

Natural selection of mammalian brain components

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The debate about whether the brain and accompanying cognitive architecture were designed by natural selection or by some other process originated with Alfred Russel Wallace and Charles Darwin. Today, this debate is no longer about vitalism versus mechanism, as it was for Wallace and Darwin, rather it is between the adaptationist and developmental constraints accounts of internal brain organization. New work by de Winter and Oxnard rules out the possibility that developmental constraints are the sole explanation for mammalian brain evolution. Moreover, it appears that the internal organization of the mammalian brain is adapted to specific ecological and ethological niches.

Contrary to Charles Darwin's hypothesis¹ that natural selection shaped the brains and minds of all animals (including humans), Alfred Russel Wallace² proposed that some other agent or process primarily influenced the mental faculties of humans. Today, debates over natural selection and the human brain deal less with 'vitalism'³, but instead are concerned with the possibility that adaptation and natural selection shaped mammalian brain components independently of developmental constraints.

According to the 'developmental constraints hypothesis' of comparative mammalian neuroanatomy, brain components increased predictably in size, both ontogenetically and phylogenetically, in concert with the entire brain⁴. On the 'adaptationist' side of the debate are those who believe that brain components were shaped independently by natural selection, just like any other organ⁵. Recently, this debate has been resolved in a multi-dimensional comparative study of mammalian brain volumes⁶. de Winter and Oxnard⁶ investigated the brain component volume data from 363 species of primate, bat, insectivore, tree and elephant shrew^{7,8} that had been previously used to support a developmental constraints hypothesis⁴. In the reanalysis⁶, the authors provide evidence that corroborates Barton and

Harvey's finding⁵ that mammalian brain evolution is characteristically 'mosaic' rather than 'concerted' within orders (i.e. structurally related nuclei evolved together regardless of other nonstructurally related areas). Mosaic brain evolution contrasts with the less probable, but commonly held belief that the whole brain increased in size for nonadaptive reasons via concerted evolution. Furthermore, de Winter and Oxnard⁶ begin to unravel the various ethological and ecological causes of mosaic brain evolution in mammals.

Here, I detail the three principal components that account for 85% of the information in de Winter and Oxnard's principal components analysis (PCA)⁶. Each order is clearly demarcated, illustrating that each one differs uniquely in terms of internal brain proportions. Primates, bats and insectivores are the most clearly differentiated, dispersing in almost orthogonal directions (i.e. the primates and insectivores dispersions are linked via some bat lineages). Tree and elephant shrews occupy their own distinct locations in the brain data space. All three orders show examples of convergent evolution of internal brain components (i.e. structural proportions) between lineages that have been separated from each other for between 30–60 million years. Importantly, brain component convergences echo morphological and lifestyle similarities between phylogenetically distant species.

Primate brains – locomotor convergences

Previous morphological studies of primate limbs suggest that they are specialized for particular locomotor styles. According to de Winter and Oxnard⁶, the analysis of internal brain proportions reflects the spectrum of locomotion in primates, and it appears that the internal brain proportions correspond to previous morphological studies of primate limbs⁹. The locomotor capacities range from hindlimb leaping, to quadrupedality, to forelimb arboreality to human bipedality, and clear cases of convergent evolution of brain components echo the previously found locomotor

convergences⁹. Specifically, the brain component data differentiate prosimians (plus marmosets and tamarins) from all cercopithecoid monkeys (including howlers and sakis). Spider monkeys *Ateles* spp., woolly monkeys *Lagothrix* spp. and apes are differentiated from humans.

There is evidence for evolutionary convergence of brain components. For example, New World prehensile-tailed spider and woolly monkeys have independently evolved an analogous forelimb-dominated, climbing–feeding complex that is considered to be a primarily hominoid locomotor adaptation. Specifically, these New World monkeys have internal brain proportions that are similar to those of their larger-brained Old World ape cousins.

In a second stage of the PCA, de Winter and Oxnard⁶ investigated the clusters of individual brain components that contributed to the dispersions of the species. Dispersions in the primate direction appear to reflect a concerted increase in internal brain proportions of neocortex, striatum, cerebellum and diencephalon relative to the medulla. These brain areas are tightly integrated into a distributed system (i.e. the functionally related component is spread across several different areas of the brain, such as the neocortex, striatum and the cerebellum) for voluntary motor control. The primate trend can be characterized as an expansion of areas governing increasing levels of flexible motor control and behaviour.

