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Fibre Divergence in the Distal Optic Radiation: possible basis of functional plasticity in adult primate visual cortex

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With 4 Figures

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Summary: The precision of retinotopy in primate visual cortex is commonly thought to result from highly ordered arrangement of fibres in the visual pathways. However, rigid point-to-point representation is hardly compatible with findings of a substantial reorganization of visual cortical maps after peripheral and central lesions. Such observations could be accounted for by divergence in the optic radiation. To explore the hypothesis of fibre divergence, we made small knife cuts in the distal optic radiation of *macaca fascicularis*. After subsequent axonal tracing by injecting WGA-HRP into lateral geniculate nucleus, we studied the course of distal fibres in white matter. The amount of divergence was assessed by measuring, relative to the prevailing fibre course, length and orientation of labelled fibres between lesion and entry into cortex. Lesion sizes between 1 mm to 3 mm did not result in any detectable diminution of terminal labelling in layer IVC of striate cortex. Individual labelled fibres were found to diverge symmetrically from both sides into the gap distal to the lesion. Divergence starts at a distance of about 3 mm before cortex. At the white matter boundary, less than 10% of all fibres still retain the original direction, with the remaining fibres taking any other orientation without preference. We estimate that this corresponds to a divergence of visual afferents encompassing about 6–10 mm of cortical distance, if intracortical arborization of terminal fibres is taken into account. Possible consequences for functional plasticity in the adult primate visual cortex are discussed.

Key words: Visual system – geniculo-striate projection – tract-tracing neuroanatomy – neuronal plasticity

Introduction

Wilbrand (1890) and Henschen (1910) were the first to correlate perimetrically assessed visual field defects with the site of cortical lesions proven at autopsy. It is since established that in man the visual field is orderly represented on the primary visual cortex. Subsequent experimental studies in subhuman primates have confirmed electrophysiologically the precise topographic mapping of the visual fields onto striate cortex (Talbot and Marshall 1941, Daniel and Whitteridge 1961, Hubel and Wiesel 1974). Also, the neurons of the lateral geniculate nucleus (LGN) have been found electrophysiologically to represent the visual map in a precise, highly ordered manner (see, for the monkey, Malpeli and Baker 1975). This retinotopic organization is traditionally thought to depend on the orderly arrangement of fibres in the visual pathways maintaining their neighbourhood relationships throughout ontogenetic development (see Polyak 1957). Retrograde tracing experiments in which discrete cortical injections of tracer into closely neighbouring visual field representations resulted in discrete, non-overlapping columns of labelled LGN cells (Perkel et al. 1986, Salin et al. 1989), have supported that view. Similarly, injections of tracer at the border of chronic lesions of striate cortex resulted in labelling of LGN cells only within the non-degenerated part of LGN but not its degenerated part (Cowey and Stoerig 1989).

However, microelectrode recordings in cat optic nerve (Horton et al. 1979) and anterograde fibre tracing experiments of the optic tract at the entry into the LGN (Eysel and Wolfhard 1983), have shown a surprising degree of unorderliness in the arrangement of fibres representing neighbouring retinal points (but see Aebersold et al. 1981). Further, clinical and experimental findings of brain plasticity with visual field rearrangement after peripheral or central lesions of the visual pathways are hardly compatible with a rigid point-to-point representation. In adult cats with focal retinal defects, some of the LGN neurons formerly representing the region that was damaged shift their receptive fields into neighbouring, intact parts of the retina, probably by the use of normally "silent" dendrites (Eysel 1982). In patients with homonymous hemianopia, systematic training can lead to a reduction in size of the visual field defect long after cerebral damage (Zihl and von Cramon 1985). The extent of re-activated cortical tissue has been estimated to be in the range of 15 to 20 mm independent of eccentricity, if the magnification factor of the visual field representation in man is taken into account (Zihl and von

Cramon 1982). Such plasticity in cortical visual field representation has recently been demonstrated experimentally in adult cat visual cortex. Electrode penetrations after one retina had been focally destroyed (and the contralateral retina completely removed) failed to detect striate regions without visual input. Instead, retinal locations bordering the area of destruction were overrepresented. Some cortical loci even received visual input from both borders of the retinal defect. The reorganization of retinotopic cortical maps encompassed regions of 4–8 mm cortical distance, corresponding to 5 degrees (arc) or more in the visual field (Kaas et al. 1990). Similar reorganization of cortical sensory maps has been found in the somatosensory cortex of monkeys after peripheral nerve lesions (see Kaas et al. 1983, Clark et al. 1988).

