

Retinotopic organization of striate and extrastriate visual cortex in the golden hamster (*Mesocricetus auratus*)

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The visual topography within striate and lateral extrastriate visual cortices was studied in adult hamsters. The cortical areas 17 and 18a in the left hemisphere were electrophysiologically mapped upon stimulation of the right eye, correlating receptive field positions in the visual field with cortical recording sites. Reference lesions were placed at selected cortical sites. Like in rats and other mammals, the lateral extrastriate cortex contained multiple representations of the visual field. Rostral area 18a contained the rostralateral maps, with medial and lateral divisions. More caudally and sharing a common border with V1, maps in lateromedial, posterolateral and posterior areas were found. More laterally and forming a "third tier" of visual maps, anterolateral, laterolateral-anterior, laterolateral and laterolateral-posterior areas were found. There was also an indication of a possible parahrinal map. The plan so defined is virtually identical to that of rats. The results may be useful to understand a basic mammalian plan in the organization of the visual cortex.

INTRODUCTION

Previous studies have demonstrated the existence of two extrastriate retinotopic maps in the visual cortex of several rodent species, including hamsters (24), rats (1), mice (3) and guinea pigs (2). One of the representations was located laterally and the other medially to the main map (V1) in area 17, corresponding to Krieg's cytoarchitectonic areas 18a and 18b, respectively. Latter observations in the rat (4, 11, 22) have shown a multiplicity of retinotopic arrangements in areas 18a and 18b. Anatomical studies in mice (16, 20), squirrels (8) and guinea pigs (21) suggest that arrangements of visual areas similar to those in the rat also exist in these species, raising the possibility that the visual cortex of all rodents may be similarly subdivided. In the present study we tested this hypothesis by comparing the visual topography in the hamster with that of rats and related species. To this aim, we used

microelectrophysiological recording techniques in the adult animal, correlating cortical recording sites with the locations of receptive fields (RFs) of visual units or clusters of units in the visual field (VF).

Since the visual cortical areas may be involved in specific visual functions, the issue of topography seems important. The results demonstrate that in the hamster there are multiple retinotopic arrangements lateral to V1. The results confirm the hypothesis (10) of a common plan of visual cortical organization in the rodent.

MATERIAL AND METHODS

Experiments were performed on 7 adult hamsters. Cortical areas 17 and 18a in one hemisphere were mapped through microelectrode recordings of single cell action potentials evoked with visual stimuli delivered to the contralateral eye. Reference lesions were placed at selected recording sites. At the

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end of recording sessions, the brains were perfused and processed for demonstration of the recording sites in stereotaxic coordinates.

For positioning of the electrodes, each animal was anaesthetized with urethane, supplemented as needed. A wide opening was made in the skull over the occipital cortex of the left hemisphere. The dura was left intact. Next, the topography of the VF representations within the left cortex was determined. The positions of RFs for single neurons or clusters of neurons were related to the locations of the corresponding recording sites. The head of the animal was held in a modified stereotaxic frame at an approximately normal angle for straight ahead, unobstructed viewing, with the Bregma and Lambda horizontal. Epoxy coated tungsten microelectrodes were stereotaxically guided, taking Lambda as reference. We focused the attention on the lateral extrastriate cortex, most of whose visual maps lay on the convex surface of the brain, requiring the recording electrode to be tilted laterally by 25°. This ensured penetrations perpendicular to the pial surface, providing accuracy in the mappings and reconstructions. RF boundaries were delimited by using a moving bar of light of the smallest effective size. It was manually lit with a slide projector on the concave side of a perimeter centered over the right eye. The left eye was permanently occluded by an opaque tape.

The right eye was instilled with a few drops of 0.1% atropine sulphate to dilate the pupils and then immobilized by suturing it through the equator to the tissues of the orbit. The adequacy of this technique was ascertained by repeatedly plotting the projection of the optic disk. The vertical meridian was located 55-65° nasally to this projection. It usually coincided with the midsagittal plane of the animal. The horizontal meridian was located 25° under this projection (24).

