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Retinogeniculostriate Pathway Components Scale with Orbit Convergence Only in Primates and Not in Other Mammals

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Key Words
Optic nerve · Lateral geniculate nucleus · Primary visual cortex · Binocular vision · Orbit orientation · Mammals

Abstract
Studies of the relative sizes of brain components in mammals suggest that areas responsible for sensory processing, including visual processing, are correlated with aspects of ecology, especially activity pattern. Some studies suggest that primate orbit convergence and binocular vision are correlated with the overall size of the brain as well as components of the visual pathway, such as the lateral geniculate nucleus. However, the question remains whether components of the visual pathway are correlated with orbit convergence and binocular visual field overlap in nonprimate mammals. Here, we examine the relationship between orbit convergence and the volumes of components of the visual pathway (optic tract, dorsal lateral geniculate nucleus and primary visual cortex). Data on orbit orientation are combined with those on overall brain volume as well as brain component volumes in a taxonomically diverse sample of mammals. Our results demonstrate that nonprimate mammals scale isometrically for component volumes along the visual pathway, whereas primates display negatively allometric relationships. However, only among primates is higher orbit convergence correlated with volumetrically larger lateral geniculate nuclei and visual cortices. Diurnal primates exhibit statistically larger visual pathway components when compared to nocturnal primates. Nonprimate mammals do not display activity pattern differences with the single exception of optic tract sizes. We conclude that binocular vision was a much stronger factor in the evolution of the visual system in primates than in other mammals.

Introduction

The retinogeniculostriate system is the primary pathway of conscious visual perception in mammals. Visual information is relayed from the retina via the optic nerve, chiasm and tract to the dorsal lateral geniculate nucleus (LGN) of the thalamus, and then terminates in the striate cortex (V1 or Brodmann area 17) [reviewed in Casagrande and Norton, 1991; also see Jones, 2007]. Although the optic nerve is traditionally named the second cranial nerve, it may be more useful to consider it a white-matter tract of the diencephalon, composed primarily of the axons of retinal ganglion cells streaming away from the eye [e.g. Brooks et al., 1999].

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The volumes of components of the retinogeniculostriate pathway covary. Intraspecific scaling studies on humans and sheep *(Ovis aries)* demonstrate that, despite variability between individuals, volumes of the optic tract, LGN and V1 are positively correlated [Ebinger, 1975; Andrews et al., 1997]; individuals with volumetrically larger optic tracts, probably reflecting greater fiber numbers from the retina, also have larger lateral geniculate nuclei and primary visual cortices. Interspecific studies on retinogeniculostriate components in various other mammals also demonstrate scaling similarities, although the impact of ecological demands on the component sizes of the retinogeniculostriate pathway as well as downstream visual cortical areas is highly debated [Frahm et al., 1984; Barton et al., 1995; Stevens, 2001; Kaskan et al., 2005; Barton, 2007]. For example, Kaskan et al. [2005] suggested that striate and extrastriate visual cortical areas are highly conservative in mammals and do not vary with ecological factors like activity pattern. However, Barton [2007], using dataset of Kaskan and coworkers, found that diurnal primates have significantly larger visual cortices than nocturnal primates. Frahm et al. [1984] also found these differences in primate visual cortex proportions.

The morphology of the mammalian retinogeniculostriate pathway may also reflect differences in visual field construction, specifically in the size of the area of binocular visual field overlap. Barton [2004] showed that, in primates, orbit convergence, a morphological surrogate for binocular visual field overlap in mammals [Heesy, 2004], is also correlated with the volumes of LGN and V1, all of which are correlated with substantial expansion of primate brain volume. These analyses support the suggestion that a major factor in primate brain size evolution is expansion of visual processing [Barton, 1998; Allman, 1999; Kirk, 2006], especially information generated by binocular vision. Barton attributed his results to the expansion of the parvocellular pathway in anthropoid primates (i.e. monkeys, apes and humans), a pathway that primarily transmits information on color and fine detail from the visual scene [Livingstone and Hubel, 1988]. Additionally, in macaques and presumably in other anthropoids, the central visual field is highly magnified in the LGN and primary visual cortex (V1) due to the density of parvocellular cells in this region of the topographically organized LGN [Malpeli et al., 1996; reviewed in Casagrande and Ichida, 2002]. Therefore, increased LGN volumes in anthropoids may be due, in part, to the increase in the number of parvocellular neurons around the area of central vision, the fovea. This led Barton [2004] to suggest that the evolution of foveal vision and the expanded parvocellular system in anthropoids is linked to magnification of the central field in the visual cortex, enhanced stereopsis and increased relative LGN, V1 and brain size volumes. However, the relationship between binocular visual field overlap, orbit convergence and the retinogeniculostriate pathway has not been studied in nonprimate mammals.

The LGN receives input from structures other than the retina. Based on data from macaques *(Macaca),* cats *(Felis),* ferrets *(Mustela)* and rabbits *(Lepus)* [Hubel and Wiesel, 1961; reviewed in Briggs and Usrey, 2009], estimates of retinal input to the LGN range from 10 to 40% [e.g. Sherman and Koch, 1986; Sherman and Guillery, 2002, 2006; Casagrande et al., 2005a, b]. Input is mostly extraretinal in origin, examples of which include a prominent corticogeniculate feedback loop from V1, several midbrain regions, other thalamic nuclei, or local modulatory or inhibitory inputs [Casagrande and Norton, 1991; Sherman and Guillery, 2002, 2006]. The best studied of the nonretinal inputs to the LGN is the corticogeniculate pathway, which provides the largest input to the LGN based on synapse number, but the function of which is still poorly understood [Casagrande et al., 2005].

Primates, as a group, tend to have greater binocular visual field overlap than other mammalian groups [Cartmill, 1974; Noble et al., 2000; Heesy, 2004, 2008, 2009]. Given the multiple inputs to LGN, it is reasonable to question whether primates differ from other nonprimate mammals in the relationships between binocular visual field overlap and the components of the retinogeniculostriate pathway. In this study, we evaluate the relationship between binocular visual field overlap, using orbit convergence as a surrogate variable, and volumetric components of the retinogeniculostriate pathway. We expand the known sample of primate orbit convergence data and include comparative data on multiple additional groups of mammals. We specifically evaluate whether the relationship between orbit convergence and the retinogeniculostriate pathway is unique to primates or is typical of all mammals. Lastly, significantly larger visual cortex volumes have been noted in diurnal primates [e.g. Barton, 2007] and activity pattern has an influence on orbit convergence and binocular visual field size in mammals [Cartmill, 1974; Ross, 2000; Barton, 2004; Ravosa and Savakova, 2004; Heesy, 2008].We therefore evaluate the effects of activity pattern on the relationships between orbit convergence and retinogeniculostriate pathway volume scaling.