These observations seem quite incompatible with the postulate of rigid point-to-point representation. To account for them anatomically, one has to assume a sprouting of axons over distances of up to 20 mm for which there is no evidence in striate cortex at present. Alternatively, one could assume a divergence of afferent axons. The precision of retinotopy in striate cortex would then be derived computationally from the weighting of input from more or less effective synapses. After destruction of active afferents, physiological "unmasking" of formerly ineffective synapses could occur (Wall 1977) and thus account for the functional rearrangement of the sensory map.

In the present study we wanted to test the anatomical basis of the latter hypothesis. As a particular feature of macaques, visual cortex folds up in the operculum. After entering it, the parallel running optic radiation fibres spread out in a thin sheet of white matter as they continue orthogonally towards the common border of areas 17 and 18 (Kuderna et al. 1984). Hence, the fibres can be cut by small knife incisions proximal from their entry into cortex and can be examined *tangentially* in a flat mount preparation. Using this experimental approach and subsequent axonal tracing with WGA-HRP, we tried to visualize the course of fibres distal to such a lesion. We especially wanted to assess orientation of individual fibres in relation to the general course of the optic radiation and to quantitate the amount of divergence. Preliminary results have been reported in abstract form (Danek et al. 1988).

Materials and Methods

Four adult macaque monkeys (M. fascicularis) of 3–5 kg weight were used. The animals were anaesthesized with a mixture of xylazine (0.5 mg/kg, i.m.) and ketamine HCl (30.0 mg/kg, i.m.) followed by sodium pentobarbital (15 mg/kg, i.v.). The head was fixed in a stereotaxic frame (David Kopf Instr.) and the skull was opened over the operculum. When striate cortex was exposed, incisions into the opercular cortex 5–10 mm away from the lunate sulcus at a site representing parafoveal visual field of 2–5 degree (arc) eccentricity were made with a small scalpel blade mounted on a micromanipulator. Great care was taken to cut through the subjacent white matter of the occipital operculum but not further.

In order to reach the LGN, one small hole of about 5 mm diameter was drilled in the skull using stereotaxic coordinates (anterior: 8, lateral: 11; Szabo and Cowan 1984). The LGN was first identified electrophysiologically using standard microelectrode technique. After recording of typical responses to visual stimulation, the microelectrode was redrawn and a microsyringe (Hamilton) was inserted into the same position through the guidance cannula. In three animals, small volumes of 0.1 to 0.3 µl of a 2% solution of wheatgerm-agglutinin coupled horseradish peroxidase (WGA-HRP; Sigma) were injected. In a control experiment, we injected 50 µCi of tritiated leucine into LGN for exclusive *anterograde* axonal transport. After 40 to 48 hours of postoperative survival, the animals were deeply anaesthetized with barbiturate and perfused transcardially with 0.9% saline, followed by fixative (3% paraformaldehyde and 0.5% glutaraldehyde in phosphate buffer, modified after Jacobson and Trojanowski 1974) and finally by phosphate buffer containing 4% sucrose.

The whole brain was removed from the skull. The occipital operculum was separated by opening lunate sulcus, calcarine sulcus (ascending and descending branch) and inferior occipital sulcus and by subsequent cutting of the Y-shaped white matter "stem" (Fig. 1). To obtain a proper flat mount, the operculum was gently pressed between two glass slides. This tissue block was cut tangentially to the cortical surface on a freezing microtome at 40 µm slice thickness and the complete set of serial sections was treated for TMB histochemistry according to a standard protocol (Mesulam 1978). The site of injection was visualized with DAB histochemistry (Fig. 2A). Slides were coverslipped and were examined at intermediate magnification under the microscope (Diaplan, Leitz) using dark field in combination with polarization optics (Fig. 2B and 2C). In the case of ^{3}H-leucine injection,