Upon completion of the recording sessions, under anesthesia, the tip of the electrode was impregnated with India ink and the full width of the left cortex was lesioned at selected recording sites. The brain was perfused with normal saline through the left carotid artery, fixed, sectioned and stained with cresyl violet to reconstruct the recording tracks in the visual cortex.

RESULTS

Visual topography in lateral extrastriate cortex

A finely grained electrophysiological exploration, with over 120 data points, was performed in one animal. This allowed us to reconstruct the visual topography in almost the entire cortex lateral to area 17 in this single experiment. For clarity, only 87 data points are shown in the figures. The results of this experiment were reproduced and confirmed in six additional animals, with a total of over 600 data points.

The recording sites (numbered dots) have been reconstructed according to the lesions. The RF for each penetration is depicted in the perimeter charts representing the right eye VF. For simplicity, the RF sizes are presented uniformly and are meant to reflect only the location of their centers. The RF plots in the charts correspond to cortical sites located within different areas of the left cortex, labeled V1, rostralateral-medial (RL-m), rostralateral-lateral (RL-l), anterolateral (AL), laterolateral anterior (LLA) (Fig. 1), posterolateral (PL), lateromedial (LM), laterolateral (LL), laterolateral-posterior (LLP) and posterior (P) (Fig. 2). Since the topography of V1 is well known in the hamster (24), the cortex was explored in medial to lateral rows of penetrations starting from V1. This served as control in the explorations.

As in previous studies (4, 6, 11), the boundaries between two neighboring areas could be defined on the basis of characteristic changes in the RF progressions when displacing the recording from one area to the next. Additional indications were changes in RF size, responsiveness and, occasionally, background activity.

The topography of the VF representation in V1 can be deduced from the recording sites and the RF plots presented in Fig. 1. The vertical meridian coincided with the lateral border of area 17 (points 6, 14, 27, 40, 55 and 69); the horizontal meridian was represented by an horizontal line running across the middle of area 17 and joining points 36 through 41; the upper and lower VF projected to the caudal and rostral portions of V1, respectively (Fig. 1). Although this topography in V1 is well known

