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VISUAL THALAMOCORTICAL PROJECTIONS IN THE FLYING FOX: PARALLEL PATHWAYS TO STRIATE AND EXTRASTRIATE AREAS

P. R. MANGER[a,c] AND M. G. P. ROSA[b,c]*

[a]*School of Anatomical Sciences, Faculty of Health Sciences, University of the Witwatersrand, 7 York Road, Parktown, 2193, Johannesburg, South Africa*

[b]*Department of Physiology, Monash University, Clayton, VIC 3800, Australia*

[c]*Vision, Touch and Hearing Research Centre, University of Queensland, Australia*

Abstract—We studied thalamic projections to the visual cortex in flying foxes, animals that share neural features believed to resemble those present in the brains of early primates. Neurones labeled by injections of fluorescent tracers in striate and extrastriate cortices were charted relative to the architectural boundaries of thalamic nuclei. Three main findings are reported: First, there are parallel lateral geniculate nucleus (LGN) projections to striate and extrastriate cortices. Second, the pulvinar complex is expansive, and contains multiple subdivisions. Third, across the visual thalamus, the location of cells labeled after visual cortex injections changes systematically, with caudal visual areas receiving their strongest projections from the most lateral thalamic nuclei, and rostral areas receiving strong projections from medial nuclei. We identified three architectural layers in the LGN, and three subdivisions of the pulvinar complex. The outer LGN layer contained the largest cells, and had strong projections to the areas V1, V2 and V3. Neurones in the intermediate LGN layer were intermediate in size, and projected to V1 and, less densely, to V2. The layer nearest to the origin of the optic radiation contained the smallest cells, and projected not only to V1, V2 and V3, but also, weakly, to the occipitotemporal area (OT, which is similar to primate middle temporal area) and the occipitoparietal area (OP, a "third tier" area located near the dorsal midline). V1, V2 and V3 received strong projections from the lateral and intermediate subdivisions of the pulvinar complex, while OP and OT received their main thalamic input from the intermediate and medial subdivisions of the pulvinar complex. These results suggest parallels with the carnivore visual system, and indicate that the restriction of the projections of the large- and intermediate-sized LGN layers to V1, observed in present-day primates, evolved from a more generalized mammalian condition.
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*Correspondence to: M. Rosa, Department of Physiology, Monash University, Clayton, VIC 3800, Australia. Tel: +61-3-9905-2522; fax: +61-3-9905-2547.
E-mail address: marcello.rosa@med.monash.edu.au (M. Rosa).
Abbreviations: dLGN, dorsal lateral geniculate nucleus; DY, Diamidino Yellow; FB, Fast Blue; FE, Fluoroemerald; FR, Fluororuby; LP, lateral posterior; MT, middle temporal area; OP, occipitoparietal area; OT, occipitotemporal area; Pi, intermediate pulvinar nucleus; Pl, lateral pulvinar nucleus; Pm, medial pulvinar nucleus; PMLS, posteromedial lateral suprasylvian; Pom, medial division of the posterior nucleus; PPc, posterior parietal cortex; TD, temporal dorsal area; TP, temporal posterior area.

Key words: megachiropteran, vision, lateral geniculate nucleus, pulvinar, lateral posterior nucleus, evolution.

The thalamus of mammals includes two main structures that give rise to projections to the visual cortex: the dorsal lateral geniculate nucleus (dLGN) and the lateral posterior (LP)/pulvinar complex (for reviews, see Jones, 1985; Casagrande and Norton, 1991; Garey et al., 1991). In the traditional view, the laminae of the dLGN are the main target of projections from retinal ganglion cells, and have efferent connections that terminate in the primary visual cortices. In contrast, there are much weaker direct retinal projections to the LP/pulvinar complex, which has been regarded as part of an indirect visual pathway that conveys information from the visual layers of the superior colliculus to extrastriate cortex (e.g. Diamond and Hall, 1969; Stepniewska et al., 1999).