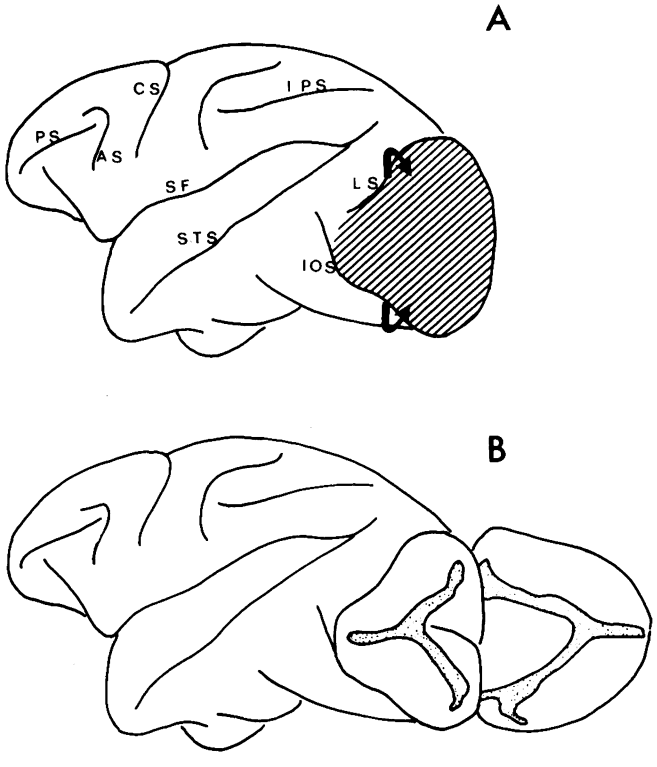
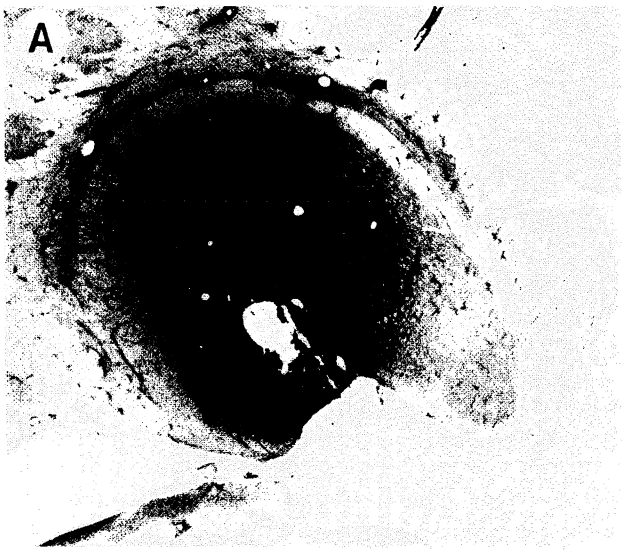


Fig. 1. Lateral view of a monkey left hemisphere (A) demonstrating the technique of separating the occipital operculum for flat mount preparation (B). The primary visual cortex on the hemispheric convexity is indicated by shading. The Y-shaped white matter "stem" of the operculum is indicated by stippling (B).



