PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B (2005) **272**, 91–100
doi:10.1098/rspb.2004.2925
Published online 07 January 2005

Peripheral variability and central constancy in mammalian visual system evolution

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Neural systems are necessarily the adaptive products of natural selection, but a neural system, dedicated to any particular function in a complex brain, may be composed of components that covary with functionally unrelated systems, owing to constraints beyond immediate functional requirements. Some studies support a modular or mosaic organization of the brain, whereas others emphasize coordination and covariation. To contrast these views, we have analysed the retina, striate cortex (V1) and extrastriate cortex (V2, V3, MT, etc.) in 30 mammals, examining the area of the neocortex and individual neocortical areas and the relative numbers of rods and cones. Controlling for brain size and species relatedness, the sizes of visual cortical areas (striate, extrastriate) within the brains of nocturnal and diurnal mammals are not statistically different from one another. The relative sizes of all cortical areas, visual, somatosensory and auditory, are best predicted by the total size of the neocortex. In the sensory periphery, the retina is clearly specialized for niche. New data on rod and cone numbers in various New World primates confirm that rod and cone complements of the retina vary substantially between nocturnal and diurnal species. Although peripheral specializations or receptor surfaces may be highly susceptible to niche-specific selection pressures, the areal divisions of the cerebral cortex are considerably more conservative.

Keywords: evolution; mammalian visual system; neocortex; retina; nocturnal; diurnal

1. INTRODUCTION

Two distinct and basic mechanistic questions underlie the relationship between the sizes of brain components and the special niches or behavioural capacities of an animal. The first concerns the fundamental relationship of structure and function in the central nervous system. Few doubt that the eye is closely adapted for vision, but is the same true of the primary visual cortex? Do features uniquely adapted to normal visual input preclude other types of sensory, motor or cognitive processing? For example, the neurotransmitter and neuromodulator systems of the visual cortex might operate in time frames particularly suitable for visual events, and axon extents might match desirable spatial integration ranges for scene processing. Given the highly elaborated structure of primary visual cortex, even prior to function (Crowley & Katz 2002), and its unquestioned involvement in normal visual processing, the answer would seem to be distinctly yes: the visual cortex *is* adapted for vision. To our knowledge, however, there have been no direct tests of the essential nature of any feature specific to visual cortex for vision.

Conversely, many aspects of cortical structure arise epigenetically and, therefore, much vision-specific structure could be imposed on the cortex (Katz & Shatz 1996). A wide variety of evidence suggests broad structure–function matches in the cortex. Of course, the cortex has a highly conserved columnar structure throughout its extent (Rockel *et al.* 1980). Originally, Lashley (1930) observed that blind rats, without visual cortex, show deficits in finding their way through a maze, implying that the visual cortex was still involved in some tasks (see also Thinus-Blanc & Gaunet 1997). More recent anatomical data indicate that primary visual cortex receives inputs from non-visual or multisensory neocortex (Falchier *et al.* 2001; Rockland & Ojima 2003). Remarkably, the primary visual cortex is activated in the congenitally blind during Braille reading (Sadato *et al.* 1996), and, recently, these findings have been expanded upon, dividing the occipital cortex of the congenitally blind into two functional regions (Amedi *et al.* 2003). Conversely, vision can find a home in 'non-visual' cortical areas after various developmental transformations (Pallas 2001). The general features of the neocortex may make it suitable for processing many different types of inputs and, therefore, the question of the specific functional adaptation of visual cortex for vision alone must remain open. This leads to the alternative view that natural selection has favoured the evolution of a domain-general architecture in the cortex, within which distinct processing abilities may reside.

The second question concerns the accessibility of individual brain parts to natural selection. Theories of the evolution of the brain and its size and structure are necessarily about adaptation, and natural selection on a particular behaviour might target particular circuitry. Even with complete functional independence of a selected circuit, evolution of the brain might not be characterized by part-by-part independence. Different components of the brain may have intrinsically different variability for selection to operate on (Glendenning & Masterton 1998). Multiple components of the vertebrate body, including the neo-

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Received 21 June 2004
Accepted 6 September 2004

cortex, under the domain of a single control gene, covary in size if the gene is altered (Nemeschkal 1999; Ragsdale & Grove 2001). Selection for each part of a distributed functional system like the visual or auditory system, even over extended evolutionary time, may simply be too unlikely. Selection on overall brain size may be the only way to select for the size of a spatially distributed neural system (Finlay & Darlington 1995).

We might hope to turn to available allometric analyses to resolve questions about the independence of parts, but the available data are problematic. Most allometric analyses employ the Stephan dataset, which includes primates, insectivores and bats (Stephan *et al.* 1981*a*,*b*). In the Stephan dataset, the major radiations have a non-random relationship to the nocturnal and diurnal classification. Bats are nocturnal, as are most of the strepsirhine primates (the lemur-like ones), while only one of the haplorhine primates (tarsiers, monkeys and apes) is diurnal (Stephan *et al.* 1981*a*). In addition, haplorhines have large brains for their body size. Work to date about the relative size of visual system components is necessarily ambiguous in separating the effects of niche and lineage on structure. Numerous ingenious ways of controlling for linked variation have been devised, and although attempts have been made, the number of species that could possibly be obtained for each contrast of interest simply does not allow revealing comparisons to be made in the case of the primate visual system (Barton 1996, 1998; Barton & Harvey 2000).

