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Retinotopy of cortical connections between the striate cortex and extrastriate visual areas in the rat

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Abstract. Previous studies have determined that the striate cortex of the rat is reciprocally connected with multiple extrastriate cortical areas that are retinotopically organized. The objective of this study was to investigate the retinotopy of the striate-extrastriate connections in the rat, by placing triple or double injections of fluorescent tracers (fluorogold, fast blue, rhodamine dextran, or rhodamine-labeled microspheres) in different regions of the striate cortex (Oc1) and mapping the distribution of cells and fibers labeled with the different tracers in the lateral (Oc2L) and medial (Oc2M) extrastriate cortex. The tracer injection sites were visualized in tangential sections of the flattened cortex and correlated with the myelin layout of the striate cortex and with an electrophysiological map from previous studies. The results showed retinotopically organized Oc1 connections with ten different extrastriate cortical areas. The location of these extrastriate areas and the retinotopy of their striate connections remained mostly invariant despite changes of the injection sites in Oc1. Thus, the quadrantic retinotopy was obtained for striate connections to areas posterior, posterolateral, lateromedial, laterointermediate, laterolateral, anterolateral and rostrolateral in Oc2L; and to areas posteromedial, anteromedial, and anterior in Oc2M. The present anatomical map correlates well with electrophysiological maps of the rat extrastriate cortex from previous studies. Furthermore, they provide a definition of the retinotopy of some areas that have not been completely mapped before. These results reaffirm the existence of multiple extrastriate visual areas in the rat.

Key words: Visual cortex – Extrastriate visual areas – Striate-extrastriate connections – Fluorescent tracers – Rat

Introduction

The visually responsive occipital cortex of the rat (Montero 1973) is composed of several retinotopically organized areas in addition to the single representation of the contralateral visual hemifield in the primary visual area (V1) in the striate cortex (Montero et al. 1973b). Each of these extrastriate areas, which were named according to their relative position to V1 (posterior, P; posterolateral, PL; laterolateral, LL; anterolateral, AL; anteromedial, AM), receives direct connections from the striate cortex (Montero et al. 1973a, Montero 1981b), and in turn, each area sends feedback connections to the striate cortex (Olavarria and Montero 1981). A double-label study of callosal and ipsilateral striate cortical connections revealed that each of the lateral extrastriate areas are contained in several distinct acallosal regions surrounded by borders rich in callosal cells and fibers (Olavarria and Montero 1984). This pattern of callosal connections is remarkably constant in the rat (Cusick and Lund 1981; Zaborsky and Wolff 1982; Olavarria and Montero 1984; Olavarria and Van Sluyters 1985), reflecting the position of the different lateral extrastriate areas. The retinotopies of the rat's areas AL, LM, and LL were confirmed in a subsequent study which, in addition, differentiated two areas medial to V1, anteromedial (AM) and posteromedial (PM), and another area, laterointermediate (LI), between LM and LL (Espinoza and Thomas 1983). Direct demonstration that independent acallosal regions contain areas AL, PL, and LL, while areas LM and LI are contained in the same acallosal region, and that a new area, rostrolateral (RL), is surrounded by another callosal ring was obtained by Thomas and Espinoza (1987).

Several other lines of evidence support the existence of the above-described extrastriate visual areas in the rat: (a) each of these areas sends separate projections to the superior colliculus (Olavarria and Van Sluyters 1982; Thong and Dreher 1986); (b) the extrastriate visual areas are interconnected (Torrealba et al. 1984; Coogan and Burkhalter, in press); (c) different medial and lateral extrastriate visual areas receive distinct thalamic and cortical connections (Olavarria 1979; Sanderson et al. 1991); (d) the laminar pattern of interconnections between the different visual areas in the rat, and their distinct terminal fields in the superior colliculus (Harvey and Worthington

1990), suggests a hierarchical order in their organization (Coogan and Burkhalter, in press).

However, the notion of the existence of multiple extrastriate visual areas in the rat has not been supported in other reports. Miller and Vogt (1984) concluded that, in general, medial and lateral parts of the rat striate cortex connect with medial and lateral extrastriate cortex, respectively. Kaas et al. (1989) speculated that the lateral extrastriate cortex in the rat is formed by a single visual area, V2, with repeating modules. Malach (1989) expanded this notion in his conclusion that the total extrastriate cortex (medial and lateral parts) surrounding the striate cortex in the rat contains a single modular global map homologous to V2 of cat and monkey.

In the present experiments the retinotopy of the striate-extrastriate connections in the rat was investigated after placing different fluorescent tracers in different regions of the striate cortex. The results should help to resolve the question of whether the retinotopy of these connections conform to a single modular map or to several distinct maps compatible with the existence of multiple extrastriate visual areas in the rat.

Materials and methods

Long-Evans (hooded) rats ($n = 7$; 310–400 g) were used in this study. The animals were anesthetized with urethane (125 mg/100 g i.p.) and ketamine (5 mg/100 g i.m.), supplemented with atropine sulfate (0.05 mg/kg s.c.) and prophylactic amoxicillin (20 mg/kg i.m.). After a craniotomy exposing most of the right occipital cortex, the striate cortex was injected through the dura mater in different sites with different fluorescent tracers according to an electrophysiological map (Fig. 1 in Montero et al. 1973b). In this map, the straight part of the lambda suture, which was used as a stereotaxic reference for the injections, is at 1.25 mm rostral to the occipital pole. Photographs of dorsal views of the skull and brain exposed in the craniotomy were used as a guide for the injection sites in the striate cortex. The following fluorescent tracers were injected through glass micropipettes (ID 0.25 mm, OD 1 mm, 30–40-μm tip; A-M Systems) using electronically controlled pulses of air pressure (Pneumatic PicoPump, World Precision Instruments): fluorogold (FG), a retrograde tracer, 4% in distilled water (Fluorochrome); fast blue (FB), a retrograde tracer, 2% in distilled water (Sigma); rhodamine dextran (RD), mostly an anterograde tracer with some retrograde label, 10% in distilled water (Molecular Probes); rhodamine-labeled latex microspheres, or "beads" (RB), a retrograde tracer, full-strength solution in distilled water (LumaFluor). Volumes of 0.02–0.05 μl of these tracers were injected at depths of 500–800 μm from the cortical surface.

After a survival time of 3–5 days, the rats were deeply anesthetized with overdoses of ketamine and pentobarbital and perfused through the heart (into the ascending aorta), using a peristaltic pump, first with phosphate-buffered saline at room temperature for about 1–2 min, followed by 1 l of cold 4% paraformaldehyde in 0.1 M phosphate buffer. The brains were immediately removed and photographed in dorsal views to localize the injection sites on the basis of the photographs used in the operation. The right cortex was carefully dissected out of subcortical structures and flattened between two slides (Olavarria and Montero 1984). The flattened cortex was photographed and jointly with a block containing the right lateral geniculate nucleus (LGN) was kept overnight in the refrigerator in the same fixative solution, plus 30% sucrose.

Tangential sections 40 μm in thickness were cut from the flattened cortex on a freezing microtome. Alternate sections were processed with a myelin hematoxylin stain or mounted unstained using Krystalon (Harleco) as mounting medium. The myelin stain in tangential sections (as shown in Fig. 1) provides a clear demarcation of the densely myelinated primary sensory visual Ocl (V1), somatosensory Parl (S1), and auditory Tel (A1) cortical areas as well as of the less densely myelinated medial (Oc2 M) and lateral (Oc2L) extrastriate cortex and densely agranular retrosplenial cortex (RSA; Olavarria and Van Sluyter 1985; Zilles 1985; Zilles and Wree 1985). The myelin pattern of V1 provided a fixed architectonic landmark that allowed an estimation of the positions of the tracer injection sites in the striate cortex with respect to its retinotopic map (Montero et al. 1973b). Alternate (40 μm) coronal sections of LGN were processed with Nissl stain or mounted unstained with Krystalon. LGN sections allowed an additional estimation of the retinotopic position of the injection sites in V1 by correlating the projection fields in LGN from the different injection sites to the retinotopic map in this nucleus (Montero et al. 1968).

The unstained sections of the cortex and LGN were examined under epifluorescence illumination (Hg, 100 W light source) in a Leitz Aristoplan microscope using filter A (BP 340–380 nm) to detect FG and FB label, and filter N2 (BP 515–560 nm) to detect RD and RB label. The microscope stage was connected through a digitizer for the x and y axes (MD2 System, Minnesota Datametric) to a 486 computer and a graphics plotter. The distribution of cells and fibers labeled with the different fluorochromes were digitized, and plots from several unstained sections as well as of myelin sections were superimposed, using vessels as fiducial marks, resulting in final diagrams as shown in Figs. 2 and 3. Likewise, the distribution of labeled cells and fibers in unstained LGN sections were plotted and related to Nissl-stained sections.