Bat brains – dietary niche convergences

The PCA revealed that the internal brain organization of bats (Chiroptera) is demarcated from that of primates and insectivores. Bats can be divided into micro- and megachiropterans (Fig. 1). Microchiropterans are found worldwide, except for the polar regions, navigate with echolocation, have short faces, well-developed tails and lack a claw on the second finger (e.g. *Macroderma gigas*). Megachiropterans are found in India, Africa, Asia and Australia, and have a claw on the second finger of each wing (e.g. *Nyctimene robinsoni*). Although some

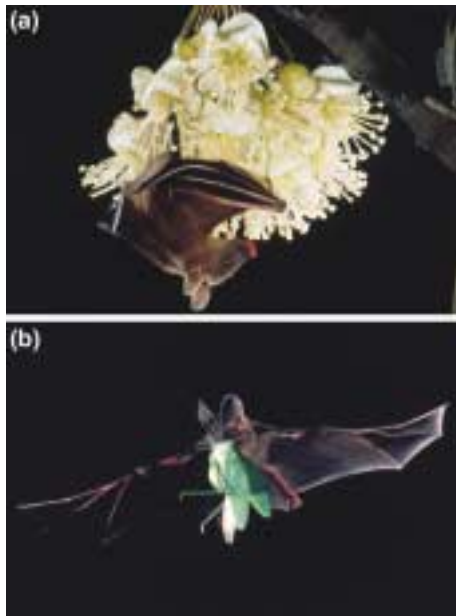


Fig. 1. Examples of Chiroptera. (a) A megachiropteran, Horsfield's short-nosed fruit bat *Cynopterus horsfieldi*, pollinating a durian flower. (b) A microchiropteran, D'Orbigny's round-eared bat *Tonatia sylvicola*, in flight carrying a katydid. Reproduced, with permission, from Merlin D. Tuttle, Bat Conservation International, Inc.

species of megachiropteran navigate using echolocation, those that forage for fruit are often large and navigate using light-sensitive eyes. It appears that phyllostomid microchiropterans (bats descended from insectivore ancestors) have radiated into a wide range of dietary niches in South America¹⁰. Brain components of frugivorous and nectivorous phyllostomid microchiropterans converge with their phylogenetically distant (and much larger-brained) megachiropteran relatives. However, insectivore phyllostomids, in spite of being close relatives of other phyllostomid frugivores, have brain components converging with those of insectivore microchiropterans.

Perhaps one of the most impressive neuroethological aspects of de Winter and Oxnard's paper⁶ is that the internal brain proportions of murinine Old World microchiropterans parallel those of New World plant-visiting microchiropterans, even though the consensus among field naturalists was that there were no Old World plant-visiting microchiropterans. Motivated by these findings of internal brain component convergences, the authors refer to unpublished field observations of others that document, for the first time, that some murinine Old World microchiropterans are nectivorous

– it is rare to predict behaviour based on analyses of internal brain components. Further convergences were found depending upon diet and the lifestyles related to acquiring food. Specifically, phylogenetically distant Old and New World microchiropterans that have independently evolved carnivorous lifestyles that require similar hunting strategies (e.g. acquiring surface-dwelling prey using echolocation) have also evolved similar internal brain proportions.

The variables associated with the dispersion from microchiropterans to megachiropterans in the data space are the expansion of septohippocampal limbic structures, the olfactory bulb and the palaeocortex relative to medulla. According to de Winter and Oxnard⁶, these dispersions suggest an elaboration of the capacities of frugivorous bats to form spatiotemporal maps of goal location¹¹ based on olfactory information provided by a patchy food source¹⁰.

Insectivore brains – 2D nocturnal niche convergences

Within the brain data space, there are separations between the insectivores of a semi-aquatic–burrowing lifestyle and the shrews and tenrecs that are surface dwellers. Nocturnal prosimians and microchiropterans (which are surface-gleaning hunters) are less demarcated from insectivores. Species that depend upon finding prey via tactile and olfactory cues in a 2D nocturnal niche have internal brain proportions that are similar to those of insectivores. Subsequently, insectivores are separated from other mammals that are able to use cross-modal information to exploit complex 3D niches.

The dispersal of species along the insectivore trend is associated with brain proportions of the functionally integrated septohippocampal system (i.e. hippocampus, septum, schizocortex, diencephalon and schizocortex), striatum and palaeocortex relative to neocortex. Insectivores have an interconnected and functionally integrated septohippocampal system that is designed to establish spatiotemporal location of desired goals. This particular system (and its links to the ventral striatum via the amygdala) has been referred to as a 'mesotelencephalic goal attainment system'¹¹. Subsequently, moving away from tenrecs and shrews on the periphery of the insectivores, the brain proportion data space suggests an

expansion of the neocortex relative to the mesotelencephalic goal attainment system. In addition, there is a similar expansion of the midbrain relative to the medulla. The insectivore expansion of neocortex and midbrain relative to the medulla is orthogonal to the primate neocortical (and linked motor structure) expansion. Because the midbrain has visual and auditory structures, the neocortex and midbrain expansions of the insectivores support the idea that there has been an elaboration in mammals of neural capacities to integrate multimodal information to create perceptual representations of increasingly complex 3D niches⁶.