The major predictor of the sizes of particular brain structures is brain size, controlling 80–97% of the variation in all estimates and each structure in the brain enlarges with respect to brain size at different predictable slopes (Finlay & Darlington 1995; Finlay *et al.* 2001). For structures with 'positive allometry', such as the neocortex, which increase in size at a greater slope than the entire brain, absolutely larger brains will predictably be composed of proportionately more neocortex. Most work to date suggests that morphologically identifiable cortical areas have predictable allometry (Frahm *et al.* 1984; Jerison 1997; Stevens 2001; Semendeferi *et al.* 2002). Without knowing the underlying allometry, taking the simple ratio of the sizes of cortical areas of animals of different brain volumes and drawing meaningful conclusions about the adaptation of brains to ecological niches is impossible.

Although data on the relative sizes of functional areas within the mammalian cerebral cortex have existed, at least since Brodman's early twentieth-century maps, they have yet to be analysed in a truly comparative sense. Using modern physiological and anatomical methods, primary and secondary visual, somatosensory and auditory cortical areas have been mapped in diverse species, including primates, rodents, various marsupials and the monotremes. These studies can help clarify cross-species allometric trends, effects of lineage and effects of niches (Luethke *et al.* 1988, 1989; Krubitzer & Kaas 1990, 1993; Felleman & Van Essen 1991; Krubitzer *et al.* 1993, 1997; Preuss *et al.* 1993; Krubitzer 1995, 1998; Beck *et al.* 1996; Preuss & Kaas 1996; Van Essen & Drury 1997; Beck & Kaas 1998; Lyon *et al.* 1998; Catania *et al.* 1999; Huffman *et al.* 1999; Rosa 1999; Rosa *et al.* 1999; Slutsky *et al.* 2000). This report attempts to systematically examine neocortical organization in 30 mammalian species, using the method of independent contrasts to control for lineage effects (Harvey & Pagel 1991; Purvis & Rambaut 1995). In addition, we present new data on the relative number of rods and cones in selected New World primates to contrast stability in neuronal numbers and organization between the sensory periphery and the cerebral cortex.

2. MATERIAL AND METHODS

(a) *Species and cortical maps utilized in this study*

The published literature offers 30 maps generated by a number of methods, including electrophysiology, cytoarchitectonics and connectional studies (see table 1 in electronic Appendix A). Our analysis includes 10 primate, two monotreme, three rodent, six marsupial and seven insectivore species, plus one species representing each of the orders Megachiroptera and Scandentia. Multiple cases were averaged for some species. For others, we used the published general map or a summary diagram (see § 4 for discussion on individual variability). All maps with scale bars were traced into NIH Image v1.61 with a Wacom 6 in × 8 in (1 inch = 2.54 cm) data tablet. For some species, only one or more modality had been measured, and possible comparisons vary accordingly. For other species, an exhaustive mapping of all the regions of cortex responsive to a particular modality had been done; in those cases, all contrasts could be made. In some cases, the entire area responsive to a particular modality had been measured, but the homology of particular areas was unclear. In these cases, only totals of modality-specific cortex were contrasted.

Four species differ somewhat from the others in terms of the available data. The cortical areas of the rat were reproduced from coronal sections (Zilles 1985). These sections were traced into Neurolucida v3.1 and serially reconstructed to give cortical surface areas. Data for the macaque neocortex come from two sets of investigators (Felleman & Van Essen 1991; Krubitzer *et al.* 1995). These two maps are averaged to yield a composite map. The neocortical map for *Homo* is produced by overlaying Brodman's cytoarchitectonic map upon a mathematically flattened human cerebral cortex (Drury *et al.* 1999). Maps for the squirrel monkey do not contain any information on auditory cortex (Krubitzer & Kaas 1990) and, therefore, this information is obtained from another map (Jones & Burton 1976). Using the SII area of each map, auditory fields on the Jones & Burton (1976) squirrel monkey map are scaled to fit into the full maps of Krubitzer & Kaas (1990) Most of the maps used in this analysis do not include all four of the targeted cortical areas. In these cases, an average map was produced which allows appropriate comparisons to be made.

The platypus and echidna (monotremes) are outliers in visual cortex organization and, possibly, primary somatosensory cortex organization. Their neocortex is organized differently from that of all other mammals, with the visual cortex located medially and the auditory cortex embedded within the somatosensory (Krubitzer *et al.* 1995; Krubitzer 1998). They are also the only mammals to possess a sense of electroreception. Owing to these significant *a priori* divergences and very obvious differences in the scaling patterns of their neocortices, we have separated these two species from the main data analysis, when appropriate.

(b) *Statistical analyses*

Because simple and multiple regression analyses assume the independence of data points, they are not completely valid methods for comparative problems: related species may share certain traits through common descent rather than through independent adaptation. Felsenstein (1985) develops an appropriate method for testing comparative relationships using phylogenetic trees. Harvey & Pagel (1991) build on Felsenstein's ideas of finding a set of