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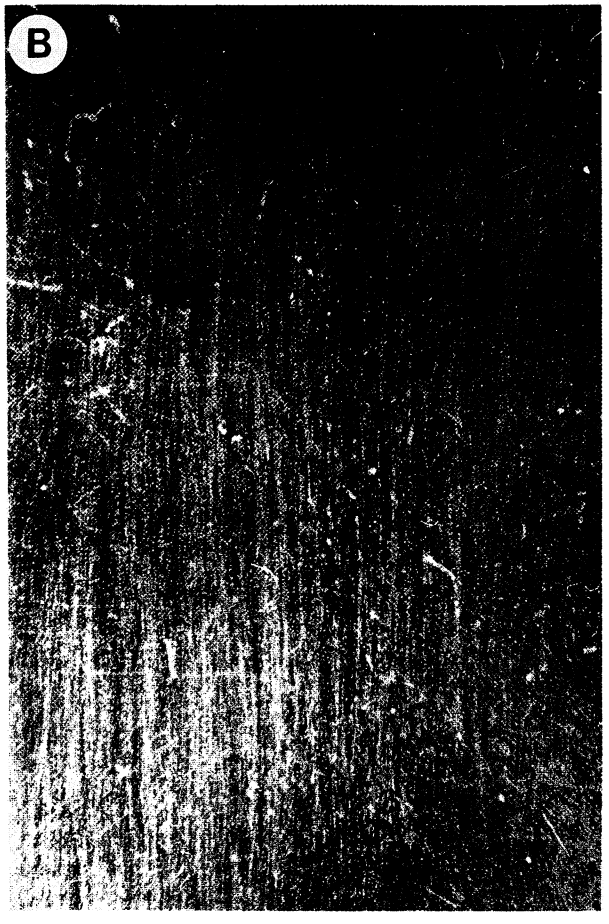

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Fig. 2. (A) Low power photomicrograph of the injection site in the lateral geniculate nucleus (WGA-HRP as tracer and DAB histochemistry, coronal section from the left hemisphere).
(B) Microphotograph of labelled geniculo-striate fibres in a section tangential through opercular white matter, taken at a distance from striate cortex of about 10 mm. Note the high degree of orderliness. (C) In the same preparation, a **conical** gap appears in the spread of labelled fibres behind a small incision at about 5 mm distance from striate cortex. Calibration bars: 1 mm.

the hemisphere was sectioned horizontally, and the sections were treated for autoradiography (Cowan et al. 1972).

Quantitative assessment of divergence was performed in one case. Labelled fibres were photographed at high magnification (Wild MPS 51 camera, Agfa Pan 100) covering the lesion and adjoining region. They were individually drawn from the negatives of the photomicrographs that were projected onto a drawing board for further magnification (×20). These drawings were mounted to large composits for each section. For the analysis, length and orientation of labelled fibres were measured on the composits in circular regions with a diameter corresponding to 0.55 mm (Fig. 3). These circular regions were placed in two pairs of columns to the right and left of the lesion extending along the main fibre course to the border of grey matter. A total of 108 circular regions from three sections was analyzed.

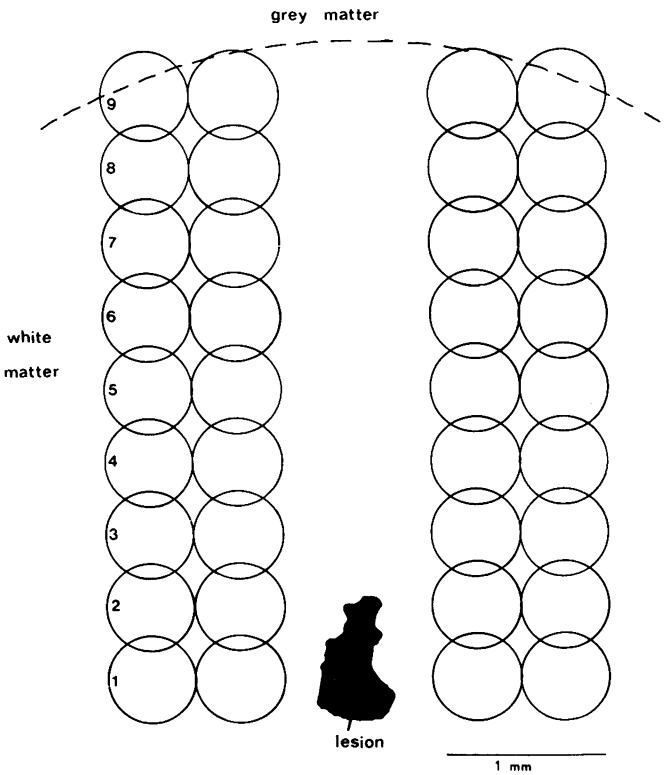

Fig. 3. Schematic drawing of the arrangement of circular regions for analysis of fibre orientation in tangential sections of flat mounts of the occipital operculum. The site and extent of the lesion is indicated in black. Calibration bar: 1 mm.