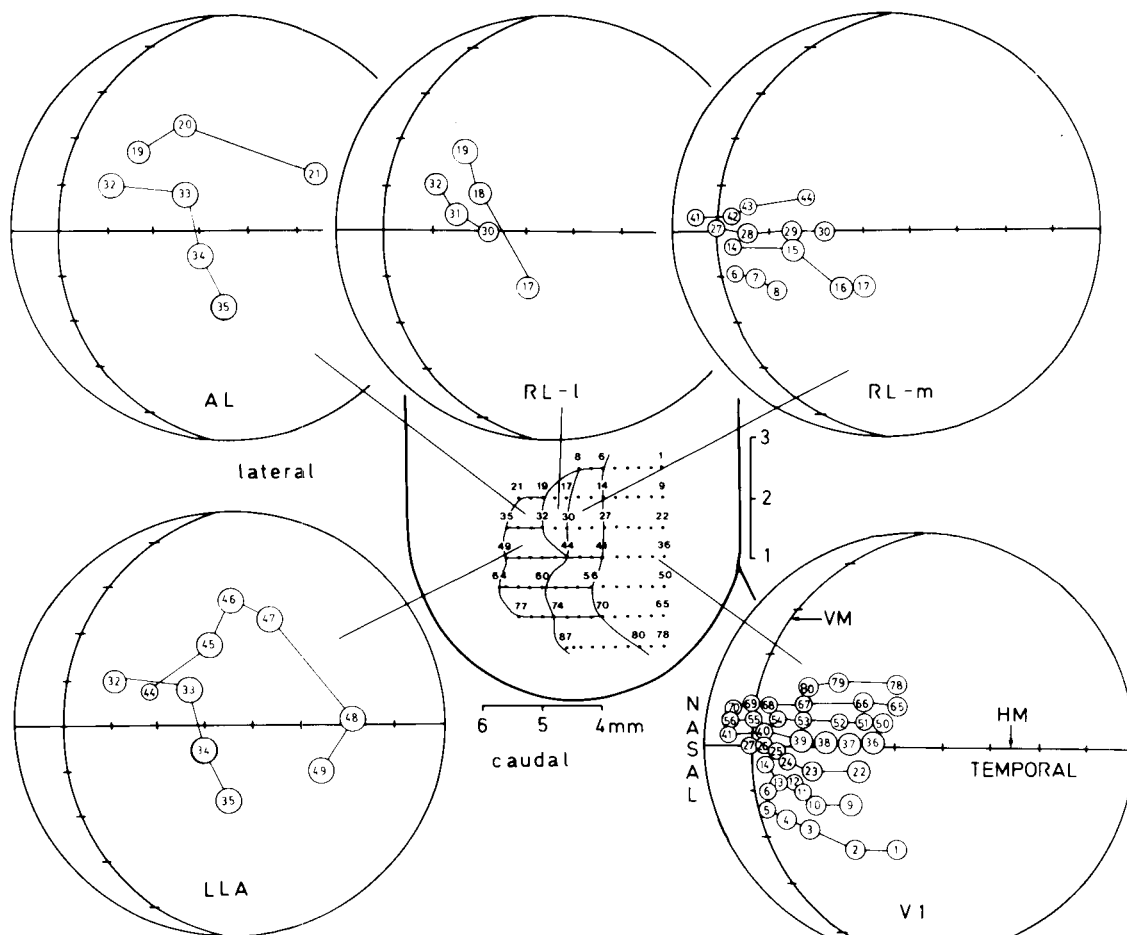


Fig. 1: At the center: surface view of left posterior cortex in stereotaxic coordinates. Recording sites (numbered from right to left and from top to bottom) reconstructed according to lesions placed at selected sites. The locations of areas containing representations of the right eye VF are indicated: primary visual (V1), rostromedial-medial (RL-m), rostromedial-lateral (RL-l), anterolateral (AL) and laterolateral-anterior (LLA). Lambda was taken as reference for the stereotaxic axes; scale in mm. RFs identically numbered and corresponding to recording sites in V1, RL-m, RL-l, AL and LLA plotted in perimeter charts of the right eye VF. HM and VM in lower right chart indicate horizontal and vertical meridians, respectively; scale subdivisions, 20°.

for several mammalian species (25) and also for the hamster (24), it is presented here for comparison with the other areas.

The topography in RL-m and RL-l can be deduced from the plots presented in Fig. 1. Notice that in RL-m, the medial to lateral displacement in cortex determined a nasal to temporal progression of RFs (points 6 to 8, 14-17, 27-30 and 41-44). The rostral to caudal displacement in cortex corresponded to a lower to upper progression of RFs (RFs 6-8 are located lower than RFs 41-44) in the VF. Notice that the RFs in this area did not progress temporally beyond about azimuth 60°, and that points 8, 17, 30 and 44 make up the RL-m /RL-l border. In RL-l, the medial to lateral displacement in cortex gave rise to

an oblique progression of RFs, from lower temporal to upper nasal VF (points 17-19, and 30-32). The rostral to caudal displacement resulted in a temporal to nasal progression of RFs (RFs 17-19 are located more temporally than RFs 30-32). By their topography and location these maps appear identical to those described in the rat (22), and hence we adopted a similar nomenclature.