Future directions

The de Winter and Oxnard paper⁶ supports the growing literature from independent research groups that suggests a mosaic evolution of mammalian brain structure^{5,12}. It is apparent that a uniform developmental constraint was not an overriding influence on mammalian brain evolution. Internal reorganizations of the brain are not simply size related. Increases in functionally related brain components occur along different axes in separate orders. For example, both bats and primates that are frugivorous are highly encephalized compared with insectivores, but this is due to a proportional expansion of different neural systems in each of those orders. This suggests that brain structures with functional and anatomical links evolved independently of other structures.

Future work should explore mosaic brain evolution in cetaceans and birds. One study of internal brain components in bottlenose dolphins *Tursiops truncatus* and common dolphins *Delphinus delphis* found that cerebellum volumes were larger than in primates (including humans) in spite of having similarly sized brains¹³. These findings from aquatic mammals are consistent with the expansion of brain components independently of strictly allometric processes. Timmermans *et al.*¹⁴, investigating mosaic brain evolution in birds, found that, in 17 avian taxa, the neostriatum–hyperstriatum ventrale complex could have a similar role as that of the primate neocortex in behavioural flexibility¹⁴. Future comparative research in birds, cetaceans and primates should be performed with attempts to correlate social transmission capacities or aspects of the social environment with brain components.

A contentious issue in de Winter and Oxnard's paper⁶ is the degree to which the primate line is unique in reflecting 'an increase in voluntary over more stereotyped control of behaviour'. de Winter and Oxnard⁶ could be misconstrued as supporting a model of 'lower organisms' being simple reflex automata. Alternatively, Menzel and Giurfa¹⁵ have suggested that insects (like most other organisms) have evolved flexible information-processing capacities (e.g. central integrators connecting domain-specific modules) to adapt to their particular environment. It is unlikely that de Winter and Oxnard would disagree with the idea of evolved mechanisms mediating flexibility across several lineages, because they endorse that, rather than a single evolutionary progression in 'general intelligence', different 'intelligences' most probably evolved independently in different ethoecological contexts. Indeed, de Winter and Oxnard (pers. commun.) do not support the lower organism or 'reflex automaton' viewpoint of animal cognition. Studies, such as that by de Winter and Oxnard, contribute towards a future

resolution of the debate between Darwin¹ and Wallace² over the degree to which human and nonhuman cognitive capacities have been shaped by natural selection.

Acknowledgements

I thank Natasha Crewdson, Chris Moore and Charles E. Oxnard for helpful comments on this article. This work was supported by the Natural Sciences and Engineering Research Council of Canada and an Isaak Walton Killam Memorial Postgraduate Scholarship.

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For your eyes only? The role of UV in mate choice

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A proliferation of experiments emphasizing the importance of the near-ultraviolet (UV) in avian mate choice has led to the proposal that this might be used exclusively by birds to signal to each other without alerting UV-insensitive mammalian predators. However, a new study suggests that information offered in the UV is no more 'special' than that offered in other wavebands.

Most avian species tested to date have revealed visual sensitivity to wavelengths of 315–400 nm, which is the near-ultraviolet (UV, specifically UV-A) part of the spectrum. Explanations for this sensory ability have ranged from the potential use of UV in orientation and foraging to a role in social and sexual signalling¹. It is the role of UV in sexual signalling, and in mate choice in particular, that has been most intensively scrutinized. Strong evidence for the use of

UV during avian mate assessment has led to the speculation that the evolution of UV vision in birds could have been driven by the need for a class-specific communication channel². However, a new report from Sarah Hunt *et al.*³ suggests that we should not get too carried away with this idea.

Studies of the role of the UV waveband in mate choice have continued since the early experiments of Bennett *et al.*⁴, which showed that female zebra finches *Taeniopygia guttata* directed their behaviour towards males under full UV illumination (UV+) in preference to males behind UV-eliminating filters. Furthermore, this attraction to UV+ partners was probably an aspect of mate selection rather than of simple species recognition. Female zebra finches preferred symmetrical leg bands⁵, and, by varying the appearance of male bands, the authors showed that the

females found symmetrical males more desirable. As the bands could only be distinguished on the basis of their visibility in UV, this wavelength was clearly instrumental in impressing the females.

This experimental paradigm has proved fruitful in subsequent studies underlining the hidden role that UV plays in the evaluation of prospective mates in other avian species, including starlings *Sturnus vulgaris*⁶ and blue tits *Parus caeruleus*⁷. Additionally, Sheldon *et al.*⁸ found that female blue tits mated with males with highly colour-saturated crests tended to produce more male offspring, whereas low colour-saturated males tended to father more females. Also, the highly colour-saturated males were significantly more likely to survive the following winter. The component of the signal used to indicate male quality lay within the UV band.