Materials and Methods

Collection of Volumetric Data on the Retinogeniculostriate Pathway

Data on the volumes of the optic tract, dorsal LGN and V1 are primarily taken from the literature. All data are summed bilaterally and the original sources are cited in table 1. For those data taken from developmental ablation studies, only the normal control volumetric data are used here. Data on wild-type species were collected whenever available. Data on the platyrrhine primate *Callicebus* sp. (titi monkey) [Bush and Allman, 2004a, b] were sufficiently different from previously published data on *Callicebus moloch* [Frahm et al., 1984; Stephan et al., 1984] to justify separate treatment of these taxa. Volumetric data on V1 in *Lepus* (rabbit), *Rattus* (rat) and *Felis* (cat) V1 [Hughes, 1971] were computed by multiplying V1 area by average V1 thickness. Brain volume data on New Zealand rabbits were computed from data in Mace et al. [1981]. Brain volume data for *Canis familiaris* (dog) were not reported, so volume data were taken from Gittleman [1986] for *Canis latrans* (coyote), which is similar in overall body mass. Analyses were run both including and excluding data on *C. latrans*, and the results were not materially affected in either instance. Frahm et al. [1984] report data on LGN volume in several afrosoricid, erinaceomorph and soricomorph taxa, which are used here. In addition, Frahm et al. [1984] estimate V1 volume in these taxa using a primate-scandentian regression equation for LGN to V1 volume ratio. We do not include the estimated V1 data for afrosoricids, erinaceomorphs and soricomorphs in our analyses because scaling similarities between 'insectivorans' and primates have never been established.

In this study, data on LGN volume for *Mesocricetus auratus* (golden hamster), *Mus musculus* (mouse), *Lepus* (rabbit) and *Rattus* (rat) were collected in order to both expand the available data as well as verify data from the literature. For the hamster, mouse and rat, images were imported into SigmaScan Pro 5 (SPSS Inc., Chicago, Ill., USA) from published digital datasets [Morin and Wood, 2001; Paxinos and Franklin, 2001; Paxinos and Watson, 2007] and calibrated, and the area of LGN measured on each slice in which it was present. Areas were multiplied by the distance between slices; these volumes were summed to estimate the unilateral LGN volume, and lastly multiplied by 2 to compute a bilateral LGN volume estimate to match the other data in our dataset. Data on the rabbit LGN were generated following a similar method after photographic images were digitized from Girgis and Shih-Chang [1981].

Our data fall within the range of values found by Kruska and Schott [1977] for the rat LGN volume. Kruska and Schott [1977] estimated the average LGN volume for 8 rats as 3.48 mm^3, whereas we found a volume of 3.68 mm^3, a difference of approximately 5.4%, but still within their published range.

Morphometric Data Collection

Most data on orbit convergence for a number of taxa in this study were from previous studies conducted by the first author [Heesy, 2004, 2005, 2008]. In addition, orbit convergence data on 4 catarrhine primates *(Cercocebus torquatus, Cercopithecus mitis, C. ascanius, Macaca nemestrina)* are from Ross [1995]. Additional morphometric data were collected from the comparative collections at the Department of Mammalogy of the Smithsonian Institution or from the personal collection of the first author. Taxa new to this study are indicated in table 1. Orbit convergence data on *Tarsius* were the mean of species means because all volumetric data on brain components are for indeterminate species [e.g. Stephan et al., 1981]. Orbit convergence data from *Alouatta caraya* were substituted for *Alouatta palliata*, which were otherwise unavailable.

The method for collecting orbit orientation data has been detailed elsewhere [Heesy, 2005, 2008; Iwaniuk et al., 2008]. Briefly, three-dimensional coordinate data were collected for 6 landmarks on the skull with a MicroScribe-3DX coordinate data stylus (Immersion Corp., San Jose, Calif., USA). Each specimen was mounted on an elevated clay base so that all coordinate data could be collected in a single series [e.g. Lockwood et al., 2002]. Each specimen sits within its own three-dimensional coordinate data space with this arrangement.

Convergence is measured as the dihedral angle (an angle between two planes) between the orbital margin plane and the midsagittal plane. The sagittal plane is defined by prosthion, nasion and inion. The orbital plane is defined by the points orbitale superius (point on the orbital margin farthest from the alveolar margin), orbitale anterius (point on the orbital margin most distant from the inion) and orbitale inferius (point on the orbital margin closest to the alveolar margin). Orbit convergence was calculated from these coordinate data following a macro available in Iwaniuk et al. [2008]. Convergence can be used as a surrogate variable for degree of binocular visual field overlap because of the isometric relationship between these variables in mammals [Heesy, 2004, 2008].

Activity pattern, the time of day during which an animal is primarily awake and active, has an influence on orbit convergence and binocular visual field size in mammals [Cartmill, 1974; Ross, 2000; Barton, 2004; Ravosa and Savakova, 2004; Heesy, 2008]. Data on activity pattern were categorized as nocturnal, diurnal and cathemeral. These data were taken from Fleagle [1999] and Heesy and Ross [2001] for primates, and Novak [1991a, b] for all other taxa included in this study.

Statistical Methods

First, we investigated the relationship between brain volume and the components of the visual pathway: optic tract, dorsal LGN, and V1. We conducted a second set of analyses to examine the regression slopes between the components of the visual pathway in order to determine whether the relationship between orbit convergence and the volumes of the optic tracts, lateral geniculate nuclei and V1 scale with geometric similarity. In order to control for size effects, we included body mass and brain size as additional predictors in our models. This is statistically similar to the common approach of using size-corrected residuals [Allen, 1997]. The goal of both approaches is to examine the relationship between orbital convergence and visual pathway components independent of body mass and brain size. Using residuals removes variation due to body mass and brain size from the model [Allen, 1997]. Using body mass and brain size as additional predictor variables directly accounts for the variation in these variables and allows us to examine the independent effect of orbital convergence.