Results

Retinotopy of connections between the striate cortex and the lateral extrastriate cortex

Multiple fluorescent tracers were injected in different quadrants of the striate cortex (V1) to obtain a layout of the nasotemporal and upper-lower axes of visual field representation in its projection fields in the extrastriate cortex. Figure 2A illustrates a case (R59) in which injections of three tracers were closely placed in the striate cortex. Injections sites (arrows) are related to the estimated positions of the horizontal and vertical meridians of the visual field representation in V1 (Montero et al. 1973b). In this map the zero vertical meridian (VM) bounds V1 laterally, the zero horizontal meridian (HM) bisects obliquely the caudal (upper visual field) and rostral (lower visual field) parts of V1, and the 60° vertical meridian (not drawn) bisects the medial (temporal) and lateral (nasal) parts of V1. A RD injection (in red) was placed in the lower-temporal quadrant of V1, a FB injection (in blue) was placed in the lower-nasal quadrant, and a FG injection (in yellow) was placed more caudally at about the HM. Color microphotographs of the FG, FB, and RD injection sites in this animal are shown in Fig. 4A, B, and C, respectively.

The cortical connection fields detected in the lateral extrastriate cortex from these multiple injections in V1 were clearly grouped in the different projection areas previously described: AL, LM, LI, LL, PL, P, and perirhinal (PRh; Montero et al. 1973a; Olavarria and Montero 1984). (The medial extrastriate cortex projections were not recovered in this animal (R59) as a consequence of a superficial lesion in this region.) In each of the target

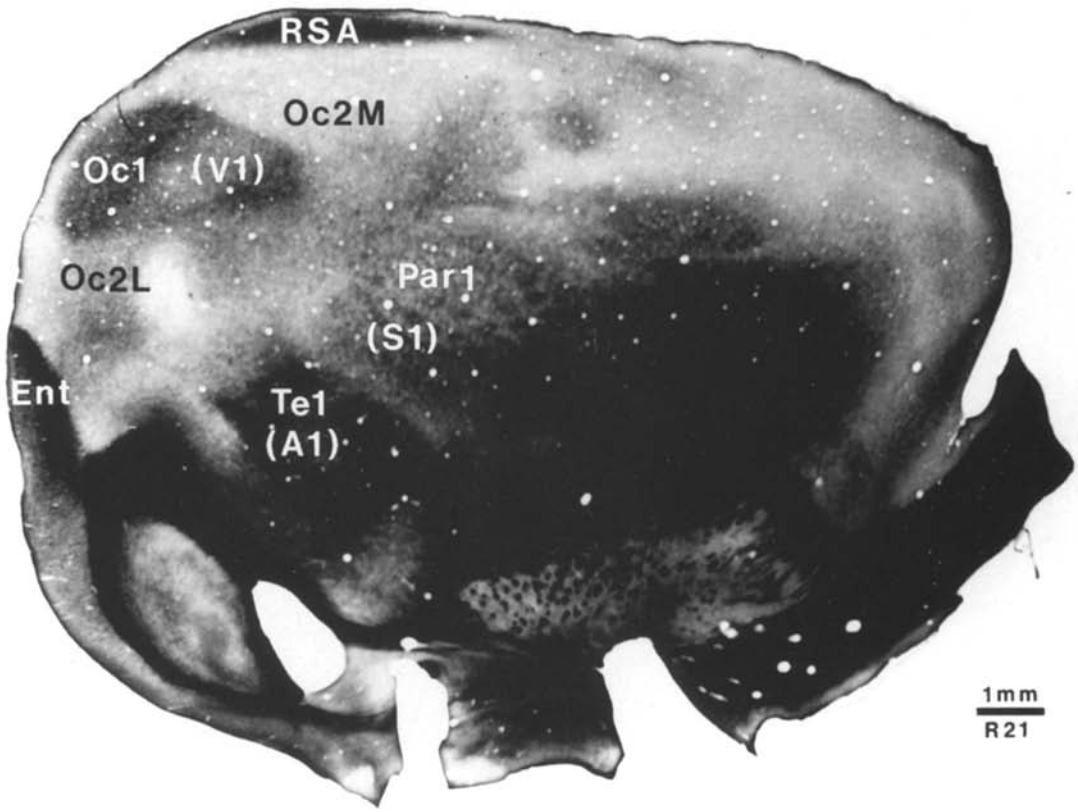
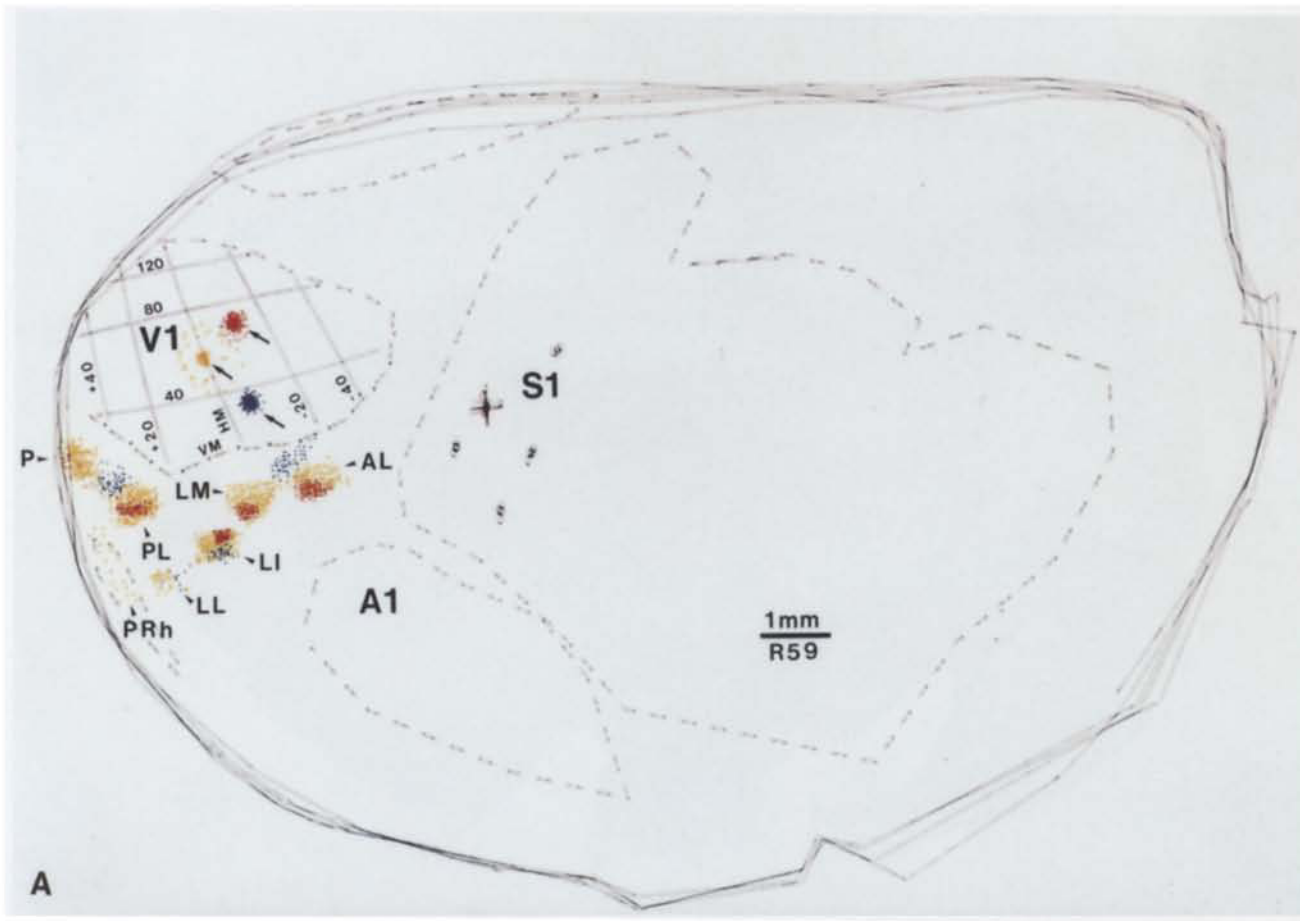


Fig. 1. Myelin-stained tangential section of the flattened cerebral cortex of rat R21. Notice the densely myelinated primary visual area *[Oc1, (V1)]* surrounded laterally and medially by less densely myelinated occipital extrastriate cortical areas *Oc2L* and *Oc2M*, respectively (Zilles 1985, nomenclature). The myelin pattern of the primary auditory cortex *[Te1, (A1)]*, primary somatosensory cortex *[Par1, (S1)]*, retrosplenial agranular cortex (*RSA*) and entorhinal cortex (*Ent*) are also indicated. *Left* is caudal and *top* is medial

areas in the extrastriate cortex, a distinct retinotopic pattern in the distribution of the multiple connection fields was observed. In area AL, connections from the RD injection in the lower-temporal quadrant and the FB injection in the lower-nasal quadrant project laterally and medially, respectively. The intermediate and caudal FG injection in V1 projects in between the RD and FB fields, but extends more rostrally in AL. In area LM, the lower-nasal FB projection lies rostrally and medially, at the boundary with area AL, while the lower-temporal RD projection is more lateral and caudal. The FG projection again occupies an intermediate position between the RD and FB projections. (Notice the larger extent of the FG projections in the extrastriate cortex, reflecting the larger injection site of this tracer in V1.) In area LI, the projections from the three tracers are inverted in a mirror image with respect to the LM projections, i.e., RD and FB projections are medial and lateral, respectively, and the FG projection is intermediate. A wide extent of extrastriate cortex devoid of projections from these injection sites exists between LM, LI, and PL, suggesting that this cortex receives projections from other retinotopic regions of V1, which is corroborated in the results of experiments described below. In area PL the projections experience a mirror-image inversion in a mediolateral plane with respect to those in LM, i.e., the lower-nasal FB projection is caudal and medial; the lower-temporal RD projection is lateral and more rostral, and the FG projection is intermediate. The boundary between areas PL and P is filled with the lower-nasal FB projection, and more caudally in area P is the relatively higher visual field FG projection. A sparse RD projection occurs caudally in area P. In area LL the FG projection is caudolateral while the FG projection is rostromedial. Scattered FG-labeled cells are present in the PRh cortex.