Although these two thalamocortical pathways appear to exist in every mammal, there is structural and functional variety among species. In many mammals, the dLGN complex is subdivided into laminae that receive connections from different types of ganglion cell, and project to different cortical areas. This laminar segregation is particularly clear in species that are heavily reliant on vision for normal behavior, such as carnivores, primates, tree shrews and flying foxes (e.g. Kaas et al., 1978; Dreher, 1986; Rosa et al., 1996; Ichida et al., 2000; Lyon et al., 2003a; see Casagrande and Norton, 1991; Garey et al., 1991 for reviews). In primates, the projections of the dLGN are highly focused on cortical area 17 (V1), with efferents to extrastriate cortices originating only from a sparse cell population concentrated in the koniocellular-dominated "interlaminar zones" (Bullier and Kennedy, 1983; Stepniewska et al., 1999). In contrast, in many other mammals, including carnivores and tree shrews, some extrastriate areas also receive parallel projections from the main layers of the dLGN (e.g. McConnell and Le Vay, 1986; Dreher et al., 1996; Lyon et al., 2003b). The LP/pulvinar complex has also been subdivided into connectional, neurochemical and functional subunits. Species with poor vision, such as rodents, have a relatively small LP/pulvinar complex, formed by a few subdivisions (Kuljis and Fernandez, 1982; Takahashi, 1985), whereas carnivores, tree shrews and primates have large complexes that are formed by many subdivisions (e.g. Graybiel 1970, 1972; Lin and Kaas, 1979; Raczkowski and Rosenquist, 1980, 1983; Simmons, 1982; Updyke, 1986; Luppino et al., 1988; Chalupa, 1991; Cusick et al., 1993; Stepniewska and Kaas, 1997; Soares et al., 2001; Lyon et al., 2003a,b). The cortical targets of LP/pulvinar projections are extensive, including visual areas in the parietal and temporal lobes (Burton and Jones, 1976).

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The present study reports the projections from the thalamus to different cortical visual areas in the grey-headed flying fox (*Pteropus poliocephalus*). Flying foxes are fruit-eating bats that have large, frontalized eyes and a well-developed visual system. According to Pettigrew (1986), present-day flying foxes are descendants of the same stock of early arboreal mammals that also gave rise to primates (for more detailed explanations of this hypothesis, see Pettigrew et al., 1989; Pettigrew, 1994). Thus, studying the visual system of the flying fox and other related species, such as prosimian primates, colugos and tree shrews (which form the superorder Archonta; Schreiber et al., 1994; Allard et al., 1996), may give us clues regarding the evolution of the complex visual system of simian primates. There have been several previous descriptions of the dLGN of flying foxes, based on both the pattern of retinal afferents (Cotter and Pentney, 1979; Pentney and Cotter, 1981) and architecture (Pettigrew et al., 1989; Ichida et al., 2000). It is therefore established that the dLGN of flying foxes is formed of various cell laminae, each subdivided into paired layers innervated by the ipsilateral and contralateral eye. The present study focuses on the organization of geniculate efferents, by labeling of the geniculocortical neurones after fluorescent tracer injections in different cortical visual areas. At the same time, arguments involving the expansion and subdivision of the LP/pulvinar complex have played an important role in the debate surrounding the evolution of the primate visual system (Grieve et al., 2000). In this context, establishing the extent and possible subdivisions of these nuclei in the flying fox may prove important. Thus, we also describe the architectural organization and pattern of interconnections between the flying fox LP/pulvinar complex and cortical visual areas.

EXPERIMENTAL PROCEDURES

The present report is based on the study of four adult flying foxes that received multiple injections of fluorescent tracers in cortical visual areas. Out of a total of 16 injections, 12 were selected for further analysis, as histological reconstruction revealed that their core and halo regions did not invade the white matter. All experiments were approved by the University of Queensland's Animal Experimentation Ethics Committee, which also monitored the well-being of the animals according to the guidelines of the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes.

