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Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores

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CONTENTS

SUMMARY

How brains have evolved in response to particular selection pressures is illuminated by ecological correlates of differences in brain structure among contemporary species. The focus of most comparative studies has been on the overall size of brains relative to body size, hence ignoring the ways in which selection operates on specific neural systems. Here we investigate evolutionary radiations in the size of visual and olfactory brain structures within three orders of mammals: primates, bats and insectivores. The comparative relationships within these three orders show both similarities and differences. After removal of the allometric effect of overall brain size, the sizes of different structures within each sensory modality are positively correlated in all three orders. Correlations between visual and olfactory structures, however, are negative in primates, negative but non-significant in insectivores, and positive in bats. In both primates and insectivores, nocturnal lineages tend to have larger olfactory structures than do diurnal or partly diurnal lineages, and among the primates diurnal lineages have larger striate visual cortexes. Hence the apparent trade-off between vision and olfaction in primates seems to be related to the divergence of nocturnal and diurnal forms. However, negative correlations between visual and olfactory structures were also found when nocturnal strepsirhines and diurnal haplorhines were analysed separately, suggesting that ecological variables in addition to activity timing may be significant. Indeed, there were also associations with diet: frugivory was associated with enlargements of the geniculostriate visual system in diurnal primates, enlargements of olfactory structures in nocturnal primates, and possibly enlargements of both in bats. Further ecological associations were found within insectivores: aquatic lineages had smaller olfactory structures than in their non-aquatic counterparts, and fossorial lineages had smaller optic nerves than in non-fossorial forms. We conclude that activity timing, diet and habitat have each played a role in the evolutionary radiation of mammalian sensory systems, but with varying effects in the different taxa. Some of the associations between ecology and sensory systems suggest alternative explanations for correlates of overall brain size, which have in the past commonly been interpreted in terms of selection on intelligence.

1. INTRODUCTION

An animal's brain constructs sensory representations that guide its interaction with the environment. Thus, sensory systems are an integral part of the adaptive complex of a species, and they will evolve in different ways in lineages facing different ecological pressures (see, for example, Ali 1978; Finlay & Sengelaub 1981). In part, these ecological pressures are the broad characteristics of the animal's niche (whether, for example, it is aquatic or terrestrial, nocturnal or diurnal), but finer details of behavioural ecology are also likely to shape sensory systems. For example, efficient foraging depends on the ability to detect potential foods rapidly and to discriminate between them using proximate cues to profitability and toxicity; these cues depend on the type of food exploited, so that we may expect to find correlations between sensory systems and dietary specialization.

In this paper we are concerned with explaining evolutionary radiations of visual and olfactory systems, as indexed by the volume of relevant brain structures.

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Table 1. *List of primate species with ecological information*

(Ecological information compiled from Clutton-Brock and Harvey (1977), Smuts *et al.* (1987), Wright (1992) and Ganzhorn *et al.* (1985). D, diurnal; N, nocturnal; Fol, folivorous, F/O, frugivorous/omnivorous, In, strictly insectivorous/faunivorous.)

	activity timing	diet	percentage fruit
Alouatta spp.	D	Fol	31
Aotus trivirgatus	N	F/O	46
Ateles geoffroyi	D	F/O	77
Avahi laniger	N	Fol	0
Callicebus moloch	D	F/O	53
Callimico goeldii	D	F/O	–
Callithrix jacchus	D	F/O	14
Cebuella pygmaea	D	F/O	–
Cebus spp.	D	F/O	17
Cercocebus albigena	D	F/O	64
Cercopithecus ascanius	D	F/O	50
Cercopithecus mitis	D	F/O	54
Cheirogaleus major	N	F/O	–
Cheirogaleus medius	N	F/O	–
Colobus badius	D	Fol	22
Daubentonia madagascariensis	N	F/O	–
Erythrocebus patas	D	F/O	76
Galago senegalensis	N	F/O	–
Galagoides demidoff	N	F/O	19
Gorilla gorilla	D	Fol	3
Hylobates lar	D	F/O	60
Indri indri	D	Fol	–
Lagothrix lagothricha	D	F/O	79
Lepilemur mustelinus	N	Fol	5
Loris tardigradus	N	F/O	15
Macaca mulatta	D	F/O	63
Microcebus murinus	N	F/O	–
Miopithecus talapoin	D	F/O	54
Nasalis larvatus	D	Fol	39
Nycticebus coucang	N	F/O	60
Otolemur crassicaudatus	N	F/O	16
Pan troglodytes	D	F/O	66
Papio cynocephalus	D	F/O	32
Perodicticus potto	N	F/O	75
Petterus fulvus	D	F/O	29
Pithecia monachus	D	F/O	82
Propithecus verreauxi	D	F/O	40
Pygathrix nemaeus	D	Fol	–
Saguinus geoffroyi	D	F/O	56
Saguinus oedipus	D	F/O	–
Tarsius spp.	N	In	0
Varecia variegata	D	F/O	–

This partly involves the identification of ecological correlates, such as have been found in a few other studies of sensory systems. Healy & Guilford (1990) showed that olfactory bulbs are larger in nocturnal than in diurnal birds. Gittleman (1991) suggested that aquatic habits might explain the reduced olfactory bulbs of otters relative to other carnivores. Barton & Dean (1993) found an association between predatoriness and the development of the tectospinal tract in mammals. We extend these studies by examining patterns within three mammalian orders for which extensive data exist: primates, bats and insectivores. Previous studies (e.g. Baron 1981; Baron *et al.* 1983;

Table 2. *List of bat species with dietary classifications*

(Diet based on information in Walker (1964) and Eisenberg (1981). F, frugivorous/nectarivorous; P, predatory.)