The topography in AL and LLA can be deduced from the plots presented in Fig. 1. In the two cases, the medial to lateral displacement in cortex determined a nasal to temporal progression of the RFs. The rostral to caudal displacement in cortex produced in AL an upper to lower VF progression of RFs, whereas the reverse was the case in LLA. In

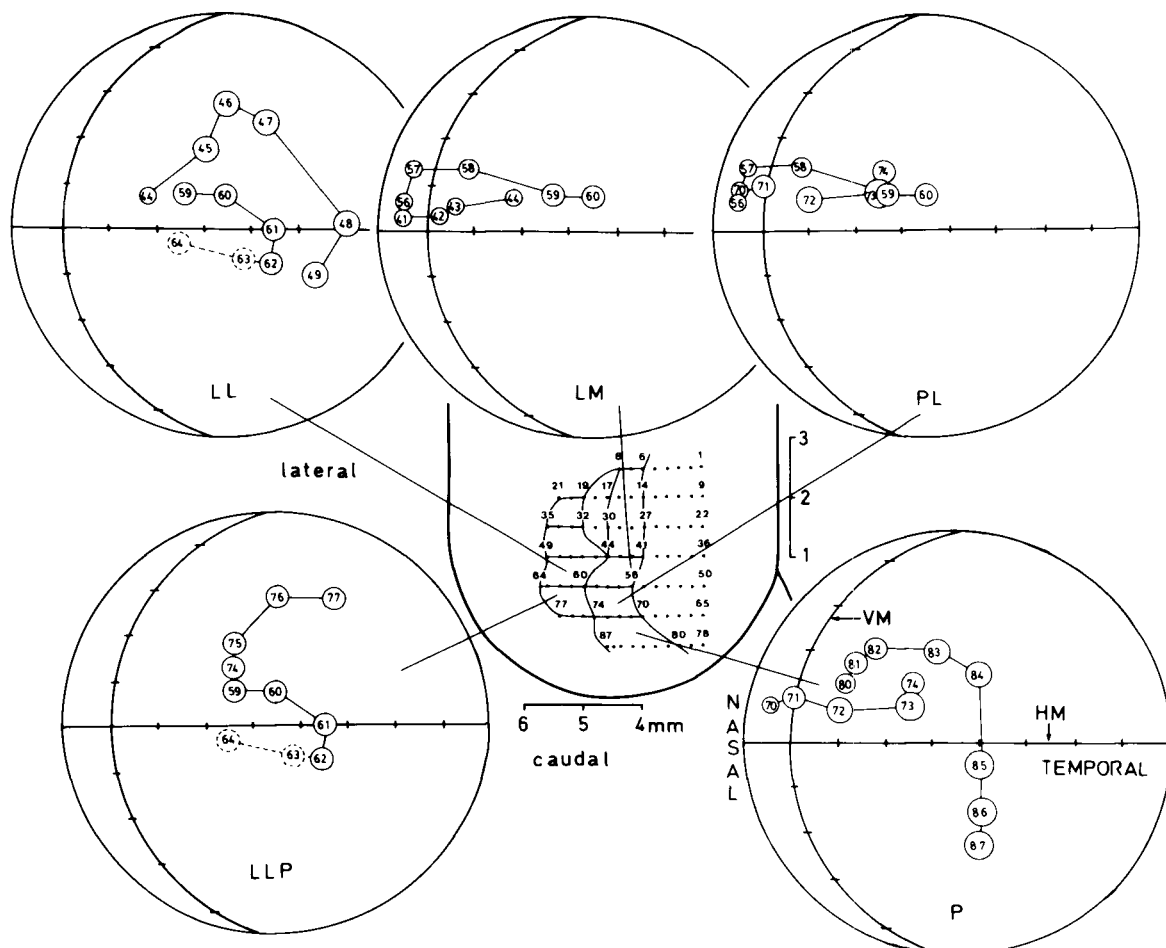


Fig. 2: Same animal as in Fig. 1, demonstrating location of maps in posterior (P), posterolateral (PL), lateromedial (LM), laterolateral (LL) and laterolateral-posterior (LLP) areas. RF distribution in each chart with corresponding recording sites. RF drawn with interrupted lines are likely to correspond to parahrinal areas.

AL, the upper and lower VF projected to its rostral and caudal aspects, respectively, while the reverse occurred in LLA. Therefore, these two areas were organized as mirror images of each other. The topography in AL is similar to area V3 in gray squirrels (6) and mice (26), to region D in albino rats (11), and to the AL maps of *Octodon degus* (13) and pigmented rats (4, 22). The topography and location of LLA seems identical to LLA in pigmented rats (22).