The topographical relations of the three tracer injections in the striate cortex in case R76 (Fig. 2B) were similar to that in the previous case, although the FB injection was more rostral (lower in the visual field), and the RD injection was more medial (more temporal in the visual field). First, notice the striking similarity in the distribution of projection fields from the FG injections in cases R76 and R59, which reflects the similar position of the FG injection sites in both animals. Second, notice that the multiple projections to the different lateral extrastriate areas followed a similar retinotopic pattern, al-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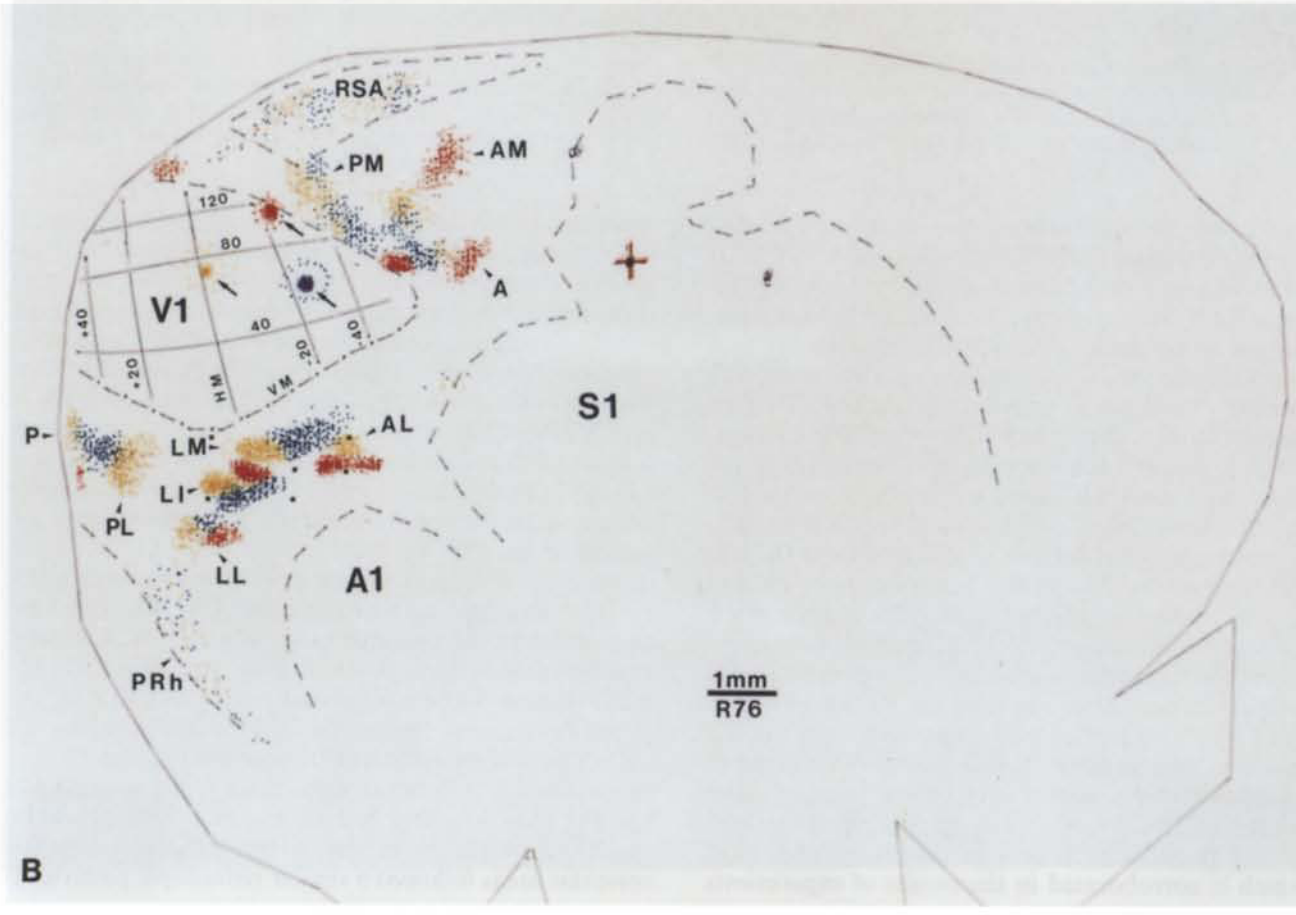
RSA
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1mm
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Fig. 2

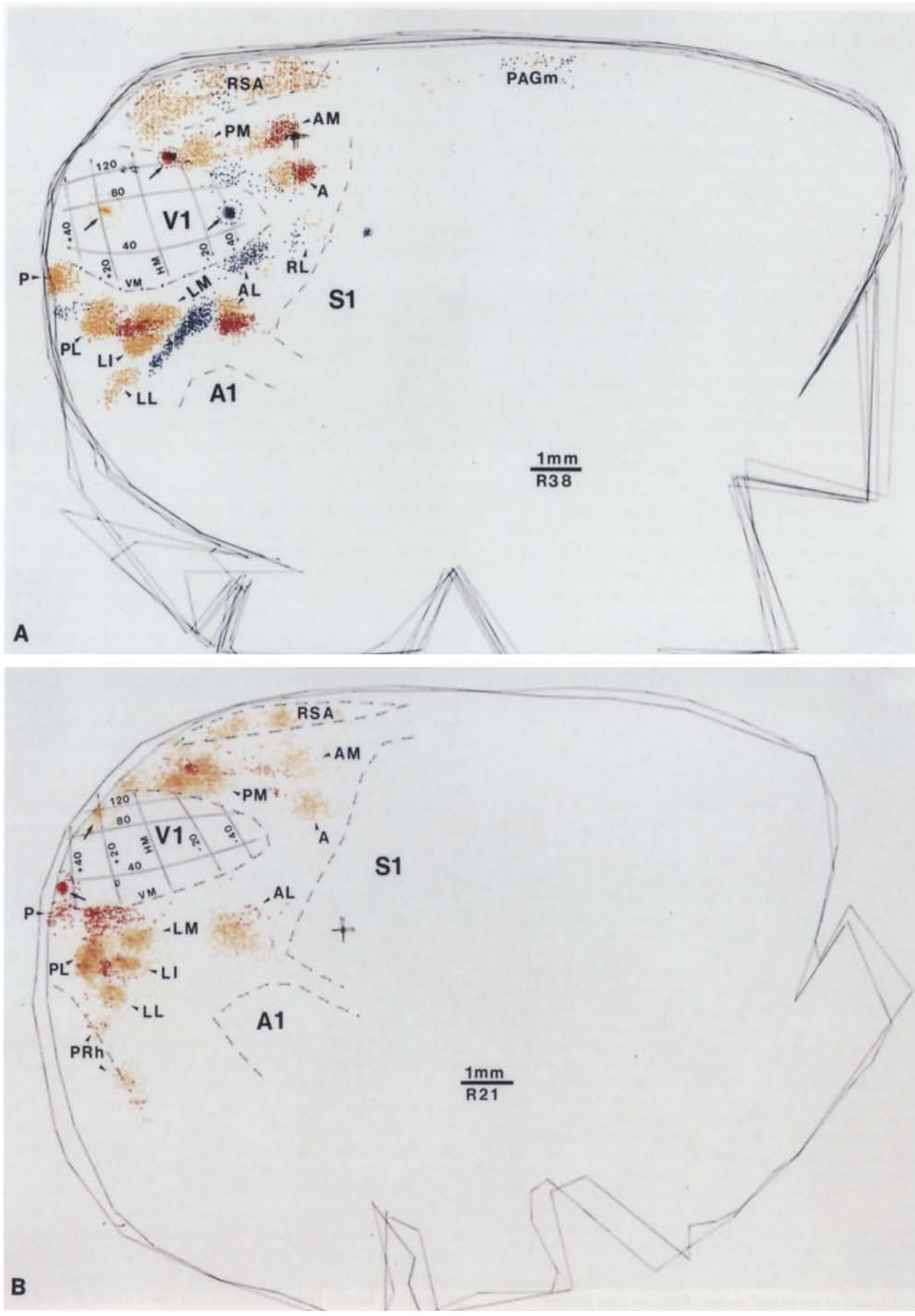
beit with some variations, to that in the previous case. In area AL, the RD injection in the periphery of the inferotemporal quadrant projects extensively laterally, while the lower and nasal FB injection projects medially, and the FG projection is intermediate. The peripheral lower-temporal RD projection between areas LM and LI, which in case R59 were separate fields, merged into a single field in R76. This is an indication that the extreme temporal field is the boundary between LM and LI, which is in good agreement with physiological results (Espinoza and Thomas 1983). In area LM, the high-to-low visual field axis formed by the FG and FB projections is oriented caudorostrally, being the FB lower visual field projection the boundary with area AL. In area LI, as in case R59, the lower visual field FB projection is lateral, but now it extends more rostral and medial, representing lower regions of the visual field in this area. In area LL, the nasotemporal axis given by the FB-RD projections is oriented mediolaterally, while the upper-lower axis given by the FG-FB projections is oriented caudorostrally. In area PL, the upper-lower axis (FG-FB projections) is oriented rostrocaudally. Projections from the temporal periphery (RD) were not found in PL. In area P, the upper-lower axis (FG-FB projections) is oriented caudorostrally and the nasotemporal axis (FB-RD projections) is oriented mediolaterally. The lower visual field (FB projection) lies at the limit between P and PL.