species	diet
Ametridia centurio	F
Ardops annectens	F
Artibeus jamaicensis	F
Artibeus lituratus	F
Asellia tridens	P
Balionycteris maculata	F
Brachyphylla cavernarum	F
Carollia perspicillata	F
Casinycteris argynnis	F
Chaerophon leucostigma	P
Cheiromeles torquatus	P
Chiroderma villosum	F
Cynopterus brachyotis	F
Cynopterus horsfieldii	F
Desmodus rotundus	P
Diaemus youngi	P
Eonycteris spelaea	F
Eptesicus fuscus	P
Eptesicus melanopterus	P
Eumops pertis	P
Glossophaga soricina	F
Hipposideros armiger	P
Hipposideros bicolor	P
Hipposideros galeritus	P
Hypsignathus monstrosus	F
Kerivoula papillosa	P
Lonchorhina aurita	P
Macroglossus lagochilus	F
Macroglossus minimus	F
Micronycteris megalotis	F
Mimon crenulatum	P
Molossus major	P
Monophyllus luciae	F
Myotis bechsteinii	P
Myotis myotis	P
Myotis natteri	P
Natalus tumidirostris	P
Noctilio labialis	P
Noctilio leporinus	P
Nyctalus noctula	P
Nycteris javanica	P
Penthetor lucasi	F
Phyllostomus discolor	F
Phyllostomus hastatus	P
Pteronotus davyi	P
Pteropus lylei	F
Rhinolophus hipposideros	P
Rhogeessa parvula	P
Rhynchiscus naso	P
Rousettus aegyptiacus	F
Saccopteryx bilineata	P
Saccopteryx leptura	P
Scotophilus temminckii	P
Sphaeronycteris toxophyllum	F
Sturnira lilium	F
Tadarida plicata	P
Taphozous melanopogon	P
Thyroptera tricolor	P
Trachops cirrhosus	P
Tylonycteris pachypus	P
Tylonycteris robustula	P
Uroderma bilobatum	F
Vampyrops helleri	F
Vampyrum spectrum	P

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Stephan *et al.* 1984*a*,*b*; Frahm *et al.* 1984) have outlined broad phylogenetic trends but, while suggesting some adaptive explanations for these, they have not analysed ecological correlates controlling for the effects of phylogeny or overall brain size (see Methods). In addition to ecological correlates, however, we are also concerned with correlated evolution among sensory systems: if different systems, such as vision and olfaction, to some extent represent evolutionary alternatives associated with different niches, specialization in one might be traded off against reduction in the other, leading to negative correlations across lineages. Alternatively, if different systems, or different parts of the same system, have interrelated functions, the size of the associated structures should be positively correlated.

2. METHODS

Volumetric measurements of visual and olfactory brain structures were obtained from published sources. Primate data (olfactory bulbs, accessory olfactory bulb, piriform lobe, striate cortex, lateral geniculate nucleus, optic tract and optic nerve) come from Stephan *et al.* (1981, 1984*b*). Bat data (olfactory bulbs, superior colliculus, and lateral geniculate nucleus – dorsal, lateral and inter-geniculate leaf) come from Stephan & Pirlot (1970), Stephan *et al.* (1974), and Baron (1977). Insectivore data (olfactory bulbs, piriform lobe, lateral geniculate nucleus, optic nerve and optic tract) come from Stephan *et al.* (1981, 1984*a*, *b*). These sources also provide information on overall brain size (volume) and body size (mass). Ecological data on primates were obtained from Clutton-Brock & Harvey (1977), expanded and updated from Smuts *et al.* (1987). Ecological classifications of bats and insectivores follow Walker (1964) and Eisenberg (1981). Lists of the species investigated and the ecological data are given in tables 1–3. Any ecological classification is likely to conceal a certain amount of variation within categories, particularly where classifications must be dichotomous as required by our method. In the diet categories, for example, species assigned to the same category often differ significantly in the exact nature and proportions of their diets. However, the key point here is that the categories can differentiate sister taxa in biologically meaningful ways. For example, the 'folivorous' primates (table 1) are not all strictly folivorous, but they are all relatively specialized for dealing with high-fibre photosynthetic and structural plant parts com-

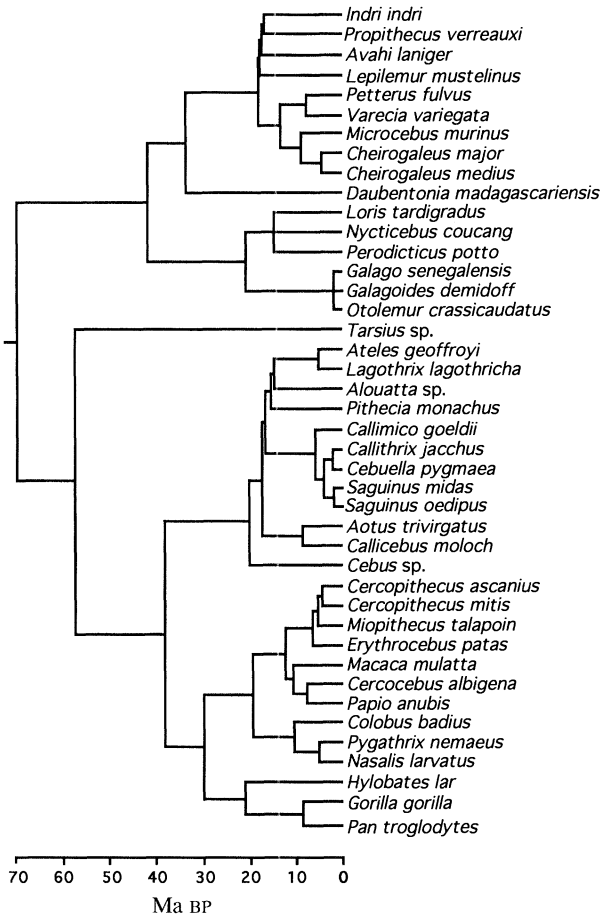

Figure 1. Phylogeny of primates used in the analyses. The topology and estimated dates of divergence were compiled from the following sources: Baba *et al.* (1980); Caccone & Powell (1989); Carroll (1988); Chiarelli (1980); Coppenhaver *et al.* (1988); Dene *et al.* (1980); Dutrillaux (1988); Ford (1986); Groves & Eaglen (1988); Martin (1990); Miyamoto & Goodman (1990); Natori (1988); Rosenberger & Strier (1989); Ruvolo (1988); Sarich & Cronin (1980); Shultz (1986); Schwartz (1986); Strasser & Delson (1987); Wayne *et al.* (1991). Since carrying out this study a new phylogeny for the whole primate order has been compiled, (Purvis 1995), differing slightly from the one used here; partial re-analysis with the new phylogeny does not indicate any substantive differences in the results.