Our third set of analyses examined the relationship between activity pattern and orbital convergence and the visual pathway components in primates and nonprimate mammals. These models also accounted for body mass and brain size. We coded activ-

Table 1. Morphometric and ecological data used in this study

Taxon	ACT	CONV	Body mass	Brain volume	Optic tract volume	LGN volume	V1 volume	Source[1]
Afrosoricida								
Echinops telfairi	N	41.0[2]	87.5	566	0.61	0.37		1, 3, 11
Hemicentetes semispinosus	N	27.7[2]	110	757	0.51	0.37		1, 3, 11
Setifer setonus	N	30.7[2]	248	1,404	1.07	1.05		1, 3, 11
Tenrec edaucadata	N	36.6[2]	832	2,315	2.73	1.46		1, 3, 11
Artiodactyla								
Ovis sp.	D	28.8		123,180	618	469	3,383	7, 12
Carnivora								
Canis familiaris	C	50.4	11,000	81,563		79.6		4, 31
Felis catus	C	65.4				41.3	698.4	8, 27
Mustela putorius	N	35.3	795.5	6,756.8		7		19, 31
Chiroptera								
Cynopterus brachyotis	N	42.7	33.9	926.8		5.14		25
Cynopterus horsfieldi	N		59.3	1,301		6.178		25
Eonycteris spelaea	N	45	58.7	1,239.9		4.68		25
Myotis sp.	N	13.5		304.4		0.34		25
Pteropus poliocephalus	N	50.9	695	6,762.2				25
Pteropus scapulatus	N	48.3	375	5,074.1				25
Dasyuromorphia								
Dasyurus hallucatus	N	41.6	912	6,686		5.97		5, 30
Monodelphis domestica	N	43.4[2]	97.6	768				20, 28
Diprotodontia								
Macropus eugenii	N	43.9	3,610	13,856		6.52		6, 30
Erinaceomorpha								
Atelerix algirus	N	31.3[2]	736	3,150.6		5.02		3, 11, 16
Erinaceus europaeus	N	32.4[2]	860	3,050	3.94	3.9		1, 3, 11
Hemiechinus auritus	N	33.5[2]	250	1,710				1
Lagomorpha								
Lepus sp.	N	20	4,500	12,329		29.05	136	8, 9, 29
Primates								
Alouatta belzebul	D	73.7	6,400	49,009		87.4	2,461	1, 3, 11
Alouatta palliata	D	76.5	5,350	43,520		90	1,860	17, 18
Aotus trivirgatus	N	67.5	830	16,195		32.9	1,203	1, 3, 11
Ateles geoffroyi	D	80.8	8,000	101,034	204	151	4,738	1, 11
Avahi laniger laniger	N	54.7	1,285	9,798		27.6	542	1, 3, 11
Avahi laniger occidentalis	N	54.7	860	9,124	38.3	29.3	527	1, 3, 11
Callicebus moloch	D	85.4	900	17,944		54.2	1,524	1, 3, 11
Callicebus sp. (= *caligatus*)	D	76.5	880	11,900		30	840	17, 18
Callithrix jacchus	D	63.5	280	7,241		25.1	685	1–3, 11
Cebuella pygmaea	D	66.7	140	4,302	23.8	16.9	415	1, 3, 11
Cebus apella	D	74.8	3,100	66,939	207	137	4,703	1, 11
Cercocebus torquatus	D	70.1	5,500	117,080		200	5,120	17, 18
Cercopithecus ascanius	D	80.2	3,400	63,505	320	147	5,106	1, 11
Cercopithecus mitis	D	73.4	6,300	70,564		150	5,274	1
Cercopithecus nictitans	D		4,260	64,740		120	4,140	17, 18
Cheirogaleus major	N	55.8	450	6,373	18	21.5	478	1, 11
Cheirogaleus medius	N	66.9	177	2,961		10.8	217	1
Daubentonia madagascarensis	N	56.4	2,800	38,130		48	1,028	1, 13
Eulemur fulvus	C	56	1,400	22,106	108	51.8	1,527	1, 3, 11
Eulemur mongoz	C	57.8	1,560	22,240		50	1,060	17, 18
Galago senegalensis	N	46.3	186	4,512		16	334	1
Galagoides demidoff	N	47	81	3,203	11.5	10.9	237	1, 11
Gorilla gorilla	D	107.7	105,000	470,359	671	384	15,185	1, 11
Homo sapiens	D	79.3	65,000	1,251,847	823	416	20,226	1, 11
Hylobates lar	D	79.8	5,700	97,505	302	175	5,750	1, 3, 11
Indri indri	D	61.7	6,250	36,285		94.5	1,961	1, 3, 11
Lagothrix lagotricha	D	78.5	5,200	95,503	203	164	6,082	1, 3, 11
Lepilemur ruficaudatus	N	55.9	915	7,175	20.7	15.6	357	1, 11
Lophocebus albigena	D	87.8	7,900	97,603		182	6,831	1

Table 1 (continued)

Taxon	ACT	CONV	Body mass	Brain volume	Optic tract volume	LGN volume	V1 volume	Source[1]
Loris tardigradus	N	61.6	322	6,269	15.7	24.6	588	1, 11
Macaca mulatta	D	73.9	7,800	87,896		158	6,586	1, 24
Macaca nemestrina	D	75	6,500	102,317	308	113		14
Microcebus murinus	N	45.3	54	1,680	6.17	7.07	149	1, 3, 11
Miopithecus talapoin	D	80.6	1,200	37,776		109	3,046	1, 3
Nycticebus coucang	N	63	800	11,755		35.9	823	1, 3
Otolemur crassicaudatus	N	55	850	9,668	33.9	23.2	548	1, 3, 11
Pan troglodytes	D	80	46,000	382,103	630	356	14,597	1, 11
Papio anubis	D	84	25,000	190,957	601	395	13,741	1, 3, 11
Perodicticus potto	N	61.6	1,150	13,212	19.5	24.3	552	1, 11
Pithecia monachus	D	67.7	1,500	32,867		76.3	2,130	1, 3, 11
Procolobus badius	D	84.8	7,000	73,818	201	128	3,984	1, 11
Propithecus verreauxi	D	62.2	3,480	25,194	125	64.5	1,355	1, 3, 11
Saguinus midas	D	70.82	340	9,569		36	1,061	1, 3, 11
Saguinus oedipus	D	74	380	9,537	50.5	34.2	977	1, 3, 11
Saimiri sciureus	D	69.9	660	22,572	117	62.9	2,326	1, 11
Semnopithecus entellus	D	88.2	9,890	107,540		140	4,320	17, 18
Tarsius sp.	N	55	125	3,393	15.5	20.8	370	1, 11
Varecia variegata rubra	D	54.6	3,000	29,713		68.9	2,112	1
Rodentia								
Mesocricetus auratus	N	55.8	135	5,163.89		1.96		10
Mus musculus	C	38.3		354.77		0.76		26
Rattus norvegicus (wild type)	C	32	300	2,252.3	7.83	3.48/3.68		8, 22, 23
Rattus (Sprague-Dawley)	C	32	300			1.3		21, 29
Spalacopus cyanus	D		85	2,094.6		0.52		15, 29
Spalax ehrenberghi	NA	59.2	197	2,384.2		0.0388		15, 29
Scandentia								
Tupaia belangeri	D	36.7	173.3	3,291.4			119.5	32
Tupaia glis	D	32	170	2,999	39.3	12.9	179	1, 3, 11
Tupaia minor	D	22.6	70	2,430		9.88	164	1, 3, 11
Urogale everetti	D	27.8	275	3,997		9.98	136	1
Soricomorpha								
Crocidura flavescens	N		29.3	399.6	0.25	0.28		3, 11, 16
Crocidura russula	N		11.2	190.8	0.12	0.08		3, 11, 16
Sorex araneus	C	6.8	11.3	204.6	0.14	0.07		3, 11, 16
Sorex minutus	C	6.8	4.9	112.6	0.11	0.06		3, 11, 16
Suncus murinus	N		33.8	369.7	0.23	0.18		3, 11, 16

