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Metabolic costs of brain size evolution

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In the ongoing discussion about brain evolution in vertebrates, the main interest has shifted from theories focusing on energy balance to theories proposing social or ecological benefits of enhanced intellect. With the availability of a wealth of new data on basal metabolic rate (BMR) and brain size and with the aid of reliable techniques of comparative analysis, we are able to show that in fact energetics is an issue in the maintenance of a relatively large brain, and that brain size is positively correlated with the BMR in mammals, controlling for body size effects. We conclude that attempts to explain brain size variation in different taxa must consider the ability to sustain the energy costs alongside cognitive benefits.

Keywords: mammals; encephalization; basal metabolic rate; cognition

1. INTRODUCTION

Ever since Darwin, anthropologists have been intrigued by the dramatic contrast in relative brain size between humans and our great ape relatives, as brain size differences are generally thought to underlie the striking differences in cognitive performance (e.g. Johnson *et al.* 2002; Lefebvre *et al.* 2004). Recent work on the evolution of brain size has largely focused on the benefits of enhanced cognitive abilities in dealing with the challenges imposed by living in social groups (e.g. Byrne & Whiten 1988; Dunbar 2003; Barrett & Henzi 2005) or in the realm of foraging (Milton 1981; Byrne 1997). However, brain tissue is energetically expensive, requiring nearly an order of magnitude more energy per unit weight than several other somatic tissues during rest (Mink *et al.* 1981). The high proportion of energy necessarily allocated to brain tissue may therefore constrain the response of natural selection to the beneficial impact of increased brain size on an animal's survival and/or reproductive success. To date, most of the work that considered the cost side of the equation has focused on trade-offs between the brain and other expensive tissues such as gut or testes (e.g. Aiello & Wheeler 1995; Pitnick *et al.* 2006). The other possibility to nourish a relatively large brain, a raised metabolic turnover (cf. Brody 1945), has been largely neglected because a comparative analysis of 172 eutherian species (McNab & Eisenberg 1989) found no significant correlation between basal metabolic rate (BMR) and brain size, controlling for body size effects. However, this rejection may be premature. First, while this analysis controlled for the effect of body size, it did not control for phylogenetic non-independence. Second, 40% of species data were rodent brain sizes from Mace *et al.* (1981), which were systematically biased by having 0.59 g added to every species' brain mass (G. Mace 2005, personal communication). Third, Martin (1998) found a significantly positive correlation between the relative brain mass and the BMR in a more balanced sample of 51 mammalian species, using both raw data and phylogenetically independent contrasts.

In this paper, we aim to re-evaluate a possible correlation between relative brain size and metabolic rates with contemporary methods and using a large sample of mammalian species.

2. MATERIAL AND METHODS

Brain mass and BMR for 347 mammalian species were assembled from several sources listed in appendix A of the electronic supplementary material. The data on BMR (W) and the corresponding body mass (g) are taken from the compilations of White & Seymour (2003) and Lovegrove (2000, 2003). Thirty-four species were excluded from the analysis following White & Seymour (2003): Soricidae enter a state of hyperactivity as soon as they are truly post-absorptive, Artiodactyla digest very slowly and the measurements of BMR might have not been truly post-absorptive, and Lagomorpha have a heightened BMR owing to foregut fermentation. However, inclusion of those species did not alter the levels of significance of our results.

To test whether phylogenetic effects are present in our data, we used Pagel's software CONTINUOUS (Pagel 1994) on a composite molecular supertree (see appendix B of the electronic supplementary material). The maximum likelihood estimations of Lambda, which measures the degree to which the phylogeny predicts the pattern of covariance among species (Pagel 1999), were close to 1 for all parameters, indicating that phylogenetic correction is indeed required. Thus, we conducted both an analysis of family means and an analysis using phylogenetically independent contrasts, as proposed by Felsenstein (1985). Contrasts were generated using the PDAP : PDTREE package (Garland *et al.* 1992) of the MESQUITE computer program (Maddison & Maddison 2005).

In order to minimize the correlation between the absolute values of the standardized contrasts and their standard deviations (square roots of sums of branch lengths, Garland *et al.* 1992), we estimated branch lengths using the method of Nee (cited in Purvis 1995), where each node is set at a depth equal to the log of the number of descendant tips. The appropriateness of these branch length estimations was then tested using CONTINUOUS (Pagel 1994). The maximum likelihood estimation of Kappa, which differentially stretches or compresses individual phylogenetic branch lengths (Pagel 1997), was close to 1 for all parameters, justifying the use of Nee's branch length estimations. All the variables were $\log_e$ transformed before analysis.