Table 3. *List of insectivore species with ecological information*

(Ecological classifications based on Walker (1964), Eisenberg (1981) and Churchfield (1986). D, diurnal/cathemeral; N, nocturnal.)

species	aquatic?	fossorial?	activity timing
Aethechinus algirus	no	no	N
Chlorotalpa stuhlmanni	no	yes	D
Chrysochloris asiatica	no	yes	D
Crocidura occidentalis	no	yes	N
Crocidura russula	no	yes	N
Desmana moschata	yes	yes	N
Echinops telfairi	no	no	N
Erinaceus europaeus	no	no	N
Galemys pyrenaicus	yes	yes	N
Hemicentetes semispinosus	no	yes	D
Hemiechinus auritus	no	no	N
Limnogale mergulus	yes	no	—
Microgale cowani	no	no	D
Micropotamogale lamottei	yes	no	N
Neomys fodiens	yes	no	D
Nesogale dobsoni	no	no	D
Nesogale talazaci	no	no	D
Oryzoryctes talpoides	no	yes	—
Potamogale velox	yes	no	D
Setifer setosus	no	no	N
Solenodon paradoxus	no	no	N
Sorex aranaeus	no	yes	D
Sorex minutus	no	no	D
Suncus murinus	no	no	N
Talpa europaea	no	yes	D
Tenrec ecaudatus	no	no	N

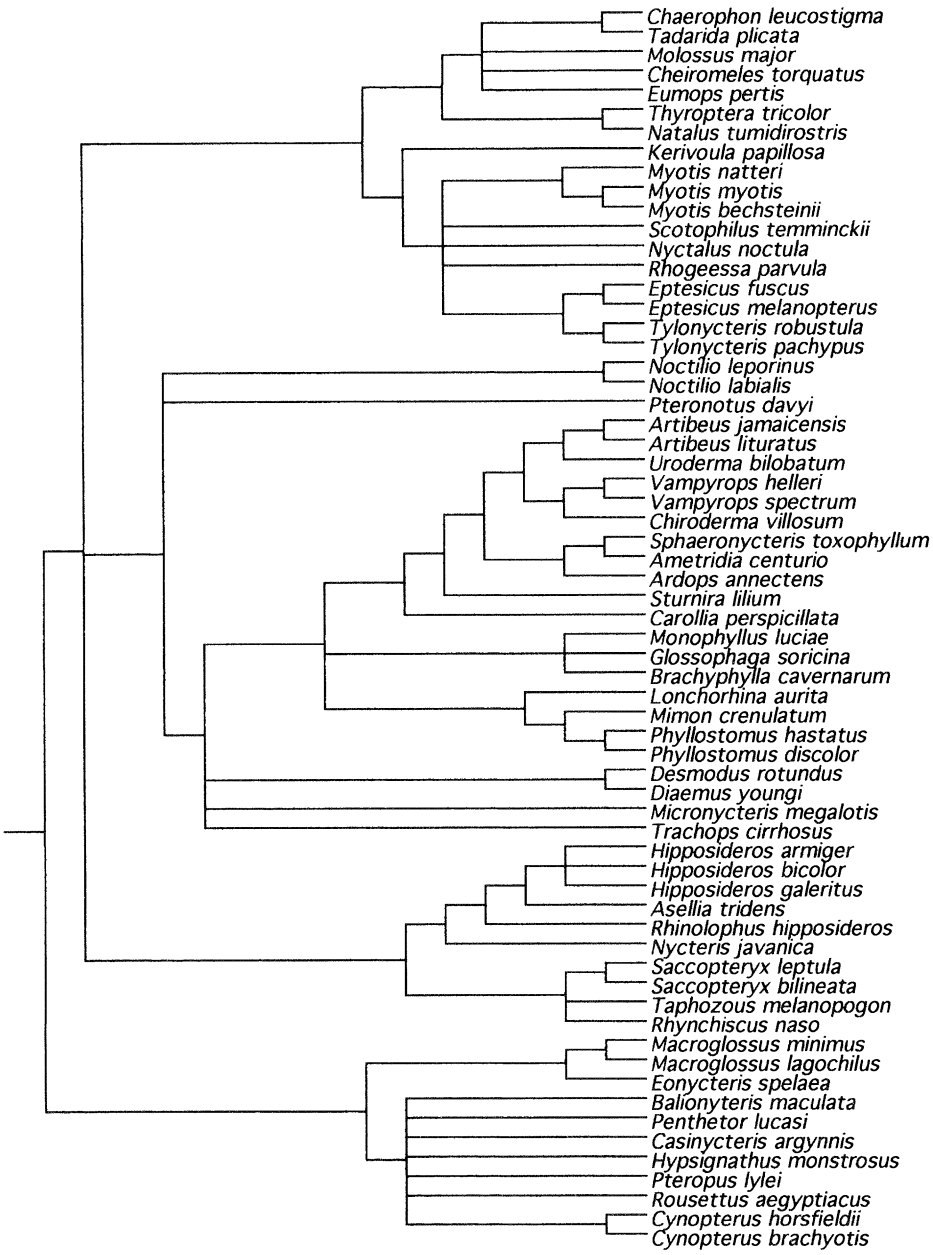

Figure 2. Phylogeny of bats used in the analyses. Branch lengths not available; topology compiled from: Findley (1972); van Valen 1979; Eisenberg (1981); Hill & Harrison (1987); Honeycutt & Sarich (1987); Owen (1987); Robbins & Sarich (1988); Baker *et al.* (1989); Corbet & Hill (1991).

pared with the 'frugivore–omnivores', whose diets tend to include large proportions of ripe fruit and flowers. The main effect of imprecision in these classifications will be conservative: the increase in error variance will tend to result in underestimation of the strength of statistical relationships.