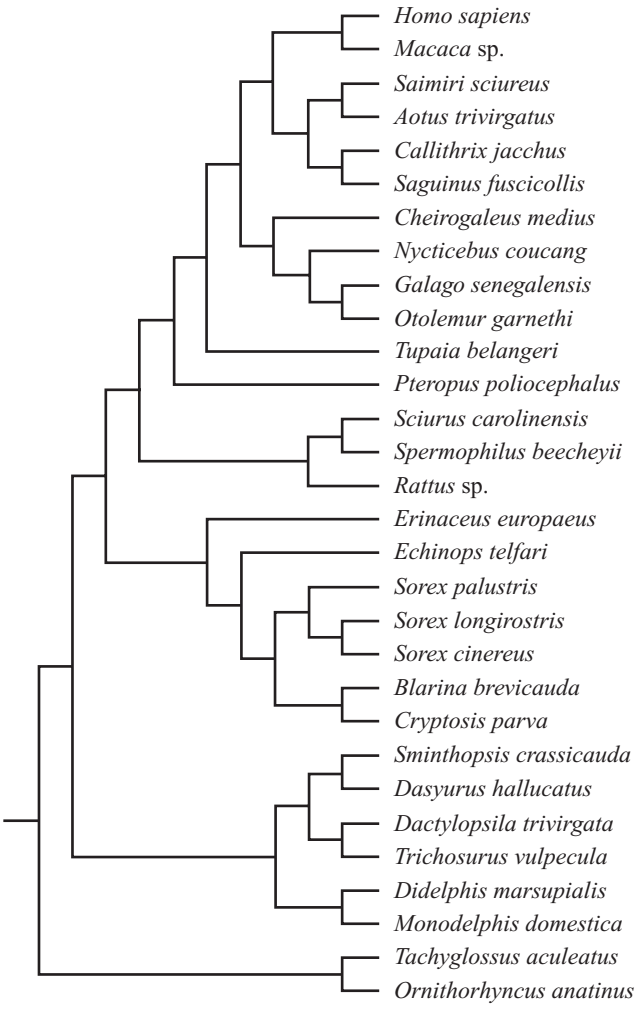

Figure 1. Phylogeny of 30 mammalian species. This tree was complied from the literature (Allard *et al.* 1999; Butler 1988; Fleagle 1999; George 1986, 1988; Kirsch *et al.* 1997; Novacek 1993; Shoshani & McKenna 1998).

independent comparisons between two species, or sub-taxa, for a bifurcating tree. These comparisons or differences can be analysed by the techniques of regression and correlation. The computer application *Comparative Analysis of Independent Contrasts* (CAIC) allows valid analyses of comparative datasets that include several continuous variables and one multicategorical variable (Purvis & Rambaut 1995). CAIC uses a phylogenetic tree to partition variance among the species into independent comparisons or linear contrasts, with each contrast made at a different node in the phylogeny. A completely resolved phylogenetic tree was compiled from the literature and is reproduced in figure 1 (George 1986, 1988; Butler 1988; Novacek 1993; Kirsch *et al.* 1997; Shoshani & McKenna 1998; Allard *et al.* 1999; Fleagle 1999). Branch lengths were set to be equivalent, assuming a punctuational model of change (Purvis & Rambaut 1995). Kaskan (2000) gives a more complete description of the data and statistical methods.

(c) *Estimation of cone and rod numbers in primate retinas*

Sample sizes varied owing to the availability of the primate species from animals bred or housed in the Centro Nacional de Primatas (CENP) in Pará, Brazil. All animal housing and procedures complied with the principles defined in the NIH *guide for the care and use of animals*. Animals were dark adapted for 30 min, while lightly anaesthetized with an intramuscular injection of a 1 : 4 mixture of 2% xylazine hydrochloride (Rompun, Bayer, Porto Alegre, Brazil) and 5% ketamine hydrochloride (Ketalar, Parke-Davis, Sao Paulo, Brazil). They were then deeply anaesthetized with the same mixture, and perfused with a phosphate-buffered saline solution (PBS). One or both unfixed eyes were then removed for the project described here, and further tissue samples were then taken for use in other procedures. Body and brain weights were recorded for each animal. The cornea and vitreous humor were removed, and the eye was post-fixed for 10–15 min in formal–saline and then dissected as rapidly as possible from the choroid layer. The retina was then post-fixed for 2 h in 10% formal–saline. At this point, the retina was rinsed in PBS, flat-mounted and drawn to calibrate for further shrinkage. The retina was then remounted on a non-gelatinized slide in distilled water, and cleared with dimethylsulphoxide overnight, rinsed, covered with glycerol, and cover-slipped. The retina was redrawn at the time of counting for calibration of shrinkage, considering principally the distance between the fovea and optic disc, the area examined in this study. The retinal area, and the retinal hemi-circumference from the nasal to the temporal ora serrata that intersected both the fovea and optic disc, were measured from the flat-mounted retinas (drawn before and after slide mounting) using a digitizing tablet. The photoreceptors were counted at a constant magnification of $\times 1500$, but the sampling area varied with retinal location, reflecting differential cell density. For cones, a 256 μm^2 sampling area was used for the foveal centre (to 0.1 mm); a 1024 μm^2 sampling area for additional locations up to 2 mm from the fovea; and a 6400 μm^2 area for regions outside 2 mm of the fovea. For rods, the sampling area was always 1024 μm^2. Cells were counted at 0.05 mm intervals up to 0.1 mm from the foveal centre, up to 2 mm at 0.25 mm intervals (0.08 mm intervals in *Saguinus*), and at 1 mm intervals more peripherally. Photoreceptor numbers were then summed over the various sampling regions.

3. RESULTS

(a) *Scaling of individual and modality-specific cortical areas*

This study examines the extent to which different structural or functional areas are represented equally across species for a particular neocortical size. The method of independent contrasts is used to control for phylogenetic relatedness (Felsenstein 1985; Pagel 1992; Purvis & Rambaut 1995). The hypothesis that either primary visual, auditory, somatosensory and motor areas, or their aggregates, appear in equal proportion in brains of different sizes is equivalent to the hypothesis that the regression slopes of primary and total neocortical areas do not significantly differ from one another. The slope of the regression of log V1 is significantly different from S1 ($n = 22$, $p = 0.021$) and from A1 ($n = 13$, $p = 0.011$). In addition, the slope of the regression of total visual cortex is significantly different from total auditory cortex ($n = 24$, $p = 0.011$). No other contrasts were significantly different. The inclusion or removal of the monotremes had no effect on these results. Figure 2 contrasts the relative slopes of primary and total neocortical areas of a single modality with total cortical area, with intercepts of the lines adjusted for easier visualization of relative slope.