Comparing brain mass to BMR requires the removal of the effects of body mass on both variables. For BMR, we used body mass data from the original studies of BMR to calculate residuals using least-squares regression (JMP v. 6, SAS Institute Inc., Cary, NC, USA). For brain mass, we used the corresponding body mass from the brain mass sources, if available, and species mean body mass otherwise, to calculate residuals. The same procedure was applied to family means and to independent contrasts. For independent contrasts, the regression lines were constrained to pass through the origin (Garland *et al.* 1992). Alternatively, the use of orthogonal regression with equal variances (major axis regression) to calculate residuals does not affect the level of significance of our results.

To account for possible grade shifts, data for species with altricial and precocial developmental modes were analysed separately. Species were defined as precocial if the young open their eyes at birth or shortly thereafter. Most families of Chiroptera produce a single, large offspring after a long gestation time, but the young opens its eyes only after some days. Thus, all Chiroptera were omitted from the analyses where the data are split by development mode, but included in the analysis of the combined dataset.

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Table 1. Least-squares regressions of ln(brain mass) residuals versus ln(basal metabolic rate) residuals in mammals. (Significant correlations are shown in bold face. Note that Artiodactyla, Soricidae and Lagomorpha are not included in the analysis. Within any possible group of insectivores (Eulipotyphla, Afrosoricida, or both combined), there is no significant correlation between brain mass residuals and BMR residuals.)

group	method	N	p par	slope	r^2
species means	raw	313	**<0.0001**	0.290	0.053
	IC	312	**0.005**	0.149	0.026
family means		61	**0.011**	0.557	0.104
Altricial	raw	206	**<0.0001**	0.339	0.082
	IC	205	**0.049**	0.127	0.021
Precocial	raw	49	**0.016**	0.535	0.117
	IC	48	**0.019**	0.333	0.133
Carnivora	raw	44	0.141	0.159	0.051
	IC	43	0.124	0.192	0.054
Chiroptera	raw	58	**0.032**	0.244	0.080
	IC	57	0.517	−0.047	0.008
Primates	raw	23	**0.0009**	0.614	0.417
	IC	22	**0.025**	0.395	0.202
Rodentia	raw	157	0.065	0.160	0.022
	IC	156	0.103	0.136	0.018

3. RESULTS

There is a positive correlation between brain mass residuals and BMR residuals in mammals, using either species values, family means or independent contrasts, which also holds among altricial and precocial taxa separately (table 1). Within large mammalian orders, the relationship is significant only in primates. Thus, controlling for body size effects, a positive correlation between BMR and brain mass exists in our sample of mammals (figure 1).

4. DISCUSSION

We tested the hypothesis that, all other things being equal, the costs of an increase in brain size must be compensated by increased metabolic turnover, indexed by BMR. Our analysis lends support to that hypothesis for mammals, as we showed that brain mass correlates significantly with BMR, controlling for body size effects. However, the amount of brain size variation that can be attributed to differences in BMR is rather small in most groups (e.g. 2.6% in all mammals, but 13.3% in precocial mammals, independent contrasts method). We do not expect BMR variability to explain a large amount of brain size variation, as there are other possibilities for

