Transneuronal Retinal Projections to V1 Form “Minicolumns” in Layer 1: Comparison with Projections to Layer 4 in Normal and Visually Deprived Long Evans Rats

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Introduction

In addition to their well-known projections to cortical layers 4 (L4) and L6, thalamic nuclei also project to cortical L1. The thalamic cells projecting to L1 are considered to constitute the “matrix” or M-type cells, while the cells that primarily project to L4 constitute the “core” of C-type cells (see Rubio-Garrido et al., 2009, and references therein). Injections of anterograde tracers into the LGN of mice reveal that projections to L1 in primary visual cortex (V1) form a lattice pattern when observed in tangential cortical sections (Ji et al., 2015). To distinguish the ipsilateral and contralateral components of this projection, we examined the labeling pattern in L1 following unilateral intravitreal injections of the transneuronal tracer WGA-HRP in Long Evans rats, a strain in which projections to L4 form ocular dominance columns (ODCs, Laing et al., 2015). We compared the projection patterns in L1 with previous data on projections patterns in L4 from normal rats and from rats that had been either monocularly enucleated or monocularly deprived by eyelid suture during development (Olavarria et al., 2021).

Methods

Following intravitreal injections of the transneuronal tracer WGA-HRP and TMB histochemistry, the retino-geniculo-cortical projections to L1 and L4 were revealed in postnatal day ten (P10) normal rats, in adult normal rats, and in rats visually deprived by either monocular enucleation or monocular eyelid suture. The data from L4 in normal and visually deprived rats come from a recent publication (Olavarria et al., 2021). Images of the WGA-HRP labeled patterns in L1 and L4 from histological sections cut tangentially to the surface of the flattened cortex were analyzed using Photoshop CS5. Thresholded images were analyzed using ImageJ. See Olavarria et al. (2021) for additional details regarding surgical, histological, data acquisition and analysis procedures.

References

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Results

Fig. 1. Contralateral eye projections to L1 and L4 in normal adult rats. The black line in Figure 1A indicates the perimeter of V1, as revealed in the myelin pattern, lateral is to the right, posterior is down. The WGA-HRP labeling in L1 of the hemisphere contralateral to the injected eye forms a lattice pattern that extends over the entire area of V1 (Fig. 1A). In contrast, the contralateral projection to L4 (Fig. 1B) does not encroach into regions occupied by the ipsilateral eye projections (white areas in Fig. 1B).

The lattice pattern in V1 is visible by P10.

In normal P10 rats, as in adult rats, the contralateral labeled patches in L1 occupy the entire V1 (Fig. 1D). Also similar to adult rats, the contralateral projection to L4 (Fig. 1E) does not encroach into regions occupied by the ipsilateral eye projections (white areas indicated by arrows in Fig. 1E).

LGN labeling patterns. The LGN projections ipsilateral (left) and contralateral (right) to the injected eye in adult rats (Fig. 1C) is similar to those in normal P10 rats (Fig. 1F). Contralaterally, in both normal adult and young rats, the labeling is uniformly dense throughout the LGN, except for a small central region where the labeling was reduced or absent, presumably corresponding to the ipsilateral eye recipient zone.

Fig. 2. Contralateral eye projections to L4, but not to L1, are susceptible to monocular enucleation. Figure 2A shows contralateral projections to L1 from the remaining eye in a rat that was monocularly enucleated at P10 and perfused at the beginning of the critical period for ocular dominance plasticity (~P20). Figure 2D shows contralateral projections to L1 from the remaining eye in a rat that was monocularly enucleated at P19 and perfused at P40. The arrows point to superficial blood vessels. The lattice patterns in Figures 2A and 2D are similar to the contralateral eye pattern in L1 in normal rats (cf. Fig. 1A), suggesting that contralateral projections to L1 are not susceptible to monocular enucleation. However, contralateral projections to L4 are susceptible to monocular enucleation. Indeed, in normal rats the contralateral projections to L4 avoid ipsilateral eye territories (Fig. 1B,E), but in monocularly enucleated rats they invade these territories (Figs., 2B,E). Note that the ipsilateral eye territories in the LGN are not invaded by contralateral projections (unlabeled areas in central regions of the LGN, right sides in Figs. 2C,F), indicating that the geniculo-cortical projections change due to the enucleation, but the retino-geniculo projections do not.

Figure 1

Figure 2

Fig. 3. Monocular deprivation at the beginning of the critical period. Contralateral projections to L1 from either the deprived eye (Fig. 3A) or the non-deprived eye (Fig. 3D) form lattice patterns similar to those observed in monocularly enucleated (Fig. 2A,D) and normal rats (Fig. 1A,D). Figure 3B shows the contralateral projection from the deprived eye to L4. As in normal animals, these projections do not invade areas of ipsilateral eye representation (unlabeled areas in the center of V1 in Fig. 3B), while contralateral projections from the non-deprived eye to L4 do invade these ipsilateral eye regions (Fig. 3E). Again, ipsilateral eye territories are free of label in the LGNs contralateral to the injected eye (right sides in Figs 3C and 3F). These observations suggest that, unlike contralateral projections to L4 from the non-deprived eye (Fig. 3E), contralateral projections to L1 are not susceptible to monocular deprivation.

Fig. 4. Ipsilateral eye projections to L1 and L4 in normal and monocularly enucleated rats. Figure 4 A,B shows the ipsilateral eye projection to L1 and L4, respectively. Projections to L4 are segregated into ODCs (Laing et al., 2015), while projections to L1 form a lattice pattern that occupies an overall area in lateral V1 that is similar in extension as that occupied by ODCs. In rats monocularly enucleated at P10 and perfused at P21, the overall area in V1 occupied by the ipsilateral lattice pattern in L1 is proportionally larger than the corresponding area in normal rats (cf. Fig. 4A). This reflects the fact that the ipsilateral projection to L4 (Fig. 4E) and to the ipsilateral LGN (cf. left sides in Figs. 4C,F) also increases in these rats. Additional data are necessary to determine whether the distribution of L1 patches closely reflects the distribution of ODCs in L4. Comparing the distributions of ipsilateral and contralateral projections to L1, our observations suggest that ipsilateral projections to L1 extend over a territory similar to that occupied by projections to L4, (Fig. 4), while contralateral projections to L1 occupy a more extensive area that includes ipsilateral eye territories (cf. Fig. 1).

Figure 3

Figure 4

Discussion

The diameter of patches or the width of “minicolumns” in the lattice patterns was approximately 50-80 μ m in adult and P10 normal rats, as well as in rats monocularly enucleated or monocularly deprived by eyelid suture, consistent with the idea that retino-geniculo-cortical projections to L1 are less plastic than retino-geniculo-cortical projections to L4. Moreover, in all groups analyzed, the labeled lattice patterns in L1 occupy about 50% of the areas sampled within the rectangles in the figures. Since the territories occupied by ipsilateral retino-geniculo-cortical projections to L1 overlap with territories occupied by contralateral retino-geniculo-cortical projections to L1, it will be important to investigate if in these regions, the ipsilateral and contralateral lattice patterns either interdigitate or overlap with each other.

Unlike retino-geniculo-cortical projections to L1, retino-geniculo-cortical projections to L6 do not form lattice patterns similar to those in L1. Instead, they segregate into patches that are in register with ODCs in L4 (Laing et al., 2015).

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