(b) *Effects of visual niche on cortical area scaling*

'Visual niche' refers to an animal's activity pattern. The platypus and the echidna were not used in this analysis, as

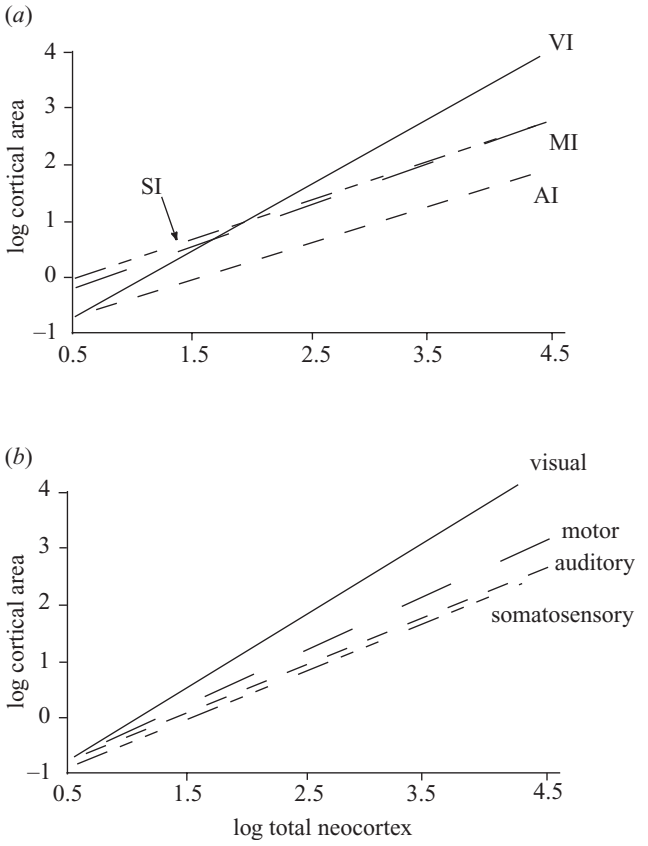

Figure 2. Cortical area scaling. Contrasts of log primary neocortical areas A (primary somatosensory, S1; primary visual, V1; primary motor, M1; and primary auditory, A1) and log totals of auditory, somatosensory, motor and visual neocortical areas B Log(primary neocortical areas A) and log totals of auditory, somatosensory, motor and visual neocortical areas B are regressed on log(total neocortex size) (y-axis). The intercepts of the lines have been adjusted for easier visualization of the relative slope. The slopes for primary and total visual cortices are greatest. The slope of the regression of log V1 is significantly different from S1 ($n = 22$, $p < 0.021$) and from A1 ($n = 13$, $p < 0.011$). The slope of the regression of total visual cortex is significantly different from total auditory cortex ($n = 24$, $p < 0.011$). The equations and r^2 values are as follows: $V1 = 1.086x - 1.225$, $r^2 = 0.907$; $V_{tot} = 1.27x - 1.49$, $r^2 = 0.935$; $S1 = 0.664x - 0.292$, $r^2 = 0.794$; $SS_{tot} = 0.796x - 0.337$, $r^2 = 0.881$; $A1 = 0.697x - 1.075$, $r^2 = 0.919$; $A_{tot} = 0.895x - 1.363$, $r^2 = 0.93$; $M = 0.84x - 0.826$, $r^2 = 0.86$; $M_{tot} = 1.044x - 1.34$, $r^2 = 0.903$.