Volumetric data are reported in cubic millimeters. Body mass data are reported in grams. ACT = Activity pattern, denoted as N for nocturnal, D for diurnal, C for cathemeral, or NA for not applicable; CONV = orbit convergence, measured in degrees; source of data.

[1] 1 = Stephan et al. [1981]; 2 = White et al. [1998]; 3 = Stephan et al. [1984]; 4 = Lee et al. [1999]; 5 = Crewther et al. [1988]; 6 = Marotte et al. [1989]; 7 = Piggins and Phillips [1996]; 8 = Hughes [1971]; 9 = Urban and Richard [1972]; 10 = Morin and Wood [2001]; 11 = Frahm et al. [1984]; 12 = Ebinger [1975]; 13 = Kaufman et al. [2005]; 14 = Blasco et al. [1999]; 15 = Cooper et al. [1993]; 16 = Stephan et al. [1991]; 17 = Bush and Allman [2004a]; 18 = Bush and Allman [2004b]; 19 = Williams and Jeffrey [2001]; 20 = Karlen and Krubitzer [2006]; 21 = Satorre et al. [1985]; 22 = Kruska and Schott [1977]; 23 = Paxinos and Watson [2007]; 24 = Malpeli et al. [1996]; 25 = Baron et al. [1996]; 26 = Paxinos and Franklin [2001]; 27 = Weber et al. [1983]; 28 = Karlen and Krubitzer [2006] and pers. comm.; 29 = Mace et al. [1981]; 30 = Pirlot [1981]; 31 = Gittleman [1986]; 32 = Drenhaus et al. [2006].

[2] Orbit convergence digitized for this study.

ity pattern as an ordinal variable from 0 to 2: nocturnal = 0, cathemeral = 1, and diurnal = 2. This approach has been commonly implemented in comparative analyses [e.g. Jones et al., 2003; Kamilar and Paciulli, 2008].

Continuous biological data potentially violate standard statistical assumptions of independence due to phylogenetic relatedness [Felsenstein, 1985; Harvey and Pagel, 1991] and taking phylogeny into account reduces the variance of the estimated regression or correlation coefficients [Rohlf, 2006]. There are several methods available to comparative biologists to account for data nonindependence due to phylogeny [Nunn and Barton, 2001; Felsenstein, 2004]. In this study, we used the phylogenetic generalized linear model function in the CAIC package for R [Purvis and Rambaut, 1995; Paradis et al., 2004; R Development Core Team, 2007]. This method accounts for phylogeny in our comparative datasets and also has the benefit of producing a Pagel's

lambda value for each model [Pagel, 1999], which indicates the strength of phylogeny in the analysis. The parameter lambda ranges on a continuous scale from 0 to 1. A value of 0 indicates that phylogeny has little impact on the relationship between the independent and dependent variables. This is equivalent to a species values regression without accounting for phylogeny. In contrast, a value of 1 indicates that phylogeny plays an important role in the model, with the residuals being weighted based on species evolutionary relationships following Brownian motion. Pagel's lambda and similar metrics are becoming increasingly popular in a wide variety of comparative biology research [e.g. O'Neill and Dobson, 2008; Kamilar and Muldoon, 2010; Kamilar and Bradley, in review].

The tree used in this study to evaluate the potential effects of phylogenetic relatedness is from Bininda-Emonds et al. [2007], which is a species level phylogeny of 4,510 extant mammals. This study included a small subset of these taxa and the tree was reduced to include only taxa for which data were available.

All of the analyses reported herein were performed on three groups: (1) an all-mammal sample including primates and nonprimates; (2) a primate-only sample that excludes all other mammals, and (3) a nonprimate mammal sample that excludes all primates.

Results

Relative Scaling among Retinogeniculostriate Components and Brain Volume

The phylogenetic generalized linear models (PGLM) of optic tract and lateral geniculate nuclei volumes, as well as lateral geniculate nuclei and area V1 volumes are statistically significant for the all-mammal and primate-only datasets (table 2). The nonprimate mammal datasets approach statistical significance with p values <0.10 for both analyses and slopes that are similar to the primate-only dataset. Lambda values are high for the analyses using all mammals, but are very low for the primate-only and nonprimate mammal datasets. All of these results are independent of brain size and body mass. The 95% confidence intervals of the slopes for the nonprimate mammal analyses of LGN versus V1 include geometric similarity (i.e. isometry). The 95% confidence intervals of the slopes for the nonprimate mammal analyses of optic tract versus LGN have an upper bound of 0.7069. However, the primates-only sample exhibits negative allometry between optic tract and LGN volumes, and between LGN and V1 volumes.

While accounting for body mass, the all-mammal dataset displays significant relationships between overall brain volume and optic tract, LGN and V1 volumes. For all three analyses, the 95% confidence intervals include isometry. The nonprimate mammal data have positive allometric slopes for the brain size versus V1 and optic tract models. In contrast, primates exhibit negative allometric relationships between brain size and both optic tract and LGN, with an upper bound of 1.01 for V1.

Scaling of Orbit Convergence with Retinogeniculostriate Components

While accounting for body mass, orbit convergence and brain volume are positively correlated at the $p = 0.051$ level in the all-mammal dataset, yet do not approach statistical significance for the primate-only and nonprimate mammal datasets. In addition, the directions of the slopes differ between these latter two datasets, in a negative direction for primates and a positive direction for nonprimate mammals. Lambda values are moderate to high in these analyses, ranging from 0.67 for primates to 0.99 for nonprimate mammals (table 2).