Angular orientation of each fibre within each circular region was measured and the deviation from the main fibre course was noted in classes of 10 degrees. The *lengths* of all fibres within a given class were added, rather than the *number* of fibres, in order to avoid a bias in favour of other fibre systems not running parallel to the plane of sectioning (and hence the plane of the optic radiation). The data from circular regions of identical distance from grey matter border were pooled and histograms of the distribution of total fibre lenght within each orientation class were constructed for each level of distance between lesion and grey matter.

Results

The injections of tracer were confined to the LGN (Fig. 2A) and the optic radiation was labelled at varying extent, mostly covering central and paracentral parts of the visual field representation. Since WGA-HRP is axonally transported both in anterograde and retrograde direction, the bulk of labelled fibres contained also cortico-geniculate axons. Comparison with the autoradiographic data, however, showed good qualitative agreement in topographic distribution, main fibre direction and pattern of fibre deviation. Thus, we conclude that the findings reported below refer indeed to optic radiation fibres, even if the contribution of cortico-geniculate fibres cannot be separated.

The arrangement of labelled fibres in the opercular white matter, seen tangentially, is highly parallel before the lesion site (Fig. 2B). One would therefore expect to see a parallel stripe devoid of labelled fibres behind the knife cut. Yet, examination at lower magnification showed that the unlabelled gap did not have the shape of a rectangular "corridor", but was of a conical shape with decreasing distance of the edges as they approached grey matter (Fig. 2C). This appearance was due to the deviation of fibres from the main course, diverging symmetrically from both sides into the gap. The degree of deviation increased as the distance from the visual cortex decreased. Axons begin to deviate approximately 3 mm before they enter the visual cortex.

In cortical layer IVC no discontinuity or diminution in the intensity of terminal labelling could be detected. It was evenly distributed along the complete extent of these layers. In the autoradiographic control, a similarly diverging course of single fibres was seen at the entry into striate cortex.

For quantitative assessment, 2283 individual fibres were measured. Each circular region taken for measurement (Fig. 3) contained 21.2 ± 10 fibres on average. The distribution histograms of axon orientation demonstrate that the orientation class of 0 degree deviation, i.e. the main fibre course, predominates in white matter at a distance of 3–4 mm from the border to striate cortex. Here, it accounts for about half the length of all fibres (Fig. 4, levels 1–4). In contrast, the orientation of fibres at the level immediately underneath the cortex shows an equal distribution in all classes. Here, less than 10% of fibre length still runs in the main course (Fig. 4, level 9). At levels in between, the proportion of fibres that deviate between 30 and 90 degrees from the main fibre course increases gradually (Fig. 4, levels 5–8). The symmetry of deviation to the right and left of the main fibre course, seen qualitatively in the histological pictures (Fig. 2C), is reflected by the shape of the histograms in the quantitative evaluation (Fig. 4). This argues against the presence of possible systematic artifact due to an obliquely running system of fibres that still could be organized in parallel.

These findings indicate that optic radiation fibres, immediately before they enter striate cortex, give up their neighbourhood relationships which they have maintained along the course of the optic radiation.