The comparative method for investigating adaptation works by identifying multiple independent cases of correlated evolution between biological traits, or between such traits and ecology (see, for example, Harvey & Pagel 1991). Thus it is not enough simply to show statistical associations based on the use of species or other taxonomic units as individual data points, because similarity due to common regimes of selection may be confounded by similarity due to phylogenetic propinquity. Instead, it is necessary to demonstrate that traits have evolved together repeatedly in separate lineages. It is the number of evolutionary events, not the total number of taxa, that is relevant here. We use the C.A.I.C. computer package (Purvis 1991), which implements Pagel's (1992) variant of Felsenstein's (1985) method of independent comparisons. In brief, the method uses phylogenetic information to produce contrasts in character values, which represent independent evolutionary events. For continuous variables, the contrasts can be scaled to have the same variance and analysed with standard methods of correlation and regression. The effect on a dependent variable of a dichotomous ecological variable, such as activity timing (nocturnal as opposed to diurnal), can also be examined; the program computes differences in the value of the dependent variable for each evolutionary transition between ecological states. If the resulting contrasts are predominantly either positive or negative, this suggests an evolutionary association between the continuous dependent variable and the

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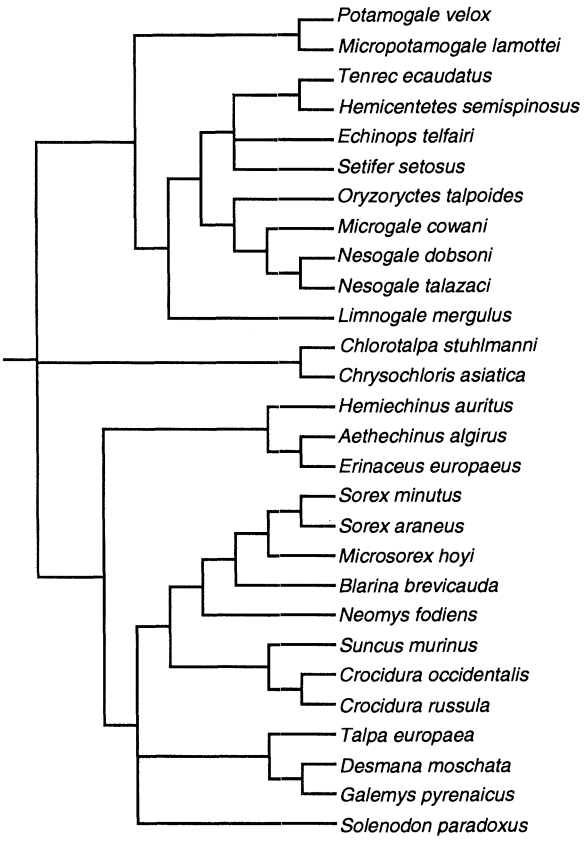

Figure 3. Phylogeny of insectivores used in the analyses. Branch lengths not available; topology compiled from: Eisenberg (1981); George (1986); Corbet (1988).

dichotomous ecological variable. Where branch length data are available (in our case, in the primates), the difference scores can be scaled to equalize variances, permitting the use of parametric statistics such as *t*-tests to evaluate significance. Otherwise, non-parametric tests such as the sign test are more appropriate, but where sample sizes are too small to use the latter, we use *t*-tests as a guide to significance with the proviso that the assumption of homogenous variances may not be met. At present there is no satisfactory way of examining the effects of a particular categorical variable while controlling statistically for the effects of others; here we note any obvious cases where categorical ecological variables are confounded with one another, and check whether removing the contrasts affected in this way makes any difference to the results.

The phylogenies used in these analyses, and the sources of information on which they are based, are shown in figures 1–3. Recent evidence (Novacek 1992; Bailey *et al.* 1992) suggests that despite controversy (Pettigrew 1986), the Chiroptera represent a monophyletic group, and we treat them as such here. The C.A.I.C. package scales the contrast scores for the variables by using branch lengths, the length of time since bifurcation of each branch of the phylogeny. For primates, we found sufficient published information (genetic distances, etc.) to estimate branch lengths directly (see figure 1). Branch lengths for bats and insectivores were estimated with an algorithm based on the topology of the phylogeny, and assuming a gradualist evolutionary model (see Harvey & Purvis 1991). All continuous variables were log-transformed as demanded by the method (see Harvey & Purvis 1991). We controlled for the effects of overall brain size by regressing independent contrasts in the size of each structure on contrasts in the size of the rest of the brain (total brain volume minus the aggregate volume of all sensory structures investigated). Where dichotomous ecological variables were involved, we removed the effects of brain size by first estimating the phylogenetically unbiased allometric exponents with C.A.I.C., and then using these to set regression slopes and calculate residual values for each species before generating independent contrasts.

3. RESULTS

(*a*) *Primates*

Contrasts in the size of each sensory structure are highly correlated with contrasts in the size of the rest of the brain (table 4). To examine variations in the size of structures independent of overall brain size, we computed residuals from the regressions on the size of the rest of the brain. These residuals are uncorrelated with body mass (olfactory bulb residuals, $r = 0.08$; accessory olfactory bulb residuals $r = 0.15$; piriform lobe residuals, $r = 0.02$; striate cortex residuals, $r = 0.11$; LGN residuals, $r = 0.12$; optic tract residuals, $r = 0.02$; optic nerve residuals, $r = 0.05$; sample sizes as in table 4; in all cases $p > 0.05$). Correlations between the residuals are shown for the whole sample of primates as well as for nocturnal strepsirhines and diurnal haplorhines separately in table 5*a–c* (there were not enough diurnal strepsirhines in the sample to analyse separately, and there is only one nocturnal haplorhine genus: the owl monkey *Aotus*). Correlations between structures within a sensory modality (i.e. between olfactory structures or between visual structures; table 5*a*, *b*) are all positive: seven of nine correlations for the complete dataset are significant, as are 7 out of 18 correlations considering nocturnal strepsirhines and diurnal haplorhines separately. Thus, functionally related subsystems have evolved together within primates generally, and also within the two sub-clades. In contrast, all 12 correlations between olfactory and visual structures (table 5*c*) are negative when calculated across the complete dataset (binomial

Table 4. *Relationships between size of individual sensory structures and size of the rest of the brain in primates*

(The r^2 and significance values were obtained by regressing independent contrasts in the size of each sensory structure on contrasts in the size of the rest of the brain (brain volume minus the aggregate volume of these sensory structures).)

	r^2	p	n
olfactory bulb	0.56	< 0.0001	39
accessory olfactory bulb	0.41	0.0004	27
piriform	0.95	< 0.0001	39
visual cortex	0.94	< 0.0001	31
LGN	0.93	< 0.0001	31
optic nerve	0.67	< 0.0001	23
optic tract	0.91	< 0.0001	17

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Table 5. *Relations among sensory structures in primates, controlling for overall brain size*

(Correlations were computed between residuals from the regressions of contrasts in structure size on contrasts in the size of the rest of the brain. In each case, correlations were calculated for the whole sample of primate species, as well as separately for the subsamples of nocturnal strepsirhines and diurnal haplorhines. The signs of Pearson correlation coefficients and their associated probabilities are given in each case, with the signs of non-significant correlations being given in parentheses. Sample sizes shown are for the whole dataset (all species).)