When accounting for both body mass and brain size, the all-mammal analyses of orbit convergence compared to optic tract and V1 volumes are significantly and positively correlated (table 2). In contrast, orbital convergence was not related to LGN volume for this dataset. Lambda values were quite high for these three models. When primates are examined alone, there is a significant and positive relationship between orbital convergence and both LGN and V1 volumes, but not with optic tract. This latter model has a high lambda value, with the remaining two analyses displaying lambda values near 0. Finally, the nonprimate mammals exhibit no relationship between orbital convergence and any component of the visual pathway. Lambda values are near 0 for the models involving V1 and optic tract and near 1 for the model examining LGN.

Activity Pattern and Orbit Convergence Scaling with Retinogeniculostriate Components

As with previous analyses, in order to evaluate the effects of activity pattern, the primate-only sample and the nonprimate mammal sample were analyzed separately. For nonprimate mammals, we found no relationship between activity pattern and orbital convergence, LGN or area V1. In contrast, we found a statistically significant and positive relationship between the degree of diurnality and the size of the optic tract at the $p = 0.024$ level. All of these models accounted for body mass and brain size.

Similar to nonprimate mammals, there was no relationship between activity pattern and orbital convergence in this sample of primates. In contrast, there was a strong and significant relationship between activity pat-

Table 2. Results for phylogenetic generalized linear models

Variables (x vs. y) Group		Additional predictors	x variable slope	CI of x variable slope	x variable t value	x variable p value	Full model r^2	Full model intercept	Full model p value	Pagel's lambda
Optic tract vs. LGN		BM and BV								
All species	37		0.8129	0.6136, 1.0122	7.9900	0.0000	0.9334	–1.1586	0.0001	0.8634
Primates only	25		0.4868	0.2726, 0.701	4.4560	0.0002	0.9741	–0.9485	0.0001	0.0001
Nonprimates	12		0.3270	–0.0072, 0.6612	1.9177	0.0914	0.9897	–9.0303	0.0001	0.0001
LGN vs. area V1		BM and BV								
All species	54		1.0661	0.916, 1.2162	13.9136	0.0000	0.9588	1.3594	0.0001	0.9121
Primates only	47		0.7254	0.5915, 0.8593	10.6274	0.0000	0.9861	–1.8175	0.0001	0.0001
Nonprimates	7		0.8381	0.1989, 1.4773	2.5699	0.0825	0.9973	–2.9951	0.0002	0.0001
Brain volume vs. optic tract		BM								
All species	37		0.7950	0.4302, 1.1598	4.2718	0.0001	0.7907	–4.6065	0.0001	0.9999
Primates only	25		0.5552	0.2108, 0.8996	3.1594	0.0045	0.8487	–2.3379	0.0001	0.9426
Nonprimates	12		3.2296	2.5138, 3.9454	8.8437	0.0000	0.9614	–15.9978	0.0001	0.0001
Brain volume vs. LGN		BM								
All species	74		0.8730	0.5502, 1.1958	5.2992	0.0000	0.6248	–5.5228	0.0001	0.9972
Primates only	47		0.6114	0.4152, 0.8076	6.1056	0.0000	0.8886	–2.4546	0.0001	0.7435
Nonprimates	27		0.9299	–0.0672, 1.927	1.8280	0.0800	0.5328	–6.7606	0.0001	0.9999
Brain volume vs. area V1		BM								
All species	55		0.9889	0.8096, 1.1682	10.8069	0.0000	0.7837	–2.9319	0.0001	0.9999
Primates only	47		0.7847	0.5617, 1.0077	6.8951	0.0000	0.8916	–0.4833	0.0001	0.7249
Nonprimates	8		3.1580	2.7176, 3.5984	14.0523	0.0000	0.9911	–13.9803	0.0001	0.0001
Convergence vs. optic tract		BM and BV								
All species	34		1.0995	0.4298, 1.7692	3.2177	0.0031	0.8465	–7.7296	0.0001	0.9902
Primates only	25		0.7431	–1.0719, 2.5581	0.8024	0.4313	0.8581	–5.6347	0.0001	0.8769
Nonprimates	9		0.3944	–0.4696, 1.2584	0.8946	0.4120	0.9701	–16.1262	0.0003	0.0001
Convergence vs. LGN		BM and BV								
All species	68		0.3359	–0.3521, 1.0239	0.9572	0.3421	0.6262	–6.2773	0.0001	0.9977
Primates only	47		0.6660	0.1376, 1.1944	2.4706	0.0175	0.9539	–5.3162	0.0001	0.0001
Nonprimates	22		–0.3760	–1.7856, 1.0336	–0.5228	0.6075	0.5151	–5.8442	0.0039	0.9999
Convergence vs. area V1		BM and BV								
All species	53		1.5156	1.1269, 1.9043	7.6443	0.0000	0.9159	–7.3155	0.0001	0.7659
Primates only	46		1.0259	0.4487, 1.6031	3.4832	0.0012	0.9617	–5.2452	0.0001	0.0001
Nonprimates	7		0.5093	–0.858, 1.8766	0.7300	0.5182	0.9922	–13.4519	0.0012	0.0001
Convergence vs. brain volume		BM								
All species	73		0.3914	0.0055, 0.7773	1.9880	0.0507	0.8663	2.6957	0.0001	0.8872
Primates only	47		–0.5367	–1.5359, 0.4625	–1.0528	0.2982	0.8867	6.7497	0.0001	0.6666
Nonprimates	27		0.2797	–0.176, 0.7354	1.2027	0.2408	0.8939	2.9592	0.0000	0.9999
Activity pattern vs. convergence		BM and BV								
Primates only	47		0.0359	–0.0162, 0.088	1.3506	0.1839	0.3362	4.1096	0.0005	0.7936
Nonprimates	26		–0.2299	–0.5511, 0.0913	–1.4023	0.1748	0.2447	2.3089	0.0975	0.9999
Activity pattern vs. LGN		BM and BV								
Primates only	47		0.1883	0.0834, 0.2932	3.5185	0.0010	0.9233	–2.2175	0.0001	0.5710
Nonprimates	26		0.0728	–0.4768, 0.6224	0.2597	0.7975	0.7608	–6.3580	0.0001	0.9999
Activity pattern vs. V1		BM and BV								
Primates only	47		0.2096	0.0991, 0.3201	3.7145	0.0006	0.9472	–0.7008	0.0001	0.1742
Nonprimates	8		–0.0451	–0.8801, 0.7899	–0.1059	0.9207	0.9911	–14.1896	0.0001	0.0001
Activity pattern vs. optic tract		BM and BV								
Primates only	25		0.4601	0.2672, 0.653	4.6773	0.0001	0.9652	–1.8808	0.0001	0.0001
Nonprimates	12		0.7504	0.2212, 1.2796	2.7795	0.0239	0.9804	–11.7528	0.0001	0.0001

Additional predictors describe when body mass (BM) and brain volume (BV) were included in the generalized linear model. The x variable slope, confidence interval (95% CI), t value, and p value describe the predictor variable of interest, independent of the additional predictors in the model. Full model columns for r^2, intercept, and p value describe the combined effects of the predictor variable of interest, body mass, and brain volume. Pagel's lambda estimates the impact of phylogeny on the variance in the model. A value of 0 indicates that phylogeny has little impact on the relationship between the independent and dependent variables, whereas a value of 1 indicates that phylogeny contributes highly to the variance in the model.

tern and the three visual pathway components: LGN, area V1 and optic tract while accounting for body mass and brain size. For all these models, the size of the visual pathway component increased with increasing diurnality.