For the placement of the tracer injections, the animals were premedicated with i.m. injections of diazepam (3 mg/kg) and atropine (0.2 mg/kg), and, after 30 min, were anesthetized with ketamine (50 mg/kg) and xylazine (3 mg/kg). They were placed in a stereotaxic frame and the occipital cortex exposed. Different combinations of tracers were injected in each animal. In every case, small crystals (200–400 μm in diameter) of the fluorescent tracers Fast Blue (FB) and Diamidino Yellow (DY) were inserted in the cortex with the aid of a blunt tungsten wire. Other tracers (Fluororuby [FR] and Fluoroemerald [FE]) were injected in different combinations, using 1 μl microsyringes. A volume of 0.4 μl of these tracers was injected over a period of 20 min, after which the syringe was withdrawn slowly. These protocols resulted in relatively restricted injection sites with high concentrations of tracer that yielded robust retrograde transport. The placement of these injections was guided by stereotaxic coordinates obtained in the course of previous studies (Rosa et al., 1993, 1994; Rosa, 1999). Their exact location in relation to cortical layers and areal boundaries was later assessed by histological reconstruction in cytochrome oxidase-stained sections (see below). After the injections were placed, the cortex was covered with a piece of sterile soft contact lens. The piece of bone removed during the craniotomy was fixed back in place with dental acrylic, and the wound was closed in anatomical layers. The animals were allowed to regain consciousness in a quiet, warm room, under the constant supervision of one of the experimenters. They recovered full mobility within 4–5 h of the end of the surgery, and were then returned to their home cages.

After a survival time of 7 days, the animals were administered a lethal i.v. dose of sodium pentobarbitone (50 mg) and transcardially perfused with 0.9% saline, followed by 4% paraformaldehyde in 0.1 M phosphate buffer and 4% paraformaldehyde/10% sucrose in phosphate buffer. The brain was removed from the skull, and the thalamus was separated from the cortex. Frozen coronal sections (40 μm) of the thalamus were obtained and every fourth section was mounted unstained on gelatinized slides for analysis of the distribution of tracer-labeled cells. The alternate series were stained for cell bodies with Cresyl Violet, or for myelin, using gold chloride (Schmued, 1990) or were histochemically reacted to reveal the distribution of the enzyme cytochrome oxidase (Wong-Riley, 1979; Rosa et al., 1991). The block containing the cortex was sectioned in the parasagittal plane, which in our experience is optimal to reveal the boundaries between visual areas. Alternate series of sections through the cortex were kept unstained, for analysis of fluorescent tracers, or reacted for cytochrome oxidase and Nissl substance.

The criteria for identifying the borders of cortical visual areas in the flying fox have been defined previously (Rosa et al., 1994; Rosa, 1999), and their application to the present material is illustrated in Fig. 2. In cytochrome oxidase-stained sections, the first and second visual areas (V1 and V2, respectively) are characterized by a heavily stained layer 4, which sets them apart from all other visual cortical areas (Fig. 2B–D). The differentiation between these areas is possible due to the fact that in V1 the upper limit of the darkly stained layer 4, with supragranular layers, is very sharp, whereas in V2 it is gradual (Rosa et al., 1994). Moreover, in Nissl-stained material V1 and V2 are distinguished by the structure of the supragranular layers (Fig. 2A); while in V1 layer 3 has a trilaminar appearance, due to the existence of a thin, darkly stained "line" of densely packed neurones at the level of layer 3b, in V2 this is not apparent. The rostral limit of V2 also coincides with a sudden decrease in the cellular density of layer 4 (Fig. 2A).

Area V2 is bordered rostrally by two areas (Fig. 1), both of which stain lightly for cytochrome oxidase in all cortical layers. Laterally, an elongated third visual area (V3) forms a representation of the visual field that is a mirror image of that found in V2, while medially the occipitoparietal area (OP) represents both the upper and lower quadrants with large receptive fields. At all mediolateral levels, the rostral border of V2 with areas V3 and OP can be defined with precision by the sudden reduction in intensity of cytochrome oxidase staining in layer 4 (Fig. 2C–E). Rostral to V3, the occipitotemporal area (OT), which forms a first-order representation of the visual field (Fig. 1), has a moderately darkly staining layer 4 (Fig. 2E). Thus, in parasagittal sections stained for cytochrome oxidase, V3 appears as a lightly stained gap between areas V2 (caudally) and OT (rostrally). Area OT has been suggested to be a homologue of the primate middle temporal area (MT; Krubitzer and Calford, 1990, 1992). All injection sites included in this study were located in relation to these architectural transitions, and only injections that were found to be restricted to one area will be described in the following sections (Fig. 1).

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