(*a*) *Olfactory structures*

	accessory olfactory bulb ($n = 27$)	piriform lobe ($n = 39$)
olfactory bulb ($n = 39$)		
all species	+, 0.04	+, < 0.001
nocturnal strepsirhines	+, 0.03	+, < 0.001
diurnal haplorhines	(+), 0.14	(+), 0.39
accessory olfactory bulb ($n = 27$)		
all species	.	(+), 0.25
nocturnal strepsirhines	.	(+), 0.13
diurnal haplorhines	.	(+), 0.30

(*b*) *Visual structures*

	lateral geniculate nucleus ($n = 31$)	optic nerve ($n = 23$)	optic tract ($n = 17$)
striate visual cortex ($n = 31$)			
all species	+, < 0.001	+, 0.05	+, 0.05
nocturnal strepsirhines	+, < 0.01	(+), 0.23	(+), 0.41
diurnal haplorhines	+, 0.04	(+), 0.19	(+), 0.15
lateral geniculate nucleus ($n = 31$)			
all species	.	+, 0.05	(+), 0.09
nocturnal strepsirhines	.	(+), 0.07	(+), 0.48
diurnal haplorhines	.	(+), 0.43	+, 0.01
optic nerve ($n = 23$)			
all species	.	.	+, < 0.01
nocturnal strepsirhines	.	.	+, < 0.001
diurnal haplorhines	.	.	+, < 0.01

(*c*) *Olfactory and visual structures*

	olfactory bulb	accessory olfactory bulb	piriform lobe
striate visual cortex			
all species	(−), 0.25	(−), 0.17	(−), 0.34
nocturnal strepsirhines	(−), 0.48	(+), 0.63	(−), 0.51
diurnal haplorhines	(+), 0.81	(−), 0.59	(+), 0.99
LGN			
all species	−, < 0.01	(−), 0.51	−, 0.04
nocturnal strepsirhines	(−), 0.59	(−), 0.26	(−), 0.39
diurnal haplorhines	(−), 0.09	(−), 0.36	(−), 0.77
optic tract			
all species	(−), 0.09	(−), 0.14	−, 0.04
nocturnal strepsirhines	−, 0.02	(−), 0.17	−, 0.03
diurnal haplorhines	−, 0.04	−, 0.05	(+), 0.79
optic nerve			
all species	(−), 0.15	−, 0.05	(−) 0.06
nocturnal strepsirhines	(−), 0.08	(−), 0.09	−, 0.03
diurnal haplorhines	(−), 0.06	(+), 0.87	(−), 0.15

$p < 0.001$), with four of these significant at $p < 0.05$. Thus, there appears to have been an evolutionary trade-off between specialization in olfactory systems and specialization in visual systems. This may be partly due to differentiation of diurnal and nocturnal forms; however, the patterns recur within nocturnal strepsirhines and diurnal haplorhines (although perhaps less markedly in the latter, where only 8 out of

12 correlations are negative, with two significant at $p < 0.05$), suggesting that other ecological factors may also be involved.

The small number of evolutionary transitions in activity timing limits the analysis of associations between this trait and the size of sensory structures: with four possible contrasts between nocturnal and diurnal lineages, olfactory bulbs are in all cases larger in nocturnal lineages ($t = 2.35$, d.f. $= 3$, $p = 0.10$), whereas striate visual cortexes are in all cases larger in diurnal lineages ($t = 2.98$, d.f. $= 3$, $p = 0.05$). Only three contrasts could be computed for the optic tract, owing to a lack of data, each contrast showing larger optic tracts in diurnal than in nocturnal lineages ($t = 2.78$, d.f. $= 2$, $p = 0.11$). Differences in other structures are not exclusively in one or other direction (piriform lobe, $t = 0.19$, d.f. $= 3$, $p = 0.86$; lateral geniculate nucleus, $t = 1.51$, d.f. $= 3$, $p = 0.23$; optic nerve, $t = 1.50$, d.f. $= 3$, $p = 0.23$).

Diet is another potentially relevant ecological factor, because the sensory requirements for locating and selecting appropriate foods will depend on the type of food exploited. In particular, among diurnal species (i.e. where light levels permit) frugivore–omnivores may rely more heavily on vision, especially colour vision, than do folivores (Jacobs 1981), to make fine discriminations according to fruit ripeness and toxicity. For similar reasons, olfaction may also be less important for folivores than for frugivore–omnivores, particularly in nocturnal species, where the use of vision is restricted. Within diurnal haplorhines, folivores do indeed have significantly smaller striate visual cortexes ($t = 5.21$, d.f. $= 3$, $p = 0.01$) and lateral geniculate nuclei ($t = 3.53$, d.f. $= 3$, $p = 0.04$) than do frugivore–omnivores. Furthermore, among diurnal strepsirhines, the brown lemur *Petterus fulvus* is more folivorous than the ruffed lemur *Varecia variegatus* (Smuts *et al.* 1987; Wright 1992), and also has a smaller visual cortex and smaller lateral geniculate nucleus relative to overall brain size. There are no diet-related differences among diurnal haplorhines in the size of optic nerves ($t = 1.45$, d.f. $= 4$, $p = 0.22$), which project to non-cortical visual structures as well as to the geniculostriate system, or in olfactory structures (olfactory bulb, $t = 0.71$, d.f. $= 3$, $p = 0.53$; piriform lobes, $t = 1.09$, d.f. $= 3$, $p = 0.35$). Unfortunately, similar analyses could not be performed for nocturnal strepsirhines owing to a lack of data, but the quantitative measures of diet available for many primate species allow a more fine-grained analysis. Here we have used multiple regression through the origin to examine the relationship between the percentage of the diet comprising fruit and the size of each sensory structure, controlling for overall brain size. In diurnal haplorhines, the percentage of fruit in the diet is not significantly related to any of the structures tested (olfactory bulb, partial $F = 1.79$, d.f. $= 1,17$, $p = 0.19$; piriform lobe, partial $F = 1.10$, d.f. $= 1,17$, $p = 0.31$; striate visual cortex, partial $F = 1.15$, d.f. $= 1,12$, $p = 0.30$; lateral geniculate nucleus, partial $F = 1.16$, d.f. $= 1,12$, $p = 0.24$; optic nerve, partial $F = 0.07$, d.f. $= 1,12$, $p = 0.79$). In nocturnal strepsirhines, however, the percentage of the diet consisting of fruit is positively correlated with the relative size of olfactory structures (olfactory bulbs, partial $F = 13.96$, d.f. $= 1,5$, $p = 0.03$; piriform lobe, partial $F = 38.29$, d.f. $= 1,5$, $p < 0.01$), but not with the relative size of visual structures (striate cortex, partial $F = 0.60$, d.f. $= 1,5$, $p = 0.49$; lateral geniculate nucleus, partial $F = 0.67$, d.f. $= 1,5$, $p = 0.47$; optic nerve, partial $F = 0.01$, d.f. $= 1,5$, $p = 0.91$). In summary, among diurnal haplorhines (and perhaps diurnal primates generally) folivores have relatively small geniculostriate visual systems, whereas among nocturnal strepsirhines the percentage of fruit in the diet is positively correlated with relative olfactory structure size.