As a photographic documentation of the segregation of projections from different injection sites in the striate cortex to the multiple extrastriate areas observed in the present experiments, the *same* field in the regions of LM and LI bracketed by square dots in Fig. 2B (rat R76) is shown in the two color microphotographs obtained with the A filter (Fig. 5A) and with the N2 filter (Fig. 5B). Notice the same positions of vessels in both micrographs. The lower half of Fig. 5A shows the FG and FB projections to area LI, with mostly FG cells (yellowish) to the left (caudally) and mostly FB cells (bluish) to the right (rostrally). An expanse of cortex mostly devoid of labeled cells separates the LI projection from the LM projection at the top of the figure. In the latter, mainly the cluster of FG-labeled cells, caudally, and the beginning of the FB projection, rostrally (top-right corner), are seen. Figure 5B shows that the empty space between the FG and FB projections to LM and LI is occupied by a dense projection of RD anterogradely labeled axons, in which a few retrogradely labeled cells are present. Figure 5C,D shows at higher magnification the *same* field in AL of rat R76 (bracketed by square dots in Fig. 2B; notice similar position of vessels in both micrographs). Figure 5C shows the almost complete segregation of FG-labeled cells (right, rostrally) and FB cells (left, caudally) in AL, while Fig. 5D shows the RD projection filling a space left empty by the FG and FB projections.

In rat R38 (Fig. 3A) the injections of the three tracers were even wider apart than in the previous cases. The FG injection was in the upper-temporal quadrant, the RD injection was in the periphery of the lower-temporal quadrant, and the FB injection was more rostral in VI (lower in the visual field) than in the previous two cases. It is convenient to focus first on the FG (upper-temporal) projections to visualize the retinotopic changes in the projections of this case with respect to the previous cases. The FG projections were distributed in the same fields AL, LM, LI, PL, P, and LL, as in the previous cases, but now the FG projections to LM, LI, and PL are much closer than in rats R59 and R76. This approximation indicates that these three areas limit each other by representations of the upper visual field.

In area AL the same retinotopic trends as in the previous two cases of the three different projections were observed, i.e., lower-temporal (RD) is lateral, nasal (FB) is medial, and the upper visual field (FG) lies between them. However, the extreme lower visual field FB projection in this case is more rostral and medial (approaching V1) than in the previous cases. In area LM, again the same retinotopic trends of the three projections observed in the previous cases are present; i.e., the lower visual field (FB) is rostral, upper visual field (FG) is caudal, and temporal visual field (RD) is lateral. The latter is again the boundary with LI. Likewise, a similar retinotopic trend to LI, as in the previous cases, is observed: the upper visual field (FG) is caudal; temporal visual field (RD) is medial, and lower visual field (FB) is rostrolateral. The main change with respect to case R76, in which the lower visual field (FB) projections to LM, LI, and LL are separated, is that the even lower visual field (FB) projection in R38 now merges with that of LM and LL. As in case R76, the upper-lower axis given by the FG and FB projections is oriented caudorostrally. No projection to LL from the peripheral lower-temporal (RD) field was found in this case. As in the previous cases, the lower visual field (FB) projection forms the boundary between areas P and PL.

Fig. 2A,B. Distribution of labeled cells and fibers in the rat extrastriate cortex, after multiple injections of fluorescent tracers in the striate cortex (*VI*). **A** Computer reconstruction of five superimposed tangential cortical sections of R59. The position of the injection sites (*arrows*) of fluorogold (FG, in *yellow*), fast blue (FB, in *blue*), and rhodamine dextran (RD, in *red*) are indicated with respect to the myelin pattern of V1 and to the approximate coordinates of a previous electrophysiological map (Montero 1973b). *Dots* indicate maximum extent of injection sites (see also Fig. 4). The distribution of cells labelled with FG and FB, as well as fibers and cells labeled with RD, in the lateral extrastriate cortex and in the perirhinal cortex (*PRh*) are indicated with *dots of corresponding colors* to the tracers injection sites. Lateral extrastriate areas containing clusters of labeled neural elements with the different tracers are named posterior (*P*), posterolateral (*PL*), lateromedial (*LM*), anterolateral (*AL*), laterointermediate (*LI*), laterolateral (*LL*), following previous nomenclature for these striate connection fields in the rat lateral extrastriate cortex (see text). The myelin pattern of *S1* and *A1* are indicated. **B** Computer reconstruction of distribution of labeled elements from nine superimposed sections of R76 (the outline of only one section was drawn). Injection sites in V1 and their connection fields in the lateral extrastriate cortex are indicated as above. The *rectangles* limited by *square dots* in *LM*, *LI*, and *AL* indicate cortical regions in the photographs in Fig. 5. Areas in the medial extrastriate cortex containing clusters of cells and fibers labeled with the different tracers are named anterior (*A*), anteromedial (*AM*), and posteromedial (*PM*). Labeled elements in retrosplenial agranular cortex (*RSA*) and in perirhinal cortex (*PRh*) are also plotted


RSA
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LM
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1mm
R21
B

Fig. 3

No peripheral temporal visual field (RD) was found in areas P and PL in this case. FG and FB projections were found in rostral extrastriate cortex, between V1 and S1. This projection field is named RL because it corresponds in location to the homonymous area mapped by Thomas and Espinoza (1987). In RL, upper visual field (FG) is rostral and lower visual field (FB) is caudal. Clear projections to RL were not found in the other cases.

In rat R21 (Fig. 3B), a FG injection was placed in the upper-temporal quadrant of V1, and an injection of RB was placed in the upper-nasal quadrant of V1. The upper-temporal (FG) projections were distributed in a similar pattern in AL, LM, LI, LL, and PL to the upper-temporal (FG) projections in rat R38. However, in this case there was no FG projection to area P. As in case R38, the upper-temporal (FG) projections to LM, LI, LL, and PL approached each other, in contrast to the FG projections in R59 and R76, indicating again that these areas bound between them by the upper visual field representation. The upper-nasal (RB) projections were distributed in area AL rostromedially to the upper-temporal (FG) projection, while they were distributed medially to the upper-temporal (FG) projections to PL and LM. This RB projection is interpreted to represent the merged upper-nasal projection to LM and PL, being the upper-temporal (FG) projections more lateral in the two areas. Notice that the upper nasal (RB) projection in this region fills a region of extrastriate cortex that is devoid of projections in all the other cases. In addition, there was an upper-nasal (RB) projection at the confluence of the FG projections in LI, LL, and PL. This RB projection is interpreted to represent the merged upper nasal projections to LI and LL. This is consistent with the lower-nasal field (FB) projection rostrally between LI and LL observed in rat R76. Finally, there was an upper-nasal (RB) projection to area P caudally, immediately adjacent to V1.

Retinotopy of connections between the striate cortex and the medial extrastriate cortex

The striate cortex connections to the medial extrastriate cortex were distributed in three distinct areas which are named A, AM, and PM. The former two areas are named according to a previous description of these striate cortex projection fields (Olavarria and Montero 1984). Area PM is so named because by its location it appears to correspond to the homonymous area described by Espinoza and Thomas (1983).

The upper-temporal field FG projections in R38 and R21 (Fig. 3) are distributed in wide-apart regions of areas A, AM, and PM. By contrast, the lower-nasal FB projection in rat R38 (Fig. 3A; see also FB projection in R76, Fig. 2B) lies in a common center of the A, AM, and AP fields. The lower-temporal quadrant is distributed at the extreme rostral region of A and AM (RD projections to AM and A) in both R76 and R38. The upper-nasal RB projection in R21 (Fig. 3B) is to more caudal parts of A and AM, and to caudomedial parts of PM. However, in R76 there is a second RD field at the caudomedial part of A.