Discussion

Overall, when variation in body mass and brain volume are accounted for, it would appear that optic tract, LGN, and V1 volumes are correlated in mammals. Larger optic tract volumes are correlated with larger LGN volumes and with larger V1 volumes. However, these results appear to be driven by the inclusion of the primate data; the comparisons limited to nonprimates were not significant. In comparison, overall brain volume is correlated with larger visual pathway component volumes in most taxonomic samples with the single exception of LGN volume in nonprimate mammals. These results generally agree with previous studies that used smaller sample sizes or alternative taxa, types of data, or analyses [e.g. Barton et al., 1995; Barton, 1998; Kaskan et al., 2005]. We additionally found that primates display allometric relationships among pathway components, whereas other mammals display isometry. An allometric relationship between the LGN and V1 in primates has been noted before by Stevens [2001], who found that among haplorhine primates (tarsiers, monkeys, apes and humans) the LGN and V1 volumes, as well as estimates of neuron numbers contained within each of these structures, scale with 3/2 slope. We found a shallower slope in this study, but it must be noted that our primate regression also included strepsirhine primates (lemurs, lorises and galagoes) as well as accounting for variance due to brain volume, body mass and phylogenetic relatedness. Notably, primates appear to have larger V1 areas for their LGN volumes, distinguishing them from other mammals.

Barton [2004] found that primate orbit convergence is correlated with LGN and V1 expansion, all of which are correlated with substantial expansion of primate brain volume, and he related this expansion to specialization for color and fine-detail vision. Our scaling results agree with Barton, which is expected because this study uses a partially overlapping primate dataset of brain component volumes. We additionally found that diurnal primates possess relatively larger LGN and V1 volumes when compared to nocturnal primates, whereas nonprimate mammals do not display such a relationship. This finding is consistent with the work by Barton [2004], who found that elaboration of the parvocellular visual pathway, which is primarily responsible for transmitting information on color and fine detail, was an evolutionary specialization of diurnal primates.

By including nonprimates, this study provides a broader mammalian context, thereby revealing that primates are possibly unique among mammals in the relationship between orbit convergence and, by extension, binocular visual field overlap and retinogeniculostriate pathway component volumes. Nonprimates, when considered together, consistently exhibited nonsignificant relationships in our analyses between orbit convergence and visual pathway component volumes. The comparatively small nonprimate mammal sample size for some comparisons consequently reduces statistical power. However, there is a significant statistical effect in primates, whereas there is none in nonprimate mammals. This includes several comparisons, such as orbit convergence versus LGN volume, where the nonprimate mammal sample size includes a sample size of 22, which is of sufficient size and power to detect a moderate effect size. Based upon the available data, this leads us to conclude that orbit convergence and the retinogeniculate pathway are not as strongly related as these variables are in primates.

The finding that primates are possibly unique among mammals in the relationship between orbit convergence and retinogeniculostriate pathway component volumes begs the question as to why. Given the moderate amount of retinal input received by the visual LGN, it is reasonable to consider what the roles of nonretinal feedback input to the LGN may be, especially with respect to corticogeniculate feedback. The most prominently cited functional hypotheses for the corticogeniculate pathway include tuning and control of binocular disparity or control of visual attention [e.g. Schmielau and Singer, 1977; Varela and Singer, 1987; McIlwain, 1995; Casagrande et al., 2005a, b]. Control of binocular tuning may function to sharpen the borders of receptive fields fixated on an object of interest, whereas less relevant visual data would not be tuned [Briggs and Usrey, 2008]. This would potentially improve the contrast of objects within the plane of fixation relative to the background [Schmielau and Singer, 1977]. Control of visual attention could entail modulating signals in the LGN by increasing the responses of these cells to stimuli within the central portion of the visual field, which has been demonstrated empirically in macaques [McAlonan et al., 2008; Briggs and Usrey, 2009]. Casagrande et al. [2005] argue persuasively that extraretinal imputs to the LGN function to enhance spatial attention specifically for visual target selection and

saccadic responses, and that corticogeniculate feedback plays a critical role. It is important to recognize that tuning and spatial attention both may be important functions of the corticogeniculate pathway, and that greater reliance on these functions is probably reflected in the volumetric morphology of the primary visual pathway.

Based on the scaling differences exhibited by primates and nonprimate mammals in orbit orientation and visual pathway, it is reasonable to hypothesize that binocular tuning and enhanced visual attention for target selection may have exerted stronger influences on the evolution of binocular vision in primates than in the other mammals included in this study. We would specifically predict that corticogeniculate pathways are either larger in terms of cell and synapse number or at least more prominent in their effect on LGN responses in primates than in nonprimate mammals. We cannot distinguish between or evaluate any proposed hypothesis for extraretinal feedback to the LGN and its relevance to retinogeniculostriate scaling. However, we would suggest that the expansion of the zone of binocular visual field overlap that is characteristic of primates incorporated greater functional reliance on binocular tuning, spatial attention for targeting, or some advantageous combination of at least both of these functions. Furthermore, this would imply that primates should perform better at binocular tuning and attention tasks within the binocular field than many nonprimate mammals. Although we do not know of any available data at present to evaluate this hypothesis, the interest in thalamic feedforward-feedback functions in general as well as in extraretinal influences on LGN function in particular leads us to believe that relevant data are foreseeable.

We conclude that the contrast between the general similarities in geniculostriate data across mammals and the fact that only primates show a significant relationship between orbit convergence and LGN and V1 volumes provide additional correlative evidence that specialization in binocular vision has been a major theme in the evolution of the primate visual system [Cartmill, 1974; Allman, 1977; Ross, 2000; Barton, 2004; Ravosa and Savakova, 2004; Heesy, 2008, 2009].

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References

Allen MP (1997): Understanding regression analysis. New York, Plenum Press.

Allman J (1977): Evolution of the visual system in early primates; in Sprague JM, Epstein AN (eds): Progress in Psychobiology and Physiological Psychology. New York, Academic Press, pp 1–53

Allman JM (1999): Evolving Brains. New York, WH Freeman & Co.