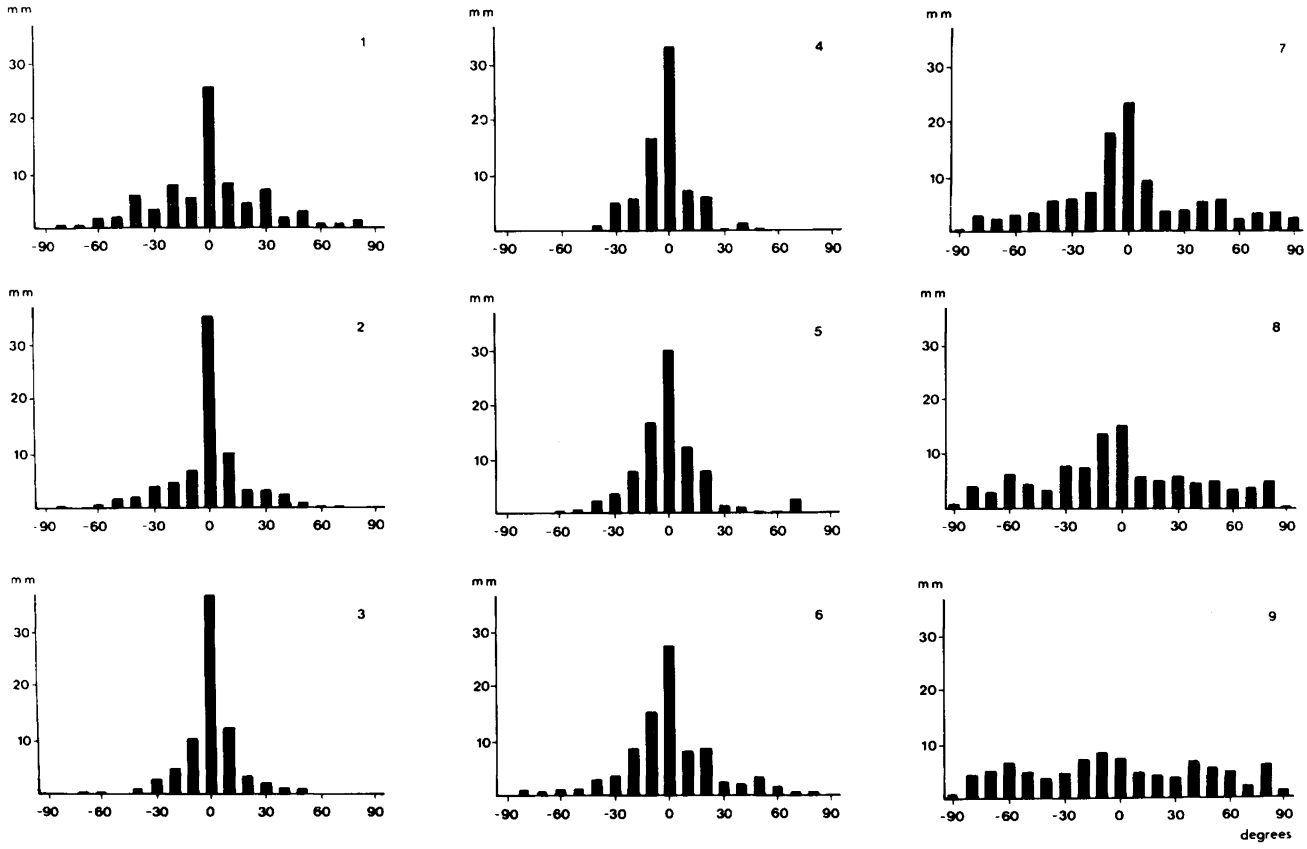

Fig. 4. Distribution histograms of fibre orientation at the nine levels between the knife cut lesion and the grey matter border as indicated in Fig. 3. The deviation to the left (−) or right (+) from the main fibre course of the optic radiation (corresponding to 0 degree) is indicated by giving the sum of lengths of all fibres within each orientation class.

Discussion

Fibres of the optic radiation run in a highly ordered, parallel fashion (see Polyak 1957), and continue so even after they have entered the operculum where they spread out in a thin sheet of white matter (Kuderna et al. 1984). Here, their main course is parallel to the direction of ocular dominance stripes and orthogonal to the 17/18 boundary (Kuderna et al. 1984). Our findings demonstrate that they diverge from this main direction before they enter striate cortex. Such divergent course of optic radiation fibres has already been illustrated by Ramon y Cajal in 1899, based on Golgi studies of the immature human striate cortex (Defelipe and Jones 1988). Geniculate fibres in many cases have shown a highly oblique course relative to the orientation of striate cortex, as demonstrated by intra-axonal labelling of single fibres in monkeys (Blasdel and Lund 1983, Freund et al. 1989). The symmetrical and gradual mode of change in axon orientation as the fibres approach striate cortex seems to leave little doubt that true fibre divergence occours. This means that the principle of strictly maintained neighbourhood relationships is abandoned and the point of final termination in striate cortex may emerge on the basis of a statistical process.