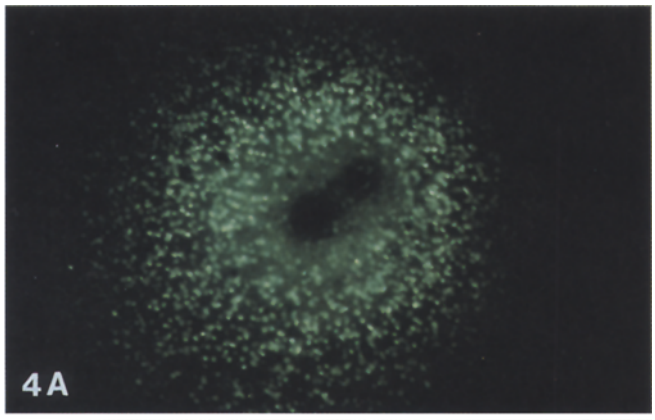
Cortical connections between striate cortex and perirhinal, retrosplenial and motor cortices

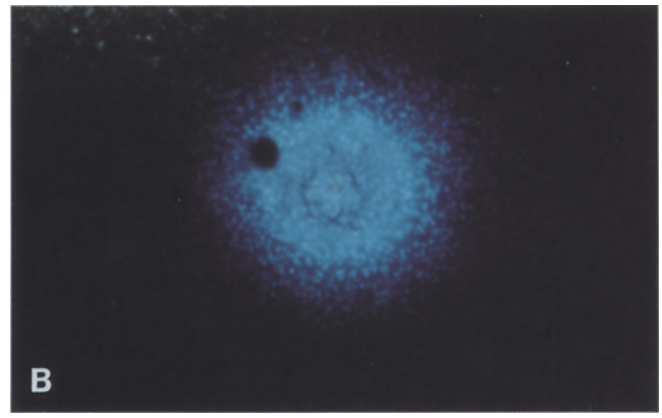
A mixture of retrogradely labeled cells from different injection sites (FG, FB, or RB) without any retinotopic order was found in the PRh cortex (R21, R76). This cortex was identified in tangential sections by its dorsal position to the highly myelinated entorhinal cortex (Zilles 1985). All regions of V1 are connected to PRh, as exemplified by PRh projections to the four visual quadrants in R21 and R76. No anterogradely RD-labeled fibers from V1 to PRh were found in the present material, although this cortical region has been observed to receive striate cortex afferents (Olavarria and Montero 1984; but see Miller and Vogt 1984).

An abundant collection of retrogradely labeled cells with FG, FB, or RD was found in the retrosplenial agranular cortex (RSA) (R21, R38, R76). This cortex was recognized in tangential sections by its caudomedial position and dense myelination (Zilles 1985). Since, owing to its border position, the RSA cortex was cut in a plane near parallel to its columns by the tangential sections, it was possible to see that retrogradely labeled cells projecting to V1 were distributed in several cortical layers, with the exception of layer 1. A periodic distribution of labeled cells along the caudorostral axis of RSA was observed; however, a substantial overlapping of cells labeled with two tracers existed in these periodic bands (R38, R76). No anterogradely RD-labeled fibers from V1 to the RSA cortex were seen. This result is consistent with previous observations (Vogt and Miller 1983; Coogan and Burkhalter, in press). However, a dense projection of anterogradely RD-labeled fibers was seen in layers 1 and 2 of the cortex adjacent medially to the caudal part of V1 (R76; Fig. 2B). It is difficult to identify with certainty this cortical region in tangential sections, although the cortex adjacent medially to the most caudal part of the striate cortex has been recognized as part of RSA (see Zilles 1985, Fig. 48). If this is the case, then the RSA cortex would have a caudal part that mostly receives afferents from V1 and a rostral part that mostly projects back to V1.

Retrogradely labeled cells projecting to V1 were clustered in a cortical region medial to S1 (indicated PAGm in R38, Fig. 3A). This posterior part of the medial frontal agranular cortex (PAGm; Donoghue and Wise 1982) has been previously described to be reciprocally connected with striate and extrastriate visual areas in the rat (Miller

Fig. 3. A Plot from six superimposed cortical sections of R38 shows distribution of injection sites with FG, FB, and RD and their respective labeled connection fields in the lateral and medial extrastriate cortex, retrosplenial agranular cortex (*RSA*), and in the medial frontal agranular cortex (*PAGm*). Conventions as in Fig. 2. **B** Plot from seven superimposed cortical sections in R21 showing distribution of FG (in *yellow*), rhodamine beads (RB, in *red*) injection sites in V1 and their respective connection fields in the lateral and medial extrastriate cortex, *RSA* and *PRh*. The outline of only two sections were drawn. Conventions as in Fig. 2





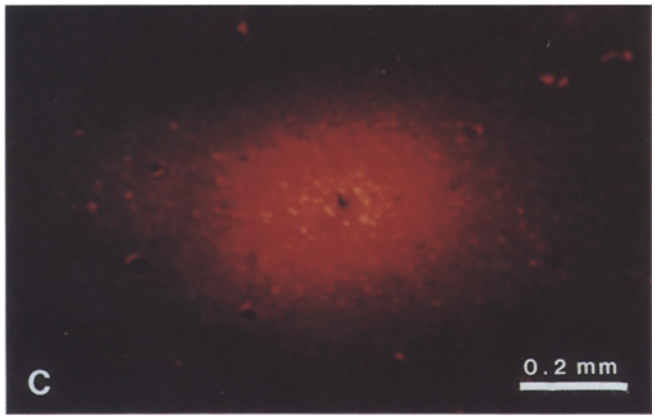
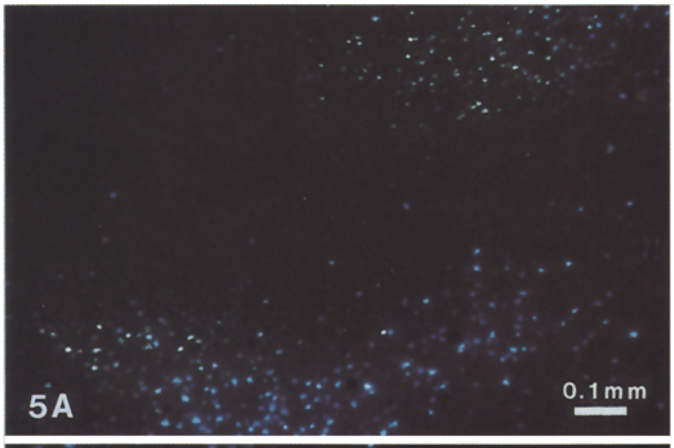
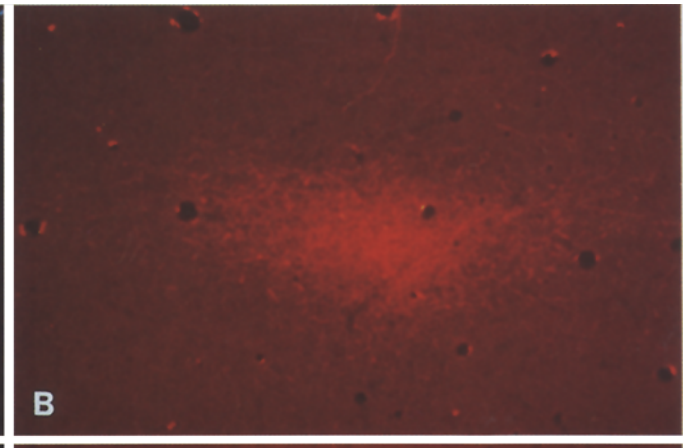
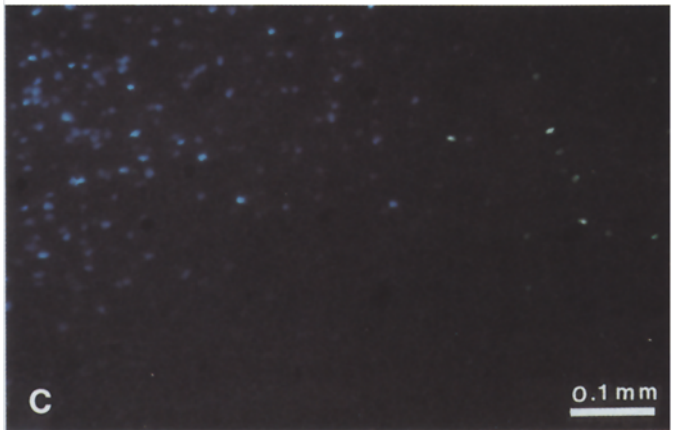


Fig. 4. Microphotographs of the injection sites of fluorogold (**A**), fast blue (**B**), and rhodamine dextran (**C**) in rat R59. *Scale* applies to all panels