Table 6. *Relations between size of individual sensory structures and size of the rest of the brain in bats*

	r^2	p	n
olfactory bulb	0.85	< 0.0001	16
LGN (dorsal)	0.50	0.0014	16
LGN (ventral)	0.38	0.0086	16
LGN (inter-geniculate)	0.64	< 0.0001	16
colliculus	0.84	< 0.0001	16

(*b*) *Bats*

As in the primates, contrasts in the size of each sensory structure are highly correlated with contrasts in the size of the rest of the brain (table 6). Again, residuals from the regressions on the size of the rest of the brain are uncorrelated with body mass (olfactory bulb residuals, $r = 0.13$; LGN_d residuals, $r = 0.02$; LGN_v residuals, $r = 0.07$; LGN_e, $r = 0.13$; colliculus residuals, $r = 0.13$; in all cases $n = 16$, $p > 0.05$). Correlations between the residuals are shown in table 7. All three correlations between separate nuclei of the LGN are positive, with one significant. Similarly, but in contrast to the primates, correlations between the olfactory bulb and LGN are also positive, with two out of three significant. Correlations between the colliculus, which has multiple sensory inputs (see, for example, Dean *et al.* 1989), and the other structures are negative but non-significant.

Investigation of ecological correlates of bat sensory systems is hampered by a paucity both of data and of evolutionary transitions in major ecological categories. Some bats do forage in daylight, but these are taxonomically concentrated within two families, the Pteropodidae and Emballonuridae, and in any case insufficient data are available to confidently classify as diurnal or 'cathemeral' (active by night and day) many of the species in our dataset. Similarly, frugivory may have independently evolved only twice, in the Pteropodidae and the Phyllostomatidae (although other dietary classifications are possible, these mainly involve distinctions between different types of prey, such as insects and vertebrates, and it is not obvious what relevance these would have for vision and olfaction; differences in the mechanisms of echolocation might be expected, but we lack the detailed neuroanatomical data to test this). However, it is

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Table 7. *Relations between sensory structures in bats, controlling for overall brain size*

(Correlations were computed as in table 5, $n = 16$. LGN, Lateral geniculate nucleus (subscripts d, v and i refer to dorsal part, ventral part and inter-geniculate leaf respectively).)

	LGN_d	LGN_v	LGN_i	superior colliculus
olfactory bulb	(+), 0.83	+, 0.03	+, 0.02	(−), 0.25
LGN_d	.	(+), 0.46	(+) 0.47,	(−), 0.17
LGN_v	.	.	+, < 0.0001	(−), 0.24
LGN_e	.	.	.	(−), 0.33

Table 8. *Relations between size of individual sensory structures and size of the rest of the brain in insectivores*

	r^2	p	n
olfactory bulb	0.83	< 0.0001	22
piriform	0.89	< 0.0001	22
optic tract	0.96	< 0.0001	8
optic nerve	0.52	0.0450	7
LGN	0.92	0.0002	7

encouraging, given the suggestions already made for primates, that both contrasts between frugivorous and non-frugivorous lineages reveal olfactory bulbs and lateral geniculate nuclei (all three parts) that are, relative to the size of the rest of the brain, larger in the frugivorous lineages. In fact these structures are also larger relative to body size, so the result cannot be due simply to the rest of the brain being smaller in frugivores (owing to less dependence on echolocation, for example). This fits neatly with the observation that the Pteropodidae locate ripe fruit by smell (Walker 1964), and additionally suggests a role for vision.

(*c*) *Insectivores*

As with primates and bats, contrasts in the size of each sensory structure are highly correlated with contrasts in the size of the rest of the brain (table 8). Residuals from regressions on the size of the rest of the brain are uncorrelated with body mass (olfactory bulb residuals, $r = -0.08$; LGN residuals, $r = -0.12$; piriform residuals, $r = 0.22$; optic tract residuals, $r = 0.42$; optic nerve residuals, $r = -0.19$; sample sizes as in table 6; in all cases $p > 0.05$). Correlations between the residuals are shown in table 9. All four correlations within sensory modalities are positive, two significantly so. All six correlations between visual and olfactory structures are negative (binomial $p = 0.03$), although none of these correlations is significant.