This divergence seems not to occur in compensation for a dearrangement of fibres earlier in the course of the optic radiation: retrograde tracing studies suggest a high degree of order and fibre parallelism immediately onward from the LGN (own unpublished observations), confirming findings of myelin or Marchi stain after cortical and white matter lesions (see Polyak 1957).

This concept of fibre divergence in the distal optic radiation seems in opposition to double-labeling studies where tracers were injected in neighbouring sites of striate cortex of macaques (Perkel et al. 1986, Salin et al. 1989). Double-labelling was absent if the cortical injections were more than 2 mm apart, and the authors concluded that axonal arborization and scatter of geniculo-striate projection is little in comparison to other afferents to the visual cortex. In a similar type of study in which in animals with long-standing large cortical resections intact cortex had been injected with HRP at the edge of the lesion, retrogradely labelled neurons were found only in the intact sector, but not in the retrogradely degenerated sector of the LGN (Cowey and Stoerig 1989). However, these experiments suffer from two shortcomings with regard to their interpretation as to the absence or presence of geniculo-striate fibre divergence. First, the mode of tracer uptake at the injection site is not completely understood: it may depend on the functional

state of the synapses and terminal boutons involved. More importantly, the fact has to be considered that the size of the structure, and hence the number of neurons, onto which the visual field is projected, differs very much between the LGN and striate cortex. The ratio between the number of cells in LGN and the receiving layer IVC in striate cortex has been estimated to be on average 1 : 130, indicating a substantial magnification of the projection surface (CONNOLLY and VAN ESSEN 1984). Since neurons in the LGN are highly outnumbered by striate neurons, divergence seems a necessary prerequisite of the geniculo-striate projection. Examination of LGN neurons that are retrogradely labelled from striate cortex in order to determine scatter and overlap of geniculo-striate projection seems hardly suited to detect divergence. This approach appears like the look through a "minifying" glass which makes the effect of divergence imperceptible. Direct visualization of the opercular white matter therefore seems better suited for a study of geniculo-striate fibre organization.

Apart from the divergence of fibres within white matter, as shown in the present study, intraaxonal labelling has demonstrated substantial intracortical branching of fibres and multiple terminal arbours. The terminal boutons of one single fibre are spread over a cortical distance of at least 2 mm (BLASDEL and LUND 1983, FREUND et al. 1989), as has also been shown previously in the cat (FERSTER and LEVAY 1978, HUMPHREY et al. 1985, FREUND et al. 1985).

Plasticity of cortical visual field representation, found both after peripheral and central lesions, cannot be explained on the basis of a rigid point-to-point representation. The studies on partial recovery from visual field defects in patients with postgeniculate lesions, as well as the experimental findings in cats indicate that an re-arrangement of cortical visual field representation is possible over cortical distances of 8 mm in cat and up to 19 mm in man (ZIHL and VON CRAMON 1982, KAAS et al. 1990). These figures are in a range comparable to the amount of divergence found in our experiments of about 6–10 mm. Since axon sprouting over such distances in primate visual cortex is unlikely, the distal divergence normally present may serve as the main basis for such functional plasticity.

Single cell electrophysiological recordings in monkey striate cortex have revealed a high degree of precision in the visual field representation, with the scatter and overlap of receptive field positions not exceeding 2 mm of cortical distance (HUBEL and WIESEL 1974). These findings have always been considered to strongly support the view of strict point-to-point projection. From our findings, however, as well as from the evidence of intraaxonal labelling it follows that the physiological precision of retinotopy depends on cortical computation rather than on the wiring of afferents. This principle allows, by "unmasking" of less effective synapses of the divergent input, the restoration of function after peripheral or central damage, as it has been shown in the somatosensory system (WALL 1977, KAAS et al. 1983).

Abbreviations

DAB diaminobenzidine
HRP horseradish peroxidase
LGN lateral geniculate nucleus
TMB tetramethylbenzidine
WGA wheat germ agglutinin

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