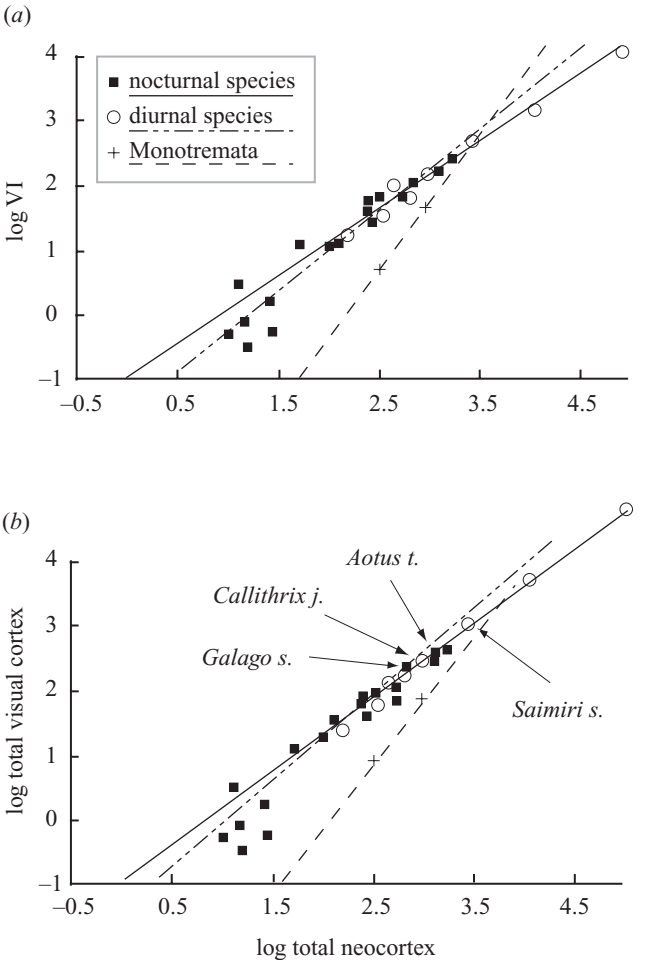

Figure 3. Visual cortical scaling in nocturnal and diurnal species. The regression slopes of V1 A and total visual cortex B for the 20 nocturnal and 8 diurnal species are plotted against total neocortex. Two important comparisons are highlighted in B, the nocturnal prosimian *Galago* and the diurnal New World monkey *Callithrix* of comparable cortex sizes, and the nocturnal owl monkey and the diurnal squirrel monkey, also of comparable cortex sizes. There is no significant difference between nocturnal and diurnal mammals in their visual cortical scaling, either in V1 or in all visual cortical areas; the regression plots are notable for their complete overlap. Diurnal V1, $y = 1.0485x - 1.0095$, $r^2 = 0.959$; nocturnal V1, $y = 1.2395x - 1.5015$, $r^2 = 0.923$; monotremata V1, $y = 2.1087x - 4.5928$; diurnal total visual, $y = 1.1536x - 1.0634$, $r^2 = 0.990$; nocturnal total visual, $y = 1.3566x - 1.6325$, $r^2 = 0.927$; monotremata total visual, $y = 2.0652x - 4.2837$.

their activities do not fit typical nocturnal and diurnal behaviour patterns, but rather vary with ambient temperature—although their data are plotted (figure 3) (Collins 1973; Griffiths 1978). Figure 3 plots the regression slopes of V1 (figure 3*a*) and total visual cortex (figure 3*b*) for the 20 nocturnal and eight diurnal species against total neocortex. Again, as measured by the method of independent contrasts, no significant difference appears between nocturnal and diurnal mammals in their visual cortical scaling—either in V1 or in all visual cortical areas. The regression plots themselves are notable for their complete overlap (with the possible interesting exception of the smallest-brained, nocturnal shrews). If diurnal animals devoted more cortex to vision, we would expect to see a 'grade shift' in these plots, with the diurnal regression line displaced upward but parallel to the nocturnal. Furthermore, no other contrast was significant: nocturnal animals did not possess more somatosensory or auditory cortex—either primary or total—as might be expected if they devoted more cortical areas to modalities of greater importance in the dark.

(c) *Rod and cone numbers in a sample of these species*

Shown in figure 4 are total rod and cone numbers for two rodent species and six primate species. The estimates of rod and cone numbers in the retinas of the common rat, the

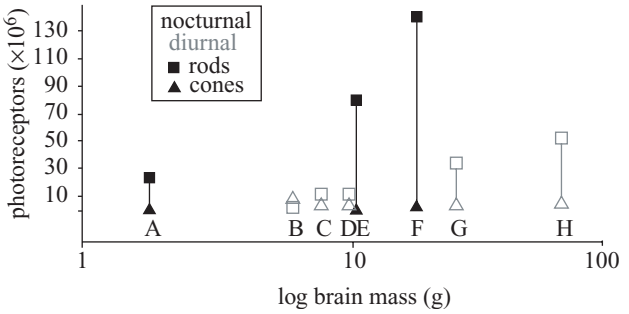

Figure 4. Numbers of rods and cones in nocturnal and diurnal species. Comparisons of total rod and cone numbers for a subset of species included in the cortical dataset. From left to right, species are A, *Rattus rattus*, B, *Spermophilus beecheyii*, C, *Callithrix jacchus*, D, *Saguinus m. niger*, E, *Galago garnetti*, F, *Aotus* sp., G, *Saimiri ustius*, and H, *Cebus apella*. The common rat (A) has eight times more rods than the much larger diurnal ground squirrel (B). The nocturnal owl monkey (F) has four times more rods than the diurnal squirrel monkey (G). The nocturnal galago (E) has about ten times more rods than the diurnal tamarin (D).

California ground squirrel and the galago are taken from the literature (DeBruyn *et al.* 1980; Hallet 1987; Kryger *et al.* 1998). The data from the New World primates are new and are presented in table 2 in electronic Appendix B. The most telling comparisons between nocturnal and diurnal mammals are those between species of comparable brain and body sizes. The nocturnal rat (A) has eight times more rods than the much larger diurnal ground squirrel (B). The nocturnal owl monkey (F) has four times more rods than the comparably sized squirrel monkey (G). Even more striking is the difference between the nocturnal galago and the diurnal tamarin retina, with near-identical body sizes. These robust differences are unaccompanied by any hints of the change in size in the fundamental morphological divisions of the neocortex (see figure 3).

4. DISCUSSION

(a) *Statistics and variability*

(i) *Data quality*

The difficulty of collecting comprehensive cortical maps in a wide variety of species necessarily limits the numbers of individual species used in our analyses. While the data we have analysed were not originally collected for the purpose of cross-species quantitative comparisons and, in some cases, the studies cited have included only one individual (as with the fat-tailed dwarf lemur, *Cheirogaleus medius*) or presented a generalized scheme of the neocortex, these collected data still show statistical predictability characteristic of other allometric studies (Stephan *et al.* 1981*a*; Frahm *et al.* 1984). For example, restricting our sample to only those animals (10 primates and the tree shrew) that intersect with those studied by Frahm *et al.* (1984) in their analysis of the volume of the area striata versus the volume of whole of the neocortical grey matter, and using the same technique of simple regression analysis, the results are very comparable. In the volumetric study, they found the following regression equation: relationship of log (area striata grey matter) $= -0.1274 + 0.7974$ log (neocortex grey area), $r^2 = 0.962$. We find log (V1 surface area) $= -0.3131 + 0.8328$ log (neocortex total surface area), $r^2 = 0.954$.