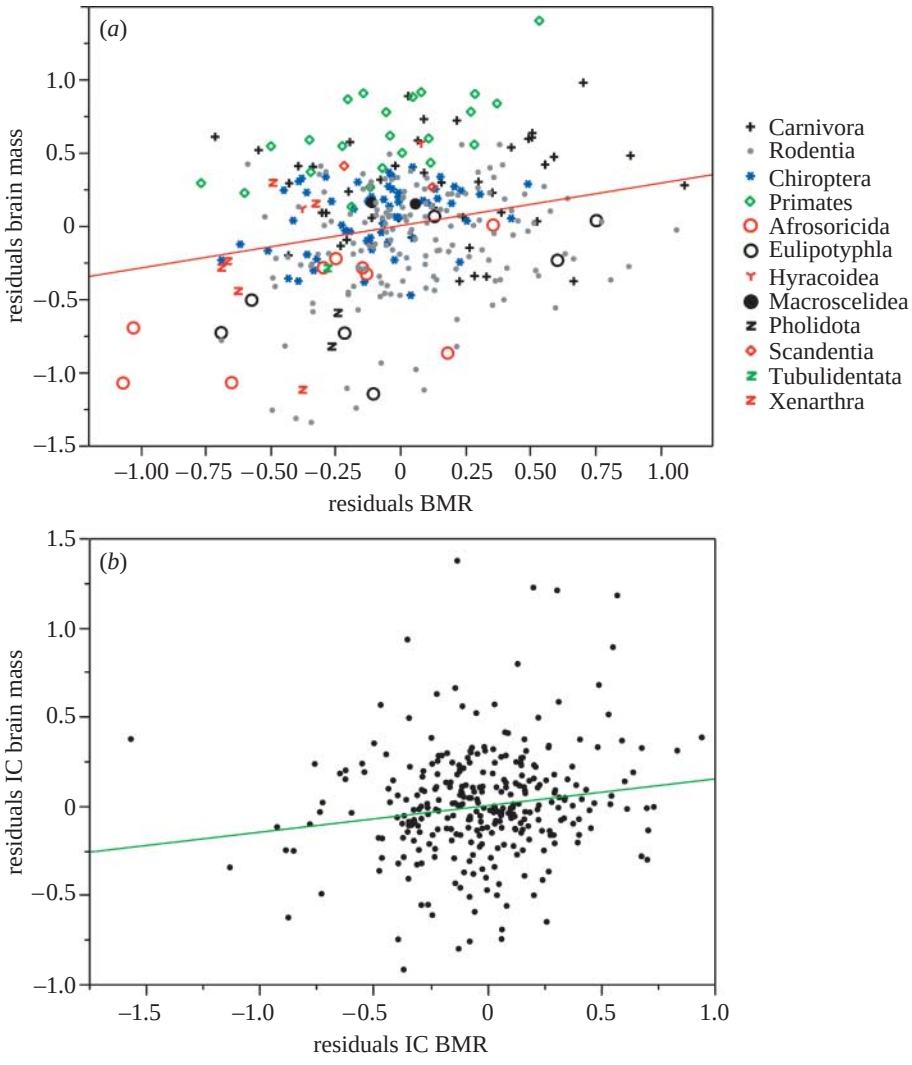

Figure 1. Least-squares regression of residuals ln(brain mass) versus residuals ln(basal metabolic rate) in mammals. (*a*) raw species values ($N=313$, $p<0.0001$, $r^2=0.053$), (*b*) independent contrasts ($N=312$, $p=0.005$, $r^2=0.026$).

maintaining an enlarged brain. Animals could reduce the size of other expensive tissues in the body (Expensive Tissue Hypothesis, Aiello & Wheeler 1995), or reduce energy allocation to locomotion or reproduction (Energy Trade-off Hypothesis, Isler & van Schaik 2006). These changes in distribution of the energy budget do not require a change in the overall energy consumption, and thus in BMR. In non-human primates, the only relatively large-brained order included in our sample, the proportion of brain size variation explained by BMR is substantial (20%, independent contrasts method). We thus conclude that energy costs play a more important role in relatively large-brained animals.

On the other hand, in a sample of 245 bird species, we could not detect a correlation between BMR residuals and brain mass residuals (Isler & van Schaik 2006). Any comparative study of avian energetics is made difficult by the limited amount of data on energetic demands in birds (McKechnie & Wolf 2004). In contrast to mammals, BMR and field metabolic rates may not be strongly correlated in birds, especially during breeding (Koteja 1991; Ricklefs *et al.* 1996). However, these studies were based on less than 30 species, mostly seabirds and temperate passerines, and it would be premature to conclude that a fundamental difference exists between the energetic physiology of birds and mammals (McNab 2002).

The results of this study indicate that increased relative brain size is often accompanied by increased BMR relative to body mass, at least among mammals. Thus, mammals tend to meet the energy costs of evolutionary changes in brain size by some combination of increased energy intake or reduced allocation to other functions such as growth, reproduction, digestion or locomotion; but, could the positive relationship found between brain mass residuals and BMR residuals be an artefact due to the confounding effects of variables that are correlated with BMR, such as home range size (Haskell *et al.* 2002; White & Seymour 2003)? It is possible, but unlikely. First, correlation coefficients remain relatively stable after the phylogenetic effects are removed, suggesting only a moderate influence of confounding variables (Price 1997; Nunn & Barton 2001). Second, the argument can be reversed: it is equally possible that home range size and BMR correlate, only owing to the confounding effect of brain size. Such patterns across evolved equilibria reflect a process of correlated evolution and are notoriously difficult to analyse. Nevertheless, our understanding of brain size evolution in mammals should increase if we can integrate the capacity to bear energetic and life-history costs of changes in relative brain size with the adaptive benefits of increased brain size, stressed by current theorizing (e.g. Dunbar 2003).

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