Andrews TJ, Halpern SD, Purves D (1997): Correlated size variations in human visual cortex, lateral geniculate nucleus, and optic tract. J Neurosci 17:2859–2868.

Baron G, Stephan H, Frahm H (1996): Comparative Neurobiology in Chiroptera: Macromorphology, Brain Structures, Tables and Atlases. Basel, Birkhäuser, vol 1.

Barton RA (1998): Visual specialization and brain evolution in primates. Proc Roy Soc Lond B265:1933–1937.

Barton RA (2004): Binocularity and brain evolution in primates. Proc Natl Acad Sci USA 101: 10113–10115.

Barton RA (2007): Evolutionary specialization in mammalian cortical structure. J Evol Biol 20:1504–1511.

Barton RA, Purvis A, Harvey PH (1995): Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. Phil Trans R Soc Lond B 348:381–392.

Bininda-Emonds ORP, Cardillo M, Jones KE, MacPhee RDE, Beck RMD, Grenyer R, Price SA, Vos RA, Gittleman JL, Purvis A (2007): The delayed rise of present-day mammals. Nature 446:507–512.

Blasco B, Avendaño C, Cavada C (1999): A stereological analysis of the lateral geniculate nucleus in adult *Macaca nemestrina* monkeys. Vis Neurosci 16:933–941.

Briggs F, Usrey WM (2008): Emerging views of corticothalamic function. Curr Opin Neurobiol 18:403–407.

Briggs F, Usrey WM (2009): Parallel processing in the corticogeniculate pathway of the macaque monkey. Neuron 62:135–146.

Brooks D, Komàromy A, Källberg M (1999): Comparative retinal ganglion cell and optic nerve morphology. Vet Ophthalmol 2:3–11.

Bush EC, Allman JM (2004a): The scaling of frontal cortex in primates and carnivores. Proc Natl Acad Sci USA 101:3962–3966.

Bush EC, Allman JM (2004b): Three-dimensional structure and evolution of primate primary visual cortex. Anat Rec 281A:1088–1094.

Cartmill M (1974): Rethinking primate origins. Science 184:436–443.

Casagrande VA, Ichida JM (2002): The lateral geniculate nucleus; in Alder FH (ed): Physiology of the Eye. St Louis, Mosby, pp 655–668.

Casagrande V, Norton T (1991): Lateral geniculate nucleus: a review of its physiology and function; in Levelthal A (ed): Vision and Visual Dysfunction, vol 4: The Neural Basis of Visual Function. London, MacMillan Press, pp 41–84.

Casagrande V, Royal DA, Sáry G (2005a): Extraretinal inputs and feedback mechanisms to the lateral geniculate nucleus (LGN); in Kremers J (ed): The Primate Visual System: A Comparative Approach. Chichester, Wiley, pp 191–211.

Casagrande V, Sáry G, Royal D, Ruiz O (2005b): On the impact of attention and motor planning on the lateral geniculate nucleus. Prog Brain Res 149:11–29.