Insectivores have radiated into a wide variety of ecological niches (Walker 1964; Eisenberg 1981). We do not have sufficiently fine-grained data on diet to make clear distinctions, but we can distinguish species according to aquatic habit, activity timing (diurnal/crepuscular or cathemeral versus completely nocturnal) and fossoriality. Unfortunately, there are insufficient data on visual structures to examine ecological associations, except for the optic nerve and fossoriality. Following Gittleman's (1991) finding that otters have reduced olfactory bulbs compared with non-aquatic carnivores, all of the four contrasts here reveal smaller olfactory bulbs and piriform lobes in aquatic than in non-aquatic insectivore lineages. It is not possible to obtain a significant result using a two-tailed binomial test when $n < 6$ (table D in Siegel 1956), but using *t*-tests, with the proviso that the assumption of homogenous variances may not be met, the difference between aquatic and non-aquatic lineages is significant both for the olfactory bulbs ($t = 8.28$, d.f. = 3, $p < 0.01$) and for the piriform lobe ($t = 5.02$, d.f. = 3, $p = 0.02$). For activity timing, six out of seven contrasts show larger relative size of olfactory bulbs and piriform lobes in nocturnal than in diurnal or cathemeral lineages (binomial $p = 0.12$). The one exception for both structures is the contrast that is confounded by aquaticness; within the Talpidae, the nocturnal and aquatic desman *Galemys* has smaller olfactory structures than the cathemeral and non-aquatic mole *Talpa* (whose greater fossoriality may make no difference; see below). The remaining six, unidirectional, contrasts (binomial $p = 0.03$) include one between two aquatic species that differ in activity timing (among tenrecs, the cathemeral/crepuscular *Potamogale velox* as opposed to the nocturnal *Micropotamogale lamottei*). Thus, both aquaticness and activity timing appear to be correlated with olfactory structure size, with aquaticness perhaps exerting the more powerful effect. Finally, it appears that fossoriality is associated with small optic nerves: all four contrasts show smaller optic nerves in fossorial than in non-fossorial lineages ($t = 3.98$, d.f. = 3, $p = 0.03$). No clear trend is apparent for the olfactory structures in relation to fossoriality: four of the six contrasts for the

Table 9. *Relationships among sensory structures in insectivores, controlling for overall brain size*

(Correlations were computed as in table 5, sample sizes as in table 8.)

	piriform	optic tract	optic nerve	LGN
olfactory bulb	+, < 0.001	(−), 0.46	(−), 0.80	(−), 0.26
piriform	.	(−), 0.93	(−), 0.83	(−), 0.30
optic tract	.	.	(+), 0.07	(+), 0.09
optic nerve	.	.	.	+, 0.03

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olfactory bulbs and three of six contrasts for the piriform lobe show smaller relative size in fossorial lineages (binomial $p > 0.5$ in both cases). Removal of the one contrast confounded by activity timing (the cathemeral and fossorial *Hemicentetes semispinosus* as opposed to the nocturnal and non-fossorial *Tenrec ecaudatus*) does not change the situation significantly (three of five contrasts negative in both cases).

4. DISCUSSION

Our results suggest both similarities and differences in the patterns of adaptive radiation of sensory systems within the three mammalian orders investigated. In all three, the relative size of separate structures within a sensory modality were positively correlated. Good evidence for evolutionary trade-offs (hence negative relationships) between structures in different modalities was found only in the primates, although there was also a suggestive trend in the same direction within insectivores. Among primates, the recurrence of negative correlations within nocturnal strepsirhines and within diurnal haplorhines implies that activity timing is not the only ecological variable associated with the evolutionary radiation of these systems. It is possible that some of the strepsirhines are not strictly either nocturnal or diurnal, but cathemeral (Engqvist & Richard 1991; Wright 1992), so there could still be variance in activity timing within the 'nocturnal' strepsirhine subsample (cathemerality is less likely in the 'diurnal' haplorhines, but see Engqvist & Richard 1991). In bats, vision and olfaction appear to have co-evolved positively, perhaps reflecting divergence between frugivorous/nectarivorous and predatory lineages; here, the main trade-off may be between vision and olfaction on one hand and echolocation on the other. Eisenberg (1981) implies that a similar trade-off has occurred in the evolution of tenrecs, which use echolocation and have small eyes. We do not at present have the necessary data on brain parts involved specifically in echolocation to test this idea for bats or insectivores. It is known that predatory bats have greatly enlarged deep (auditory) layers of the superior colliculus (Covey *et al.* 1987), and the colliculus was the one structure negatively, though non-significantly, correlated with the other sensory structures. Clearly, a better test of the echolocation versus vision/olfaction idea requires data on the separate collicular layers.

The clearest evidence for ecological associations comes from primates and insectivores. In primates, activity timing and diet appear to have been important. Among insectivores, activity timing and aquaticness are associated with differences in the relative size of olfactory structures, whereas fossoriality is associated with smaller relative optic nerve size. Sample sizes were in most cases small, but these results do tend to fit predictions, based both on results that have been obtained in other taxa and on what is known about how particular senses are used by animals and how they are constrained by ecological factors. Thus, the associations between the size of olfactory structures and activity timing in primates and insectivores accord with Healy & Guilford's (1990) finding that olfactory bulbs are larger in nocturnal than in diurnal birds. The association no doubt reflects the constraints that low light levels place on vision (see, for example, Suthers 1978), and hence the premium placed on olfaction for foraging and perhaps social interaction. Similarly, the association between small olfactory structures and aquatic habits within the insectivores accords with Gittleman's (1991) finding that olfactory bulbs are smaller in otters than in non-aquatic carnivores, and here the constraints on function are obvious. Markedly reduced visual systems have been described for a number of fossorial mammals (see, for example, Lund & Lund 1965; Finlay & Sengelaub 1981; Cooper *et al.* 1993), and our results show that the association is present within a single order, the insectivores; although we have data for only one structure, the optic nerve, it seems likely in this case that smaller optic nerves reflect generally reduced visual systems, as described by Cooper *et al.* (1993) for a rodent, the mole rat *Spalax ehrenberghi*. Finally, associations between sensory systems and diet have been proposed before (see, for example, Suthers 1978), for example in relation to the evolution of colour vision and frugivory (Jacobs 1981, 1993; Savage *et al.* 1987; Allman & McGuinness 1988), but such associations have not previously been demonstrated rigorously with comparative data. Fruits advertise their ripeness and toxicity by colour and smell, and frugivores must be able to make fine discriminations. We found that diet is correlated with the size of visual structures among diurnal primates and with the size of olfactory structures among nocturnal primates. These results accord with the fact that colour vision can only operate where light levels are sufficient (see below), placing the onus on olfaction for frugivores that forage at night.