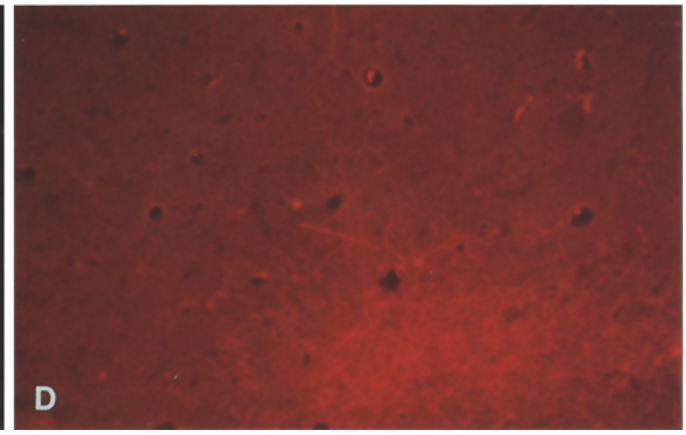


Fig. 5A–D. Microphotographs showing in the lateral extrastriate cortex of rat R76 the segregation of cells and fibers labeled with different tracers injected in different sites of the striate cortex. **A** Microphotograph (taken with the A filter) of FG- (*yellowish*) and FB- (*bluish*) -labeled cells in area LM (*top*) and LI (*bottom*). Notice the segregation of FG and FB cells in these two areas. **B** Microphotograph of the *same* cortical region taken with the N2 filter shows RD-labeled fibers and cells in a region between areas LM and LI which is mostly devoid of FG- or FB-labeled cells. **C** Microphotograph at higher magnification of a region of area LM and AL framed by the square dots (*small rectangle*) in Fig. 2B. Notice that FB- (*bluish*) and FG- (*yellowish*) -labeled cells are mostly segregated to the *left* (caudally) and *right* (rostrally) in the field, respectively. **D** The same field photographed with the N2 filter shows RD-labeled fibers and cells distributed in a region of area AL mostly devoid of FG- or FB-labeled cells

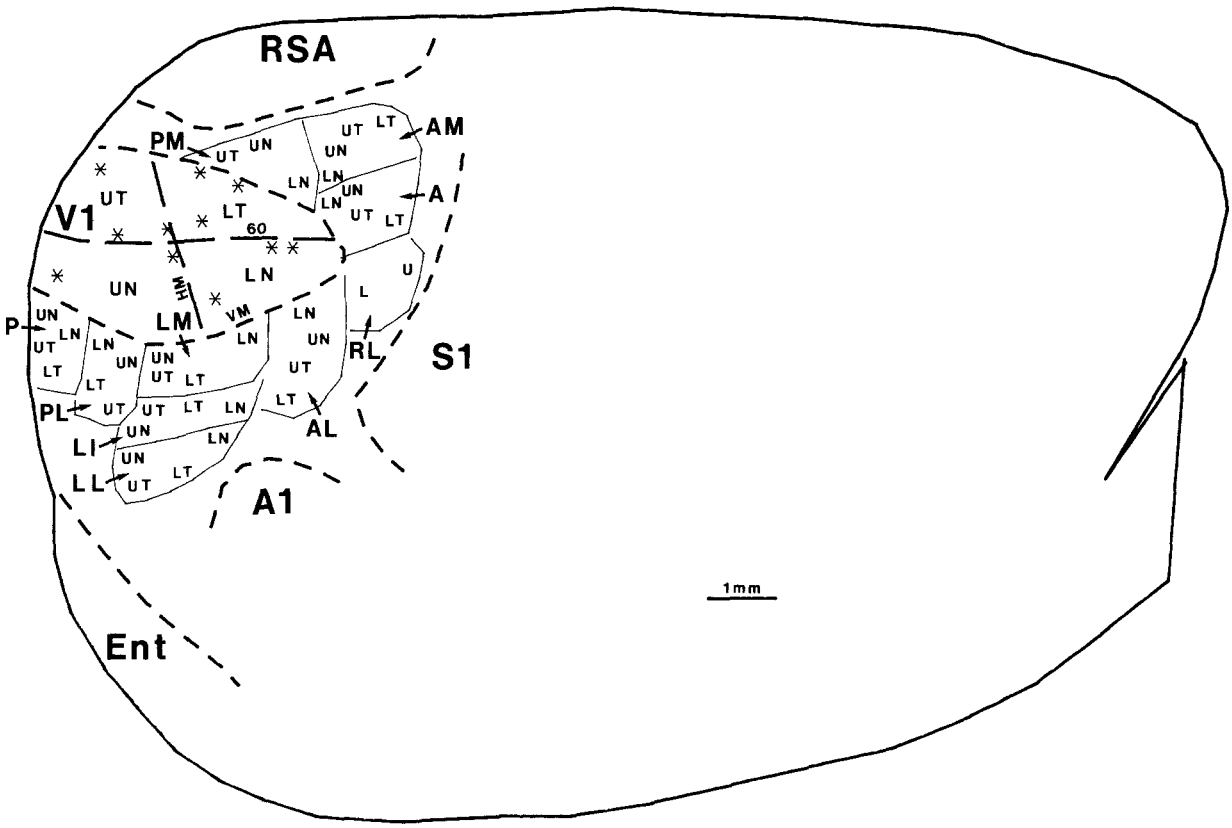


Fig. 6. Extrastriate visual areas in the rat. The flattened cerebral cortex of the rat showing the location and quadrantic retinotopy of ten extrastriate visual areas defined by their distinct pattern of striate retinotopic connections in this study. The approximate locations of the horizontal meridian (*HM*) and 60° vertical meridian in *V1* define the upper-nasal (*UN*), upper-temporal (*UT*), lower-nasal (*LN*), and lower-temporal (*LT*) quadrants of the visual field in the primary visual cortex. For diagrams of physiological maps of these areas see Fig. 1 in Montero et al. 1973b, Fig. 3 in Espinoza and Thomas 1983, and Fig. 6 in Thomas and Espinoza 1987. Abbreviations as in Fig. 2

and Vogt 1984; Torrealba et al. 1984; Sukekawa 1988; Sanderson et al. 1991). As demonstrated in case R38, cells projecting to caudal (FG label) and rostral (FB label) parts of V1 intermingle in the PAGm, indicating no retinotopy in this connection. The PAGm in the rat appears to be equivalent to the frontal eye field of the monkey (Hall and Lindholm 1974).

Scheme of extrastriate visual areas in the rat

Figure 6 shows on the flattened cerebral cortex of the rat the location and quadrantic retinotopy of ten extrastriate visual areas defined by their distinct pattern of retinotopic connections with area V1 in these results. The approximate locations of the horizonal meridian (HM) and 60° vertical meridian in V1 define the upper-nasal (UN), upper-temporal (UT), lower-nasal (LN), and lower-temporal (LT) quadrants of the visual field representation in the primary visual cortex (Montero et al. 1973b).

In the lateral extrastriate cortex, V1 is bounded caudorostrally by areas P, PL, LM, AL, and RL. Lateral to LM in second and third tiers are areas LI and LL. In areas P, PM, LM, and AL, the nasal hemifield is medial and the temporal hemifield is lateral. In the caudorostral direction, from areas P to AL adjacent to V1, the nasal field reverses several times from upper to lower (P), lower to upper (PL), and upper to lower (LM, AL). In the mediolateral direction, from areas LM to LL the visual field reverses from nasal (at the medial border of LM with V1), to temporal (at the border between LM and LI), to nasal (at the boundary between LI and LL), to temporal (at the lateral part of LL). Rostrocaudally, in areas LM, LI, and LL, the upper visual field is caudal and lower visual field is rostral. In area AL the representation of the visual field is more convoluted, with a core of upper field in the rostral center, while lower-temporal and lower-nasal fields are represented in the lateral and medial parts, respectively, of this area. For area RL only the upper field (rostral) and lower field (caudal) representations were obtained. In the medial extrastriate cortex are areas PM and A, adjacent medially to V1, and, inserted as a wedge between PM and A, area AM. In area PM, the upper visual field is caudal, lower visual field is rostral, while upper-temporal and upper-nasal fields are lateral and medial, respectively. In area A, the lower-temporal field is rostrolateral (there is an extra lower-temporal projection caudolaterally in area A of R59, Fig. 2A). The lower-nasal field is caudal, while the upper-temporal field is inserted between them. The upper-nasal field is caudomedial relative to the upper-temporal field (see R21, Fig. 3B). In area AM, the lower-temporal quadrant is repre-

sented at the rostromedial extreme, while the lower-nasal field is represented in the opposite, caudolateral extreme. The lower-nasal and upper-nasal fields are represented intermediate between the lower quadrants.

Discussion

Anatomical maps reveal retinotopy of extrastriate visual areas

Multiple injections of tracers in retinotopically different regions of the striate cortex of the rat revealed retinotopically organized connections of V1 with ten different extrastriate cortical areas in this study. The location of these extrastriate areas, and the retinotopy of their striate connections, remained mostly invariant despite wide changes of the injection sites in V1. Thus, the results indicate that striate-extrastriate connections in the rat are established according to the following principle: *striate cortex connections are distributed in a set of fixed extrastriate areas following retinotopies specific for each of these areas.* Since cortical visual areas are known to be interconnected retinotopically in mammals (e.g., correspondence of retinotopies of striate cortex projections and electrophysiological map of area MT in the monkey see: Spatz 1977; Montero 1980; Gattass and Gross 1981; Sousa et al. 1991; for similar correspondence in the cat see: Montero 1981a; Symonds and Rosenquist 1984; Ferrer et al. 1992), it is evident that the different retinotopic patterns of the striate-extrastriate connections detected in this study reflect the existence of different retinotopically organized visual areas in the rat. Although previous anatomical studies have shown anterograde and retrograde connections from single lesion or tracer injections sites in V1 to a comparable complex array of extrastriate visual areas in the rat (Montero et al. 1973a; Montero 1981b; Olavarria and Montero 1981, 1984) the use of multiple tracer injections had the advantage of simultaneously indicating the orientation of nasotemporal and caudorostral axes in the striate cortex connections with the different extrastriate visual areas. Contrary to the case of V1, which in all mammals studied so far coincides with the cytoarchitectonic striate cortex, definition of extrastriate visual areas in mammals of different orders, as obtained in the present results in the rat, has been mostly based on detection of cortical areas with distinct retinotopies by means of physiological and/or anatomical connectivity maps (see Van Essen 1979; Tusa et al. 1981; Felleman and Van Essen 1991 for reviews).