Cooper HM, Herbin M, Nevo E (1993): Visual system of a naturally microphthalmic mammal: The Blind Mole Rat, Spalax ehrenbergi. J Comp Neurol 328:313–350.
Crewther D, Nelson J, Gillard Crewther S (1988): Afferent input for target survival in marsupial visual development. Neurosci Lett 86: 147–154.
Drenhaus U, Rager G, Eggli P, Kretz R (2006): On the postnatal development of the striate cortex (V1) in the tree shrew *(Tupaia belangeri)*. Eur J Neurosci 24:479–490.
Ebinger P (1975): Quantitative investigations of visual brain structures in wild and domestic sheep. Anat Embryol 146:313–323.
Felsenstein J (1985): Phylogenies and the comparative method. Am Nat 125:1–15.
Felsenstein J (2004): Inferring Phylogenies. Sunderland, Sinauer.
Fleagle JG (1999): Primate Adaptation and Evolution, ed 2. San Diego, Academic Press.
Frahm H, Stephan H, Baron G (1984): Comparison of brain structure volumes in insectivora and primates. V. Area striata (AS). J Hirnforsch 25:537–557.
Girgis M, Shih-Chang W (1981): A New Stereotaxic Atlas of the Rabbit Brain. St Louis, Green.
Gittleman JL (1986): Carnivore brain size, behavioral ecology, and phylogeny. J Mamm 67:23–36.
Harvey PH, Pagel MD (1991): The Comparative Method in Evolutionary Biology. Oxford: Oxford University Press.
Heesy CP (2004): On the relationship between orbit orientation and binocular visual field overlap in mammals. Anat Rec 281A:1104–1110.
Heesy CP (2005): Function of the mammalian postorbital bar. J Morphol 264:363–380.
Heesy CP (2008): Ecomorphology of orbit orientation and the adaptive significance of binocular vision in primates and other mammals. Brain Behav Evol 71:54–67.
Heesy CP (2009): Seeing in stereo: the ecology and evolution of primate binocular vision and stereopsis. Evol Anthropol 18:21–35.
Heesy CP, Ross CF (2001): Evolution of activity patterns and chromatic vision in primates: morphometrics, genetics and cladistics. J Hum Evol 40:111–149.
Hubel D, Wiesel T (1961): Integrative action in the cat's lateral geniculate body. J Physiol 155:385–398.
Hughes A (1971): Topographical relationships between the anatomy and physiology of the rabbit visual system. Doc Ophthalmol 30: 33–159.
Iwaniuk A, Heesy C, Hall M, Wylie D (2008): Relative Wülst volume is correlated with orbit orientation and binocular visual field in birds. J Comp Physiol A 194:267–282.
Jones E (2007): The Thalamus, ed 2. Cambridge, Cambridge University Press, vol 2.
Jones KE, Purvis A, Gittleman JL (2003): Biological correlates of extinction risk in bats. Am Nat 161:601–614.
Kamilar, JM, Bradley BJ: Interspecific variation in primate coat color supports Gloger's rule. J Biogeog, in review.
Kamilar JM, Muldoon KM (2010): The climatic niche diversity of Malagasy primates: a phylogenetic approach. PLoS One 5:e11073. DOI:10.1371/journal.pone.0011073
Kamilar JM, Paciulli LM (2008): Examining the extinction risk of specialized folivores: a comparative study of colobine monkeys. Am J Primatol 70:1–12.
Karlen S, Krubitzer L (2006): Phenotypic diversity is the cornerstone of evolution: Variation in cortical field size within short-tailed opossums. J Comp Neurol 499:990–999.
Kaskan PM, Franco ECS, Yamada ES, de Lima Silveira LC, Darlington RB, Finlay BL (2005): Peripheral variability and central constancy in mammalian visual system evolution. Proc Biol Sci 272:91–100.
Kaufman J, Ahrens E, Laidlaw D, Zhang S, Allman J (2005): Anatomical analysis of an aye-aye brain (*Daubentonia madagascariensis*, Primates: Prosimii) combining histology, structural magnetic resonance imaging, and diffusion-tensor imaging. Anat Rec 287A:1026–1037.
Kirk EC (2006): Visual influences on primate encephalization. J Hum Evol 51:76–90.
Kruska D, Schott U (1977): Comparative-quantitative investigations of brains of wild and laboratory rats. J Hirnforsch 18:59–67.
Lee I, Kim J, Lee C (1999): Anatomical characteristics and three-dimensional model of the dog dorsal lateral geniculate body. Anat Rec 256A:29–39.
Livingstone M, Hubel D (1988): Segregation of form, color, movement, and depth: anatomy, physiology, and perception. Science 240: 740–749.
Lockwood CA, Lynch JM, Kimbel WH (2002): Quantifying temporal bone morphology of great apes and humans: an approach using geometric morphometrics. J Anat 201:447–464.
Mace GM, Harvey PH, Clutton-Brock TH (1981): Brain size and ecology in small mammals. J Zool 193:333–354.
Malpeli JG, Lee D, Baker FH (1996): Laminar and retinotopic organization of the macaque lateral geniculate nucleus: magnocellular and parvocellular magnification functions. J Comp Neurol 375:363–377.
Marotte L, Flett D, Mark R (1989): Effects of very early monocular and binocular enucleation on primary visual centers in the tammar wallaby *(Macropus eugenii)*. J Comp Neurol 282:535–554.
McAlonan K, Cavanaugh J, Wurtz R (2008): Guarding the gateway to cortex with attention in visual thalamus. Nature 456:391–394.
McIlwain JT (1995): Lateral geniculate lamination and the corticogeniculate projection: a potential role in binocular vision in the quadrants. J Theor Biol 172:329–333.
Morin L, Wood R (2001): A Stereotaxic Atlas of the Golden Hamster Brain. San Diego, Academic Press.
Noble VE, Kowalski EM, Ravosa MJ (2000): Orbit orientation and the function of the mammalian postorbital bar. J Zool 250:405–418.
O'Neill MC, Dobson SD (2008): The degree and pattern of phylogenetic signal in primate long-bone structure. J Hum Evol 54:309–322.
Nowak RM (1991): Walker's Mammals of the World, ed 5. Baltimore, The Johns Hopkins University Press, vol 1.
Nowak RM (1991): Walker's Mammals of the World, ed 5. Baltimore, The Johns Hopkins University Press, vol 2.
Nunn CL, Barton RA (2001): Comparative methods for studying primate adaptation and allometry. Evol Anthrop 10:81–98.
Pagel M (1999): Inferring the historical patterns of biological evolution. Nature 401:877–884.
Paradis E, Claude J, Strimmer K (2004): APE: analyses of phylogenetics and evolution in the R language. Bioinformatics 20:289–290.
Paxinos G, Franklin KBJ (2001): The Mouse Brain in Stereotaxic Coordinates, ed 2. San Diego, Academic Press.
Paxinos G, Watson C (2007): The Rat Brain in Stereotaxic Coordinates, ed 6. Burlington, Academic Press.
Piggins D, Phillips CJ (1996): The eye of the domesticated sheep with implications for vision. Anim Sci 62:301–308.
Pirlot P (1981): A quantitative approach to the marsupial brain in an eco-ethological perspective. Rev Can Biol 40:229–250.
Purvis A, Rambaut A (1995): Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. Comput Appl Biosci 11: 247–251.
R Development Core Team (2007): R: A Language And Environment For Statistical Computing. Vienna, R Foundation for Statistical Computing.
Ravosa MJ, Savakova DG (2004): Euprimate origins: the eyes have it. J Hum Evol 46:355–362.
Rohlf FJ (2006): A comment on phylogenetic correction. Evolution 60:1509–1515.
Ross CF (1995): Allometric and functional influences on primate orbit orientation and the origins of the Anthropoidea. J Hum Evol 29: 201–227.
Ross CF (2000): Into the light: the origin of Anthropoidea. Annu Rev Anthropol 29:147–194.
Satorre J, Cano J, Reinoso-Suarez F (1985): Stability of the neuronal population of the dorsal lateral geniculate nucleus (LGNd) of aged rats. Brain Res 339:375–377.
Schmielau F, Singer W (1977): The role of visual cortex for binocular interactions in the cat lateral geniculate nucleus. Brain Res 120:354.
Sherman SM, Guillery RW (2006): Exploring the Thalamus and Its Role in Cortical Function, ed 2. Cambridge, MIT Press.

Sherman S (2002): The role of the thalamus in the flow of information to the cortex. Phil Trans Roy Soc B357:1695–1708.
Sherman S, Koch C (1986): The control of retinogeniculate transmission in the mammalian lateral geniculate nucleus. Exp Brain Res 63:1–20.
Stephan H, Baron G, Frahm HD (1991): Comparative Brain Research in Mammals. New York, Springer, vol 1: Insectivores.
Stephan N, Frahm H, Baron G (1981): New and revised data on volumes of brain structures in insectivores and primates. Folia Primatol 35:1–29.
Stephan H, Frahm HD, Baron G (1984): Comparison of brain structure volumes in Insectivora and Primates. IV. Non-cortical visual structures. J Hirnforsch 25:385–403.
Stevens CF (2001): An evolutionary scaling law for the primate visual system and its basis in cortical function. Nature 411:193–195.
Urban I, Richard P (1972): A Stereotaxic Atlas of the New Zealand Rabbit's Brain. Springfield, Thomas.
Varela F, Singer W (1987): Neuronal dynamics in the visual corticothalamic pathway revealed through binocular rivalry. Exp Brain Res 66:10–20.
Weber A, Kalil R (1983): The percentage of interneurons in the dorsal lateral geniculate nucleus of the cat and observations on several variables that affect the sensitivity of horseradish peroxidase as a retrograde marker. J Comp Neurol 220:336–346.
White AJR, Wilder HD, Goodchild AK, Sefton AJ, Martin PR (1998): Segregation of receptive field properties in the lateral geniculate nucleus of a New-World monkey, the marmoset *Callithrix jacchus*. J Neurophysiol 80: 2063–2076.
Williams AL, Jeffery G (2001): Growth dynamics of the developing lateral geniculate nucleus. J Comp Neurol 430:332–342.