Areas LM and PL (Fig. 2) were located immediately lateral to V1. There, a relative emphasis in the representation of the nasal aspects of the upper VF was observed, while the lower VF did not seem to be represented. In the two cases, the mediolateral displacement in cortex yielded a nasal to temporal progression of the RFs. Area LM was

organized as a reduced mirror image of V1: the vertical meridian coincided with its medial border (points 41 and 56); its rostral aspects contained the representation of the RFs located lower (RFs 41-44) and its caudal aspects those located upper (RFs 56-60) in the VF. In area PL, the upper-lower VF topography was the reverse with respect to LM (RFs 56-60 were over RFs 70-73). By location and topography, LM is similar to V2 in mice (26), gray squirrels (6) and guinea pigs (2), to region C in albino rats (11), and to LM region in *Octodon degus* (13) and pigmented rats (22). Area PL of hamsters seems similar to PL in pigmented rats (22).

Areas LL and LLP seemed to contain a representation of the medial zones of the VFs (Fig. 2). In both maps, the medial to lateral displacement in cortex gave a nasal to tempo-

ral progression of RFs. The rostral to caudal exploration, however, resulted for LL in an upper to lower VF progression of RFs (RFs 44-49 are over RFs 59-64), whereas for LLP it gave a lower to upper progression of RFs (74-77 are over 59-64). Notice that for the row of points 59-62, there was first a nasal to temporal progression of RFs. From points 62-64, however, there was again an abrupt temporal to nasal progression of RFs (interrupted lines). This feature, described also in rats (22) by physiological recordings from these cortical zones, may be an indication of a parahinal area, predicted from anatomical explorations in rats (15). Area LL in hamsters seems identical by topography and location to LL in *Octodon degus* (13) and pigmented rats (22).

Finally, in the map labeled P, the rostral to caudal displacement in cortex produced a lower to upper VF displacement of RFs (70-73 are lower than 80-87). Therefore P was a mirror image of PL, and seems identical to area P in pigmented rats (22).

Visual maps in medial extrastriate cortex (area 18b).

Previous physiological studies in rats (4) and mice (26) have indicated the existence of two additional maps in medial extrastriate cortex (area 18b). In hamsters, an additional map was described (24). The present physiological recordings have confirmed its existence in some cases. Our explorations here, however, have been uncomplete, so the presence of two different maps cannot be discarded.

Figure 3 shows a summary diagram of the present results. There is a layout of the visual maps of striate and lateral extrastriate visual cortices of the left hemisphere, in stereotaxic coordinates. It was derived from the experiments shown in Figs. 1-2. The representation of the visual midline and of the horizontal meridian is there indicated.

DISCUSSION

Multiple visual areas in the hamster

The main finding of the present study is that in hamsters there are multiple retinotopic maps in the lateral extrastriate cortex, in addition to

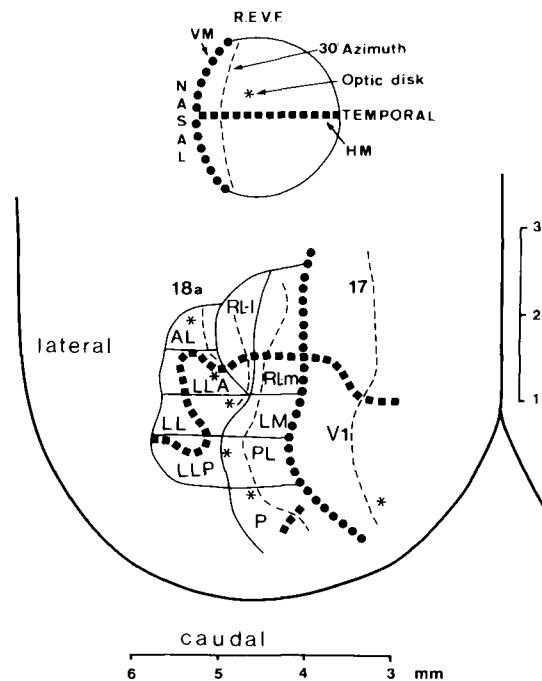


Fig. 3: Surface view of posterior left hemisphere. Schematic layout of visual maps of striate and lateral extrastriate cortex, as derived from Figs. 1-2. Abbreviations for visual maps as in previous figures.

the main representation of the VF in area 17. The plan of this visual representation in the hamster is virtually identical to that of the rat cortex.