The general association between small visual systems and low light levels (nocturnality, fossoriality) may conceal some adaptive specialization in the types of vision used. At least some nocturnal mammals (including nocturnal primates) have large eyes and large pupils with consequently increased light-gathering capability, and almost spherical lenses that concentrate the available light onto a small area of the retina (Suthers 1978). In many species there is a *tapetum lucidum*, which reflects light back through the retina and may substantially increase the sensitivity of the eye (Suthers 1978). In fact there may be a trade-off between different channels within the visual system: the emphasis in nocturnal mammals seems to be on contrast sensitivity and the detection of movement, and in diurnal species on acuity and colour vision (Suthers 1978; Jacobs 1981, 1993). Associated with this divergent specialization are differences in the density of retinal rod cells (high in nocturnal species) and cone cells (high in diurnal species). For example, the owl monkey (*Aotus trivirgatus*), a nocturnal haplorhine, lacks a distinct fovea and has a lower overall cone density and poorer colour vision than do its diurnal counterparts among the haplorhines, and similarly, nocturnal strepsirhines have lower overall cone densities than do diurnal strepsirhines (Jacobs 1981). A recent study suggests that non-foveal cone densities are

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similar in nocturnal and diurnal primates (Wikler & Rakic 1990), implying that the overall differences are largely the product of a highly developed fovea in diurnal species. We would predict corresponding differences throughout the visual system; within the geniculostriate system, the magnocellular subsystem has high contrast sensitivity and low resolution, dealing with movement detection, depth perception and the analysis of dynamic form, whereas the parvocellular subsystem has low contrast sensitivity and high resolution, dealing with colour perception and the analysis of fine details (Livingstone & Hubel 1987; van Essen *et al.* 1992; Zeki 1993). We would therefore expect a relative enlargement of the magnocellular system in nocturnal lineages and of the parvocellular system in diurnal lineages, particularly frugivores. Such differences should also be reflected in differences in the corresponding specialized target areas in prestriate visual cortex (see van Essen *et al.* 1992; Zeki 1993). In fact, there is some evidence for a higher percentage of magnocellular components in the geniculostriate system of nocturnal primates, and a relative expansion of parvocellular layers in diurnal species (Hassler 1966; Shulz 1967 (cited in Stephan *et al.* 1984*b*); Allman & McGuinness 1988). Areas of prestriate cortex receiving input from magnocellular layers of LGN and implicated in visual tasks such as the perception of direction of moving stimuli (area V_5, or MT) are present in all primates and therefore associated with the primitive nocturnal–predatory condition, whereas other areas are present only in the predominantly diurnal haplorhines (Allman 1987; Allman & McGuinness 1988). Specialization for movement detection in nocturnal primates may be partly explained by their generally predatory habits, and it has previously been shown that another pathway implicated in rapid prey-capture type responses to moving objects, the tectospinal tract, has co-evolved with predatory habits in mammals, including primates (Barton & Dean 1993).

More comparative data on the separate visual pathways and their functionally specialized target areas in prestriate cortex would help in interpreting the overall differences in striate cortex volume. It seems likely, for example, that high acuity and the analysis of form with colour are computationally more expensive and therefore require larger neural nets and more brain tissue than do high contrast sensitivity and movement detection. This would explain associations between the gross volume of striate cortex and ecological factors such as activity timing and diet in more specific terms than simply general differences in 'visualness'. Furthermore, given that cortical areas involved in visual processing compose up to about half the total volume of each hemisphere (van Essen *et al.* 1992), it is also possible that visual specialization in diurnal frugivores, together with olfactory specialization in nocturnal frugivores, help to explain previously reported correlations between frugivory and large brain size relative to body size, correlations that have usually been interpreted in terms of selection on more general cognitive abilities associated with foraging strategies (see, for example, Eisenberg & Wilson 1978; Clutton-Brock & Harvey 1980; Mace *et al.* 1980; but see also Deacon 1990). Similarly caused associations between encephalization and activity timing would not necessarily follow from this, however, because our results suggest that in nocturnal lineages smaller visual systems are at least partly compensated for by larger olfactory bulbs.

The reduction in visual abilities in highly fossorial mammals such as moles is more marked than in those that are simply nocturnal. Finlay & Sengelaub (1981) note that among the rodents, a variety of 'mole-like' fossorial forms with regressive eyes have appeared independently. In one, the blind mole rat (*Spalax ehrenberghi*), eyes are tiny and subcutaneous, visual pathways are regressed and incomplete, and there appears to be no ability to form a visual image (Cooper *et al.* 1993). It is suggested by Cooper *et al.* that the visual system is instead specialized for photoperiodic regulation of circadian activity rhythms. Not all fossorial mammals show such extreme reduction; the European mole (*Talpa europea*) can perceive moving objects and use visual cues for orientation (reviewed in Stephan *et al.* 1984*b*). We found no evidence of compensatory increases in olfactory structures of fossorial insectivores; in this case, touch may be the sensory system where the compensation is to be found – the same also applies to aquatic insectivores such as the otter shrews (Burton 1962). Once again, the divergence in sensory systems may help to explain a previously reported ecological correlate of overall brain size; an association between fossoriality and small brains relative to body size has been interpreted as an association between environmental complexity and intelligence (Mace *et al.* 1980; Harvey & Krebs 1990). Given our results, however, the possibility that the differences in overall brain size are simply a result of selection on visual systems should be investigated.

Comparative studies of the overall size of the brain relative to body size have made little headway in the effort to understand brain evolution, because of the lack of consistency across taxa in ecological correlates (Harvey & Pagel 1988), the problems with body size as the allometric reference variable (Deacon 1990), and the structural and functional heterogeneity of the brain itself (Harvey & Krebs 1990). Looking beneath the surface of the brain at individual neural systems shifts the emphasis away from a one-dimensional focus on overall size and 'intelligence', with its emphasis on progressive evolution, and towards evolutionary radiations of the mammalian brain in response to specific ecological demands. The data we have analysed begin to shed light on the evolutionary radiations of mammalian sensory systems. We need to look at patterns within more groups, rodents potentially providing a rich source of data on the neurobiological implications of invading particular niches (Finlay & Sengelaub 1981). We also need to look at auditory and tactile structures, to get a more complete picture of sensory specialization in these groups. Finally, a more detailed understanding of selection pressures and specializations requires data on functionally specific subsystems. For example, our analyses of primate visual cortex examined gross

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volumetric differences, yet in the macaque monkey there are 305 pathways connecting 32 cortical visual areas, comprising 10 levels of visual processing (van Essen *et al.* 1992). Comparative analysis at this level of neurobiological detail may reveal much about how brains have evolved.

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