Relation between anatomical and physiological maps of the extrastriate visual areas

There is a close correspondence of retinotopies between the anatomical and physiological maps for areas AL, LM, LI, and LL (Montero et al. 1973b; Espinoza and Thomas 1983; Thomas and Espinoza 1987). Anatomically defined area PL corresponds with partial physiological maps of this area (Montero et al. 1973b, where this area was indicated by the letter A; Thomas and Espinoza 1987). Anatomically defined area P, at the caudal occipital pole, has not yet been mapped physiologically. By its position at the rostral pole of V1, anatomically and physiologically defined area RL (Thomas and Espinoza 1987) may be equivalent. However, incomplete anatomical and physiological maps of this area preclude a comparison of these maps.

With respect to areas in the medial extrastriate cortex, there is a good correspondence between anatomical and physiological (Espinoza and Thomas 1983) maps of area PM. In both maps the representation of the upper-temporal quadrant is caudal, lower-nasal is rostral, and upper-nasal is rostro-medial. Anatomical area A and physiological area AM (Espinoza and Thomas 1983) are most probably equivalent, since the two areas are similarly located at the medial rostral border of V1. The name for anatomical area A has been maintained here to designate the same striate cortex projection field previously described (Olavarria and Montero 1984). There is a partial correspondence between the anatomical and physiological maps of area A (AM of Espinoza and Thomas 1983). In both maps, nasal and temporal parts of the visual field are located caudally and rostrally, respectively; but, while in the physiological map lower and upper visual fields are lateral and medial, respectively, in the anatomical map upper visual field is interposed between lower-temporal and lower-nasal projections (R38, Fig. 3A).

The anatomically defined area AM apparently was not mapped in the physiological experiments of Espinoza and Thomas (1983). However, in the original physiological description of extrastriate visual areas in the medial extrastriate cortex of the rat (see Fig. 1, field E, in Montero et al. 1973b), in the region equivalent to AM, the lower-temporal quadrant is represented at the extreme rostromedial part, while in the caudolateral direction fields move nasally, as in the anatomical map of AM. In this physiological map of the medial extrastriate areas, three divergent representations of the temporal field were found. Its anterior, medial, and caudal parts match the representations of the temporal field in the anatomically defined areas A, AM, and PM, respectively.

Relation of extrastriate visual areas with cytoarchitectonic and callosal maps

There are striking similarities between the distribution of striate and extrastriate visual areas in the occipital cortex of the rat defined in this study (Fig. 6) and the myelo- and cytoarchitectonic map of Zilles (1985). The myelin pattern of the striate cortex (V1) in the flattened section coincides quite precisely with Zilles' area Oc1 (B and M parts). This serves as a fixed reference with which to compare his cytoarchitectonic fields with the present subdivisions of the extrastriate cortex. In the lateral and dorsal views of Zilles' map (1985; his Figs. 46, 47), it is possible to recognize that the cytoarchitectonic field Oc2L, extending laterally from rostral to caudal parts of Oc1, corresponds closely to the lateral extrastriate cortex contain-

ing areas P, PL, LM, LI, LL, AL, and RL (Fig. 6). It should be noted that Zilles and Wree (1985) reported field Oc2L to be "a cytoarchitecturally heterogeneous area composed of several subareas," which is consistent with the presence of multiple visual areas in Oc2L. In the medial extrastriate cortex between Oc1 and RSA, Zilles distinguished two cytoarchitectonic fields: Oc2ML and Oc2MM. By its position relative to the rostromedial border of the striate cortex (Oc1), the rostral part of Oc2ML would correspond to visual area A. Between Oc2ML and RSA lies cytoarchitectonic field Oc2MM, whose rostral part would contain visual area AM. Finally, the caudal parts of Oc2MM and Oc2ML would correspond to visual areas PM.

Krieg's (1946) cytoarchitectonic map is inadequate to refer to striate and extrastriate visual areas of the rat for several reasons. His area 17, by not reaching the occipital pole, does not coincide with the rat primary visual area (V1) defined by its geniculate inputs (Ribak and Peters 1975), retinotopic map (Montero et al. 1973b; Espinoza and Thomas 1983), and myeloarchitectonics (Olavarria and Van Sluyters 1985; Zilles 1985; present results). Likewise, Kriegs's parietal area 7, which is interposed rostrally between his areas 18a and 18b, would probably encompass areas AL, RL, and A, which are visual, not parietal, in nature.

The pattern of callosal connections in the occipital cortex of the rat has been directly correlated with striate projections to extrastriate cortex from single tracer injections in V1 (Olavarria and Montero 1984) and with physiological maps of the extrastriate cortex (Thomas and Espinoza 1987). From these studies it is known that, adjacent lateral to the dense callosal band laterally in V1 representing the zero vertical meridian (Montero et al. 1973b), a series of acallosal islands surrounded by partial or complete callosal rings contain, caudorostrally, areas P, PL, LM, and LI, AL, and RL. Area LL lies in a callosal island lateral to that containing areas LM and LI. In these previous studies it was suggested that the callosal rings interposed between these areas were related to vertical meridian representations, as it has been reported for visual areas in higher mammals (Hubel and Wiesel 1967; Van Essen and Zeki 1978). The present results are consistent with these suggestions. For example, the callosal bridges extending laterally from V1 caudorostrally (see Fig. 5 in Olavarria and Montero 1984) correspond to vertical meridian representations at the lower-nasal boundary between P and PL, upper-nasal boundary between PL and LM, and lower-nasal boundary between LM and AL. There is no callosal boundary at the temporal periphery limit between LM and LI, whereas there is a callosal boundary at the nasal, vertical meridian representation between LI and LL. With respect to visual areas in the medial extrastriate cortex, a callosal band separates areas A and AM (Olavarria and Montero 1984), corresponding to the nasal boundary between these areas.

A single modular map in the extrastriate cortex of the rat?

A recent report concluded that the extrastriate cortex belt in the rat contains a single, global map with modules, which would be homologous to area V2 of cat and monkey (Malach 1989). The present results, and the diverse lines of evidence discussed in the Introduction, are incompatible with Malach's interpretation. For example, focusing this discussion mostly on comparisons of cat area V2 and rat extrastriate cortex, area V2 in the cat sends a single retinotopically organized projection to the superior colliculus (Kawamura et al. 1974), in contrast to the rat in which each of the retinotopically organized areas in the extrastriate cortex sends separate connections to the superior colliculus (Olavarria and Van Sluyters 1982; Thong and Dreher 1986). Area V2 in the cat receives thalamic afferents from a single group of thalamic nuclei (Niimi et al. 1981). In contrast, the retinotopically organized extrastriate areas in the rat receive different thalamic inputs (Olavarria 1979; Sanderson et al. 1991). Area V2 in the cat contains a single representation of the visual hemifield, although with some islands (Tusa et al. 1979). The medial and lateral extrastriate cortices in the rat contain multiple representations of the visual field (Montero et al. 1973b; Espinoza and Thomas 1983; Thomas and Espinoza 1987). Area V2 in the cat and monkey receives a single set of retinotopically organized afferent connections from area 17, and connections arising from a single injection site in area 17 are distributed in a single field (cat, Montero 1981a) or in closely segregated patches (monkey, Lin et al. 1982; Van Essen et al. 1986). In contrast, in the rat each of the retinotopically organized areas in wide-apart regions of the medial and lateral extrastriate cortex is reciprocally connected with the striate cortex (Montero et al. 1973a; Olavarria and Montero 1981, 1984) and each of the extrastriate visual areas receives a set of retinotopically organized connections with the striate cortex (present results). A tracer injection in V2 of cat and monkey does not label connections into distant regions of V2, but only intrinsic connections into the near vicinity of the injection site (Rockland 1985; Matsubara et al. 1987; LeVay 1988). In contrast, tracer injections in the different retinotopically organized extrastriate areas in the rat reveal distant interconnections between most of these areas (Torrealba et al. 1984; Sanderson et al. 1991; Coogan and Burkhalter, in press). It is evident that none of these results would support the notion of homology of area V2 in the cat with the multiple retinotopically organized areas in the rat extrastriate cortex.