The visual cortex in the hamster has already been explored by electrophysiological recordings (24), and apart from V1, two extrastriate visual maps were described, namely V2 and Vm, in Krieg's areas 18a and 18b, respectively. At that time, however, the existence of multiple visual areas in lateral extrastriate cortex was accepted as a possibility if more thorough explorations were done. The major finding in the present study, the indication of an elaborate plan of multiple visual maps, was the result of our finely grained explorations, in particular in rostral to caudal displacements.

A common plan of visual areas in the rodent

The plan of visual areas proposed in the present study for the hamster appears virtually identical to that reported for the albino (11) and pigmented (4, 22) rats, and shows several features in common with those reported for related species such as guinea pigs (2), mice

(26), gray squirrels (6) and *Octodon degus* (13). These latter patterns may be regarded as contained in the more complex ones of rats and hamsters. It is very relevant that the pattern of ipsilateral cortico-cortical connections in hamsters (17), interpreted as consisting of various foci of projections from V1 to lateral extrastriate cortex, is comparable to those reported for rats (9, 15), mice (16, 20), squirrels (8), guinea pigs (21) and even rabbits (10). These connections may provide the substrate for the multiple retinotopic arrangements described in the present study. Moreover, when examined in retrospect, some of the data from physiological experiments in mice (26) and squirrels (6) could be interpreted as we have done previously in rats (4, 22) and presently in the hamster. For example, the central part of the lateral extrastriate cortex in the mouse (26) exhibits a second reversal in iso-azimuth lines, indicating an additional representation of the nasal lower VF. This reversal may be equivalent to that observed at the RL-m/RL-l boundary of the present map. It was also reported (26) that the extreme posterior aspect of V2 presents a reversal in iso-azimuth lines as one proceeds laterally, yielding a partial reduplication of the upper temporal VF. There was also an indication of a small additional representation of the lower nasal VF in the extreme posterior aspect of V3. None of these zones were defined as separate in the mouse. In the squirrel, two reversals were reported in medial to lateral explorations of the lateral extrastriate cortex, comparable to the present data (ref. 6, squirrel No. 67). So far, further distinctions dependent on rostral to caudal explorations have not been reported for area 18 in squirrels, a finding difficult to reconcile with the patchy distribution there of the area 17 efferents (8). The same can be said with respect to area 19, where a single map, V3, was postulated (6), but containing at least two distinct termination fields of afferents (OTr and OTc) from areas 17 and 18 (8). From this, it is possible to assume that the lateral extrastriate cortices in mice, squirrels and guinea pigs, after pertinent studies, could yield a plan as the one we suggest now for the hamster. Additional evidence supporting the existence of separate visual maps in lateral extrastriate cortex in the rodent comes from

its patchy metabolic activation revealed with 2DG autoradiographs in rats after monocular stimulation (23).

All the above considerations support the possibility of a basic plan of visual cortical organization common to rodents, which could be extended to lagomorphs and even higher mammals, such as cats and monkeys. The present results may prove useful also to further characterize the visual areas in hamsters, through a direct comparison of the electrophysiologically derived maps with the pattern of callosal connections in the same animal. In this respect, it has been already established (7) that the main band of visual callosal connections in the hamster is in register with the striate peri-striate border, as is the case in the rat (22) and other mammals (25). The precise relation of the present maps with the pattern of callosal connections to the extrastriate areas in combined anatomical and electrophysiological explorations remains to be seen.

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