Since we are able to capture statistically significant differences both in the slope of scaling of V1 versus total cortical area, and also in the sum of all visual cortical areas versus total cortical areas, this increases our confidence in our ability to detect a difference, if present, between nocturnal and diurnal species. There is no hint of a trend that would discriminate nocturnal and diurnal groups if we had more or better data, nor excessive noise that is obscuring the relationship. In addition, we can demonstrate expected differences in the visual periphery in the same animals whose central visual structures are conserved.

The collection of species here is like other allometric studies in that primate species predominate, but with particular debt to the Kaas and Krubitzer laboratories we are fortunate also to include a number of other small mammals, including marsupials. The inclusion of these animals changes the regression equations in interesting ways, which bears further investigation with more species. For example, inclusion of the smaller mammals changes the simple regression of V1 surface area on total cortical area to positive allometry: $y = 1.0979x - 1.21$, $r^2 = 0.929$, and makes the area of the smaller human V1 a notable outlier, suggesting a 'grade shift' in either cortical or visual cortical scaling in primates. The observation that monotreme cortical areas scale unlike all those of other mammals adds a further distinction to their already atypical cortical organization.

(b) *Intrinsic variability in brain structures*

A perplexing feature in the understanding of brain size regulation is the report of remarkable individual variability in the size of cortical areas (and many features of visual system organization, to be discussed). This would seem to be in contradiction both with the very regular scaling observed in allometric studies and the claims for significant relationships to dietary or other niches with relatively minor differences in the size of cortical areas, determined from residual variation after either whole brain size or cortex size have been controlled for. This discussion is not concerned with the methodological problem of controlling for individual variability in allometric studies, and will assume that, for the most part, published allometric studies have managed to determine representative mean structure volumes for scaling work. Rather, we address the more theoretical question of how are we to understand the importance of structure sizes if individual members may occasionally differ from one another in the relative sizes of brain parts by as much as a factor of 2 (Van Essen *et al.* 1984; Purves & LaMantia 1993; Adams *et al.* 2003).

First, it is important to establish the appropriate quantitative context. Since allometric studies typically concern themselves with very large ranges of brain sizes, expressed logarithmically, large individual variations must first be considered in this context. It is often difficult to interpret standard measures of central tendency using these scales. For example, in a moderately sized sample, a normally distributed variable typically has a total sample range of about five times its standard deviation. In the Stephan dataset, we analysed previously where this assumption held, cortex volumes ranged over a factor of 142 000 (Finlay & Darlington 1995). Though absolute brain size accounted for over 96.3% of the variation in the volume of

the cortex in this sample at any particular brain size, sample range as computed above is a factor of about 2.5, tiny with respect to 142 000. This size difference, however, is impressive to any anatomist looking at a cortex twice as large as another (Finlay & Darlington 1995).

What kinds of variations are reported at the individual level, within species? The best information comes from a number of studies of the primate visual system, particularly the rhesus macaque. Van Essen *et al.* (1984) have found individual animals whose primary visual cortex differed by a factor of two or more. Similarly, the variability of the human visual cortex exceeds substantially the variability of the entire cortex (Gilissen & Zilles 1995). There are no studies, to our knowledge, of the variability at the individual level of the number and arrangement of cortical areas. The primate fovea also presents peculiar variability. Most individuals have roughly comparable high cone central densities, but 1 in 5 to 1 in 10 have an obviously aberrant, much reduced foveal specialization (Hendrickson & Kupfer 1976; Franco *et al.* 2000). The distribution of photopigments in the fovea is far from regular in humans, and shows individual variations that range from 10/90 to 90/10 L (long wave length): M (medium wave length) ratios (Roorda & Williams 1999). Conversely, the volume and number of cells in the lateral geniculate in primates are highly predictable, showing deviations of less than 4% across individuals (Williams & Rakic 1988; Blasco *et al.* 1999).

Few of these observations have as yet been tracked onto individual variation in visual capacity, and it would be interesting to do so. There is reason to believe, however, that, with the exception of variations in cell density in the visual periphery that directly affect acuity, the basic processing of the visual system will be robust to wide variations in number of neurons in interconnecting populations, owing to the stabilizing effect of processes like activity-dependent stabilization in early development (Finlay & Pallas 1989; Pallas & Finlay 1989, 1991; Rezak *et al.* 2003), or compensatory perceptual processes in adulthood (see, for example, Neitz *et al.* 2002).

These three pieces of evidence—regular allometric scaling, individual variability and developmental plasticity—all converge on the same interpretation. The regularity of major components of neural allometric scaling, best predicted by cross-mammalian developmental constraints apparently independent of function, suggests that 'mismatches' of neural ratios or of typical structure–function allocations must be a regular, compensated phenomenon in mammalian evolution. The existence of large individual differences in brain structure sizes, unaccompanied by flagrant disabilities, tells the same story about individual development, as do innumerable instances of developmental plasticity. Thus, particularly for central structures, structure and function may not be uniquely linked at neurogenesis, and neural resources may often be allocated to new functions as necessary. The fact that we have named a structure 'visual' cortex (because that is typically what it does) does not prevent it from becoming 'Braille' cortex, when circumstance permits.

