in the two eyes correspond to the same locations in visual space (13). Second, the present results, together with those from the somatosensory system, imply that basic neuronal properties such as receptive field location are maintained in a dynamic state in sensory-perceptual systems of adult mammals. Such adult plasticity may be important, not only in recoveries from brain damage and adjustments to other impairments, but also in our abilities to maintain, alter, and improve sensorimotor and perceptual skills.

REFERENCES AND NOTES
6. A single photocoagulation lesion was made with an Argon blue-green laser (Argon Medical, Athens, TX) (spot size, 500 μm; intensity, 2.5 W, duration, 5 s or longer) in the superior and nasal retina of one eye in cats anesthetized intramuscularly with ketamine hydrochloride (20 mg/kg) and xylazine (4 mg/kg). Within a few days, the contralateral eye was enucleated under Nembutal anesthesia (35 mg/kg, intraperitoneally) by standard procedures and under aseptic conditions. The animals were treated with antibiotics and maintained for 2 to 6 months before recording were made.
7. Although cats have ocular dominance columns and some neurons in layer IV respond exclusively to one or the other eye, most neurons can be activated by either eye (for example, D. H. Hubel and T. N. Wiesel, J. Physiol. (London) 160, 106 (1962); J. Neurophysiol. 28, 229 (1965)].
8. Recordings were largely from neuron clusters 800 to 1200 μm from the surface in the hemisphere contralateral to the lesioned eye. Penetrations were typically placed 200 to 300 μm apart in mediolateral rows about 1 mm apart. Recording sites in penetrations along layers in cortex of the medial wall were typically 100 μm apart. Recording methods were standard and have been described in detail elsewhere [J. H. Kaas and R. W. Guillery, Brain Res. 59, 61 (1973); M. T. Timberlake, E. Peli, E. A. Einhäuser, K. A. Augline, ibid. 28, 1268 (1987)].
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