One of Malach's (1989) main arguments for considering the rat peristriate cortical belt as a single visual area is his contention that rostral and caudal parts of V1 connect preferentially with rostral and caudal parts, respectively, of the striate cortex, indicating as examples his results in Figs. 4 and 5. However, contrary to his contention, a horseradish peroxidase (HRP) injection in the caudal (upper visual field) of V1 (his Fig. 5) labeled not only the neighboring caudal extrastriate cortex but it labeled *all* the retinotopically organized areas in the lateral

and medial extrastriate cortex described here, with the exception of area RL. Moreover, the projection in AL was to its more rostral part (as defined by the callosal pattern), consistent with the representation of the upper visual field in rostral AL (Montero et al. 1973b; Espinoza and Thomas 1983). On the other hand, the tracer injection in the rostral V1 (Malach 1989, his Fig. 4) resulted not only in projections into the neighboring rostral extrastriate cortex but as far caudal as areas P and PL, belying his conclusion that rostral striate cortex connects only with rostral extrastriate cortex. In fact, the results of these two experiments can be totally explained by the present results with multiple tracers. For example, the tracer injection in rostral V1 (Malach's Fig. 4) resulted in projections to medial and lateral extrastriate cortex that are very similar to projections obtained from rostrally located injections in V1 in the present experiments; e.g., FB injections in cases R76 (Fig. 2B) and R38 (Fig. 3A) which labeled lower visual field regions in AL, LM, LI, LL, and between PL and P, and in the confluence of PM, AM, and A. On the other hand, Malach's results with the caudal injection in V1 (Malach 1989, his Fig. 5) resulted in extrastriate label which is similar to that obtained with tracer injections in the caudal V1 in the present experiment; e.g., FG-labeled connections (in yellow) in R38 (Fig. 3A) and RB labeled connections (in red) in R21 (Fig. 3B). However, the use of multiple-tracer injections in different retinotopic regions of V1 in the present experiments allowed the simultaneous recognition (e.g., R38, Fig. 3A) that projections from upper, lower, or temporal field are distributed in a topographical pattern that is consistent with the retinotopy of the different extrastriate visual areas, as discussed above.

Kaas et al. (1989) speculated that the multiple striate cortex connection fields on the lateral extrastriate cortex in the rat (Montero et al. 1973a; Olavarria and Montero 1984) constitute "repeating modules" of a single visual area V2. In addition to the abundant morphological and physiological evidence reviewed above that supports the existence of multiple visual areas in the lateral and medial extrastriate cortex in the rat, the present results do not support the notion of repeating modules in the rat striate-extrastriate connections for the following reasons. The notion of repeating modules implies that striate-extrastriate connections in the rat are divergent and that patches of connections from different sites in the striate cortex overlap partially *within a single retinotopic map* in the extrastriate cortex, as demonstrated, for example, in the striate cortex connections to area MT in the macaque (Montero 1980) and to the lateral suprasylvian area in the cat (Montero 1981a). Contrary to this model, the present results show that *these connections from different regions of the rat striate cortex are consistently clustered around a number of fixed projection areas in the lateral and medial extrastriate cortex and that these connections follow several different retinotopic maps which are characteristic for each target area.* In addition, these target areas exist not only adjacent to V1 but also in a second (LI) and third (LL) tier lateral to V1, in which there are several inversions of the nasotemporal visual axis. If repeating modules of a single visual area V2 exist in the rat striate-extrastriate connections, then one should expect in the cases with widely spaced injections (R38, Fig. 3A; R76, Fig. 2B) that: the projections from the FG injections (in yellow) caudally in the striate cortex would be distributed in patches mostly in the caudal extrastriate cortex; projections from the rostral FB (in blue) injections would be distributed in patches mostly in the rostral extrastriate cortex, with some overlap with the FG projections; and the RD (in red) projections would be distributed in a similar number of patches overlapping the FG and FB projections in a more lateral position in the extrastriate cortex. Moreover, according to the single V2 model, all these projections should be distributed in a single tier adjacent to V1. Contrary to this model, however, the caudal FG projections are distributed throughout the span of the lateral extrastriate cortex, from the most rostral (area RL) to the most caudal part (area P), and these connection fields are distributed in first, second, and third tiers lateral to V1 (areas LM, LI, LL). Likewise, the FB connections from the rostral V1 are distributed throughout the span of the lateral extrastriate cortex, caudally from the P-PL boundary to rostrally in RL. FB projections are also distributed in first (LM), second (LI), and third tiers (LL), which is more evident in R76. Furthermore, it should be noted that projections from injections closely clustered in central parts of the striate cortex (R59, Fig. 2A) and in caudal parts of the striate cortex (R21, Fig. 3B) are distributed into as wide-apart connection fields in the lateral extrastriate cortex as in cases R38 and R76. The repeating modules model also predicts that larger injection sites in V1 should produce a greater number of connection patches in the extrastriate cortex than smaller injection sites. However, the results of case R59 (Fig. 2A) demonstrate that a large FG injection site (in yellow) induced virtually the *same* number of connection fields in the lateral striate-extrastriate cortex than the smaller RD neighboring injection site (in red). These results not only do not support the repeating modules model but they necessarily support the notion of retinotopically organized connections into a fixed number of extrastriate visual areas, in each of which the larger injection site (FG) labels a larger extent of connections into these areas than the smaller (RD) injection site. Finally, Spatz et al. (1991) have adduced a strong phylogenetic argument against the notion of Kaas et al. (1989) of "V2 repeating modules" for the striate-extrastriate connections in the rat and other rodents, in the sense that this notion could not explain their own results showing an almost identical distribution pattern of striate-extrastriate projection areas in the guinea pig as in the rat.

The present results also do not support the assertion by Miller and Vogt (1984) that, in general, lateral parts of the striate cortex in the rat are connected with lateral extrastriate cortex (their area 18a), and medial striate cortex is connected with medial extrastriate cortex (their area 18b). The multiple-tracer injections demonstrated in the *same* experimental animals that connections from the lateral (nasal) and medial (temporal) parts of the striate cortex were pervasive both in the lateral and medial extrastriate cortices.

Comparative considerations

The results of recent molecular phylogenetic studies suggest that in the evolution of eutherian mammals (McKenna 1975), rodents branched off earlier than lagomorphs, primates, artiodactyls, and carnivores (Easteal 1990; Li et al. 1990) and that caviomorphs diverged even earlier than the rest of rodents (Shoshani et al. 1985; Graur et al. 1991). A basic pattern of extrastriate visual areas similar in different degrees to that described in the rat in this and previous studies (Montero et al. 1973a,b; Montero 1981b; Espinoza and Thomas 1983; Thomas and Espinoza 1987) has been detected in a variety of rodents and in lagomorphs; e.g.: suborder Myomorpha, family Muridae, mouse (Wagor et al. 1980[1]; Olavarria et al. 1982; Olavarria and Montero 1989); family Cricetidae, hamster (Olavarria and Montero 1990); *Phyllotis darwini, Oryzomys longicaudatus, Akodon andino, Akodon longipilis* (Bravo et al. 1990); suborder Sciuromorpha, family Sciuridae, gray squirrel (Montero and Cliffer 1981; but see Kaas et al. 1989); suborder Caviomorpha, family Cavidae, guinea pig (Spatz et al. 1991); family Octodontidae, *Octodon degus* (Olavarria and Mendez 1979; Bravo et al. 1990); order Lagomorpha, family Liporidae, rabbit (Montero and Murphy 1976; Montero 1981b; Müller-Paschinger and Tömbö l 1989). These results suggest that a "rodent prototype" of visual cortex organization is generalized in rodents and lagomorphs, as proposed earlier (Montero 1981b), and consequently it is ancestral not only to these orders but also to the later divergent primates, carnivores, and artiodactyls.

Corollaries to the above assumption are: (a) extrastriate visual areas similarly located with respect to the striate cortex in the lissencephalic brains of rodents and lagomorphs are probably homologous and may perform similar visual functions; (b) at least some of the more numerous extrastriate visual areas in carnivores and primates, probably those at a lower hierarchical level (Felleman and Van Essen 1991) would have derived from and would be homologous to those of the ancestral rodent prototype, while other visual areas appeared later in the evolution of these higher mammals. Thus, it is probable that area LM of the rodent prototype is homologous to area V2 of carnivores and primates on the basis that both areas appear to be at a second hierarchical level after V1 (Coogan and Burkhalter, in press; Felleman and Van Essen 1991). In this respect, it is of interest to note that area LM in the gray squirrel is more expanded rostrocaudally than in the rat, separating anteriorly area AL from V1 (Montero and Cliffer 1981; unpublished observation). Possibly area LM developed more in the squirrel as a consequence of need for acute stereopsis in its arboreal habitat and correspondes to area V2, interposed between V1 and the rest of the lateral extrastriate areas (Kaas et al. 1989; see also Sereno et al. 1991).

Much further work is needed to establish homologies between the extrastriate visual areas of the rodent prototype with those of carnivores and primates. The interest of such comparisons resides in the fact that the rodent prototype being an ancestral organization of visual cortex in eutherian mammals, each of its component visual areas may perform different *basic* neocortical functions essential for the visually guided behavior of mammals. For example, the indemnity of visual areas in the medial extrastriate cortex of the rat needed for visuosensory interactions (Pinto-Hamuy et al. 1987) and the indemnity of rat lateral extrastriate visual areas needed for pattern recognition (Gallardo et al. 1979) is reminiscent of the dichotomy of parietal (medial) and temporal (lateral) streams in primates that appear to be involved in spatial/action-oriented tasks or object discrimination, respectively (Miskhin et al. 1983; Goodale and Milner 1992).

[1] For a discussion of similarities between maps of mouse (Wagor et al. 1980) and rat visual cortex see Montero 1981b.

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