(c) *General visual system scaling and niche*

(i) *Rods and cones*

That rod numbers are elevated and cone numbers are depressed, in nocturnal animals compared with diurnal animals, is neither a new nor a controversial observation (Hughes 1977; Ross 2000). The interesting observation is the magnitude of the retinal change in closely related animals of comparable brain size, a 4–8-fold difference in rod numbers—clear proof of the malleability of photoreceptor number in the retina given environmental pressure (see figure 4). The conservation of central structure, in the face of widely varying photoreceptor complements, extends past the gross measure of cortical area: contrasting nocturnal and diurnal primates, the 'cell-type' complement of the retina is also conserved across niche (Silveira *et al.* 1994; Yamada *et al.* 1996). Work is presently in progress to determine what differences, in the timing and rate of neurogenesis of nocturnal and diurnal primates, produce these major differences in retinal composition.

(ii) *Striate and extrastriate cortex*

The finding that V1 scales vary predictably with respect to the entire neocortex, and with a significantly different slope, has been described previously for haplorhine or strepsirhine primates and some insectivores (Frahm *et al.* 1984). While debate persists as to whether all primate species (notably humans; Gilissen & Zilles 1995) scale similarly, the bulk of evidence suggests conservation of scaling for the primary visual cortex (Frahm *et al.* 1984; Stevens 2001). The present analysis extends this observation of predictability both to non-primates and to the total visual cortex devoted to visual analysis. Primary visual cortex scales at a rate higher than other primary sensory areas, but lower, for example, than prefrontal cortex (see below), which scales with steep 'positive allometry', occupying a predictably and proportionately larger component of total cortical volume (Jerison 1997; Semendeferi *et al.* 2002). Parietal cortex, containing many of the areas included in our 'total visual cortex' sample also scales steeply with brain size. Overall, these results suggest that each morphologically identifiable component of neocortex has unique scaling properties, independent of niche.

There are many conflicting claims about whether visual niche (or dietary niche) predicts cortical area; most of the prior studies have examined only V1, and not the volume of extrastriate visual areas. This literature presents massive problems for between-species comparisons, principally because of the different ways that many have used to 'norm' animals, and thus for understanding what constitutes a 'small' or 'large' visual cortex. The central relationship, which is the most useful for comparing studies, is that identifiable brain regions scale very predictably with brain size, and that brain regions, including cortical areas, each scale with a different slope. In addition, primates have relatively more cortices, at any brain size, than do insectivores, rodents and bats (and other radiations). Therefore, if the percentage of cortical area occupied by V1, in a collection of animals of various body and brain sizes (some of which are primates), is given without accounting for absolute brain size or primate status, the results cannot be interpreted without reference to what would be expected allometrically. More unfortunately still, interpretations will

be systematically biased, in that the largest-brained animals typically examined are predominantly primates, and diurnal.

Krubitzer & Kaas (1990) have analysed the relationships among eight cortical areas in four species of primates, and report that these areas occupy a larger percentage of the cortex in diurnal monkeys than in the nocturnal owl monkeys and galago. They report that diurnal primates have proportionally more cortex devoted to the primary visual area (VI), the secondary visual area (VII), the dorsolateral visual area (DL) and the mediotemporal visual area (MT). In this case, as described above, the confounds of niche, brain and body size in primates prevent determination whether the differences are those that would have been expected allometrically.

There are, however, several studies where allometric scaling was done. These have been unable to show any relation of V1 or other cortex size to 'activity niche' owing to the same data limitations (even though these studies are often cited as if they did). Barton *et al.* (1995) state that 'there are not enough diurnal strepsirhines in the sample to analyse separately, and there is only one nocturnal haplorhine genus'. They go on to show positive correlations between visual system structures, and negative correlations between olfactory and visual system structures. In this study, they state that among diurnal primates, greater relative visual cortex size is associated with frugivory and also social group size.

Among primates, the principal contrast group to frugivores is folivores, which, overall, have smaller brains. The argument is offered that the detection of fruits requires greater detection capacities from the visual system. Nevertheless, the factual basis for a comparatively greater visual challenge posed to fruit-eaters than leaf-eaters is unclear—recent evidence suggests, for example, that the use of trichromatic vision may be optimal in distinguishing shades of green and brown in unripe foliage as much or more, as it may help discriminate fruit (Regan *et al.* 1998, 2001; Dominey & Lucas 2001). The howler monkey, *Alouatta* sp., a folivore, is so far the only New World primate described with obligatory trichomacy, and which also possesses a highly unusual fovea of doubled cone density (Franco *et al.* 2000). Frugivory is associated with larger brain size, particularly neocortex size. The general basis for an overall larger brain has often been hypothesized to be the greater cognitive requirement necessary to use fruit as a resource—memory for seasons and places, navigation to the places, manipulation and extraction of the fruit, and even the social aspects of finding and sharing seasonally abundant resources. Simple detection of fruit, though essential, is only one part of a larger capacity. If greater relative visual cortex size is not an artefact of uncorrected positive allometry with respect to whole cortex size, its association with frugivory would, if anything, weaken the association of 'visual' cortex with vision, not strengthen it.

(iii) *Regression*

At the extreme, in fossorial animals whose eyes have regressed (Bronchti *et al.* 2002), morphologically identifiable V1 may diminish in volume, and the changed scaling of V1 has been noted in these animals (Frahm *et al.* 1984). No animals of this type appear in the dataset used here. A candidate developmental mechanism for the 'loss' of V1 in this case exists, independent of neurogenesis, as the cortical region, which typically becomes the recognizable V1, changes its attributes when it loses thalamic input. Very early removal of the eyes (*in utero* in primates) causes the partial degeneration of the lateral geniculate nucleus (Finlay *et al.* 1986; Rakic *et al.* 1991). Less innervation of the cortex by the lateral geniculate body causes the specification events dictated through the thalamus to be lost or changed, including the organization of layer 4, and establishment of intrinsic and extrinsic connectivity (Niederer *et al.* 1997). Therefore, it is probably that regression of the eyes is the direct cause of reduction in V1 size.

(d) *A parallel case in the frontal cortex*

The identical comparison problem of distinguishing proportionate from disproportionate growth has plagued the understanding of the role of frontal cortex in primate evolution. Along with parietal cortex, frontal cortex scales regularly with increasing brain size, but at a slope much higher than the primary sensory and motor areas, a fact that has been known for quite some time (Uylings & van Eden 1990; Jerison 1997) but republished recently using imaging information (Semendeferi *et al.* 2002). If the relative percentage of frontal cortex is contrasted between any great ape (or any mammal with an absolutely smaller brain) and human, the human percentage will be greater. This percentage, however, is precisely what we should expect in a primate of our brain size. It does not follow from this predictability, however, that whatever functions the frontal cortex permits have not been selected for in the hominid line, or that the frontal cortex is either useless or unduly blessed with 'emergent' properties. Its percentage prominence must simply be understood in the context of coordinated brain evolution, not as a singularity.

Claims about particular social adaptations in primates, and their linkage with particular cortical regions (area 10; area 13), are aspects of the continuing debate about the modular or distributed nature of cortical evolution (Semendeferi *et al.* 1998, 2001; Holloway 2002). Several characterizations of frontal cortex exist, from a mosaic of areas each concerned with a particular spatio-temporal computation (Goldman-Rakic 1995) to a region with distributed, overlapping abilities for a wide variety of problems involving working memory, selective attention and inhibition, and weighing of past contingencies (Duncan & Owen 2000). The relationship between brain allometry and specialized behaviours is grist for this debate, but great care should be taken to understand behaviour at its actual complexity, not the laboratory tokens of it.

(e) *Decoupling of morphology and function*

There is no *a priori* reason that a nocturnal visual system should require less neural volume than a diurnal visual system (if the nocturnal computational problem is perhaps harder, it could be argued that it should require more). Our central observation reveals that it appears to require neither less nor more, in the face of greatly different photoreceptor distributions. Nevertheless, the assumption that greater usage has a direct correlation with the size of corresponding neural systems is prevalent in the literature (Barton 1996, 1998; Barton & Harvey 2000). It is perplexing that subtle differences in visual requirements for frugivory versus folivory should be associated with differences in visual system organization, while major differences to accommodate nocturnality and diurnality should not. As noted above, niche, brain size

and cortex size are difficult to dissociate in primates. It may be, therefore, that the observations are confounded by conserved scaling phenomena unrelated to function. Alternatively, frugivory and a certain visual cortical organization might be necessarily related, but with selection on gross brain size as the only means of inducing the required detail in brain organization. For example, in a study of 'dexterity' in animals whose dexterity ranged from hooves to hands, brain area devoted to control of the forelimbs showed a high positive correlation with dexterity, but the area devoted to the forelimbs was, in turn, accounted for entirely by total neocortex size (Nudo & Masterton 1988).

The hypothesis that visual cortices differ between nocturnal and diurnal mammals may yet be true, but for aspects of cortex other than simple size. Evolution might well act on variables like cell number or density, receptive field size, axonal arborization, myelination or basic cell physiology. As these data are not available for a large number of species, we have worked with the largest dataset we could build that is closest to function: the sizes of cortical areas devoted to visual processing, as defined principally by thalamic input.

Several new imaging and other functional studies, however, suggest that we may have been over-impressed by the major thalamic input to an area when cortical regions were named. Functions may play more freely over the cortical matrix specified early in development than we have imagined, perhaps through long-range intracortical connectivity (Calvert *et al.* 1997; Gao & Pallas 1999; Bavelier *et al.* 2001; Bronchti *et al.* 2002; Elbert *et al.* 2002). In the adult, our understanding of cortico-cortical connectivity is limited, but recent work shows that connections may be widespread and fail to conform to traditional hierarchies and notions of connectivity (Falchier *et al.* 2001; Rockland & Ojima 2003). Thalamocortical connections also show a distributed nature with a matrix of superficially projecting cells not confined to the intralaminar nuclei, which may serve to bind sensory experiences by connecting multiple cortical and thalamic areas (Jones 1998). On the whole, the findings that such broad structure–function matches in the cortex exist implies that the neocortex is not a piecemeal collection of areas, each with its own discrete function, but is a generalized processing device.

This work was supported by a joint CNPq no. 910149/96-98 and NSF Int-9604599 to L.C.L.S. and B.L.F., and NSF grant IBN-0138113 to B.L.F. P.M.K. was supported by a NIH training grant T32 MH19389 and an NEI training grant 5T32 EY07135. We thank Dr José Augusto P.C. Muniz, head of the Centro Nacional de Primatas during this study, for offering his resources, and Walter Augusto de Carvalho, Francinaldo Lobato Gomes, Cezar Akiyoshi Saito and Justin Crowley for research assistance.

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