

Scaling of the primate brain: implications of body size

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Abstract

Among primates, the highest degrees of encephalisation (relative brain size) are found in humans and in capuchin monkeys (*Cebus* sp.). Capuchin monkeys therefore provide an interesting source of comparison when seeking an explanation for the increase in relative brain size during hominid evolution. The question however remains: why is the human relative brain size value not paralleled among primates? A brain weight vs. body weight ratio of 4% represents the upper limit for adult brain weight vs. body weight ratios in all orders of mammals. Body size therefore appears to be a constraint on relative brain size and residual values of individual species relative to a best-fit line between brain size and body size values are not independent of body size itself.

Keywords: body size, brain size, encephalisation, primates.

Résumé

Parmi les primates, les plus hauts niveaux d'encéphalisation (taille cérébrale relative) se rencontrent chez l'homme et le singe capucin (*Cebus* sp.). Les singes capucins offrent donc une intéressante source de comparaison pour comprendre les paramètres en œuvre lors de l'augmentation de la taille cérébrale relative au cours de l'évolution des hominidés. Il demeure toutefois une question qui reste sans réponse : pourquoi la taille cérébrale relative de type humain n'a-t-elle aucun parallèle chez les primates non humains ? Il s'avère qu'un rapport de 4 % entre le poids cérébral et le poids corporel représente la limite supérieure de pourcentage de tissu cérébral atteint chez tous les mammifères. Le poids corporel a donc un effet de contrainte sur l'augmentation de la taille cérébrale relative et les valeurs résiduelles pour les différentes espèces par rapport à une droite de régression tracée entre le poids cérébral et le poids corporel ne sont pas indépendantes du poids corporel lui-même.

Mots-clefs : poids corporel, poids cérébral, encéphalisation, Primates.

1. WHY ARE HUMANS THE MOST ENCEPHALISED PRIMATES?

The most dramatic change that occurred in hominid evolution during the last 2 million years is the increase of absolute brain size (Kappelman, 1996; Wood & Collard, 1999). The question of how the size of the brain evolved relative to that of the body remains the most relevant issue in the study of hominid brain evolution. A striking characteristic of extant humans is the disproportionate enlargement of brain size relative to body size. This enlargement is defined by the relative brain size value rather than by the ratio brain size/body size. Relative brain size is expressed by the residual values of individual species relative to a best-fit line drawn between logged brain and body size values (fig. 1).

Among primates, the highest residual values are found in humans and in capuchin monkeys (*Cebus* sp.; Martin, 1990; Aiello & Wheeler, 1995) [fig. 1]. When compared to the average of placental mammals, humans show a relative brain size about 6 times larger than expected and capuchin monkeys have brains about 3.5 larger than expected. In comparison, chimpanzees have brains only about 2.5 times larger than expected. Capuchin monkeys therefore provide

an interesting source of comparison when seeking an explanation for the increase in relative brain size in hominid evolution. Recent studies have correctly stressed the energetic constraints on brain enlargement (Aiello & Wheeler, 1995; Martin, 1990, 1996). It is for instance interesting to note that capuchin monkey eats hard food items and closely resembles the robust australopithecines in its microwear pattern (Kay & Grine, 1988) but also has a high-quality diet (Milton, 1987) and resembles humans in its gut morphology (Martin *et al.*, 1985, Martin, 1990, Milton, 1987). The question however remains: why is the human relative brain size value (or encephalisation level) not paralleled among primates?

2. THE ROLE OF BODY SIZE

Sacher (1975) noticed that a brain weight vs. body weight ratio of 4% represents the upper limit for adult brain weight vs. body weight ratios in all orders of mammals. Body size therefore appears to be a basic constraint against increasing brain size and hence encephalisation. To further explore this issue, we used the published datasets of Fürst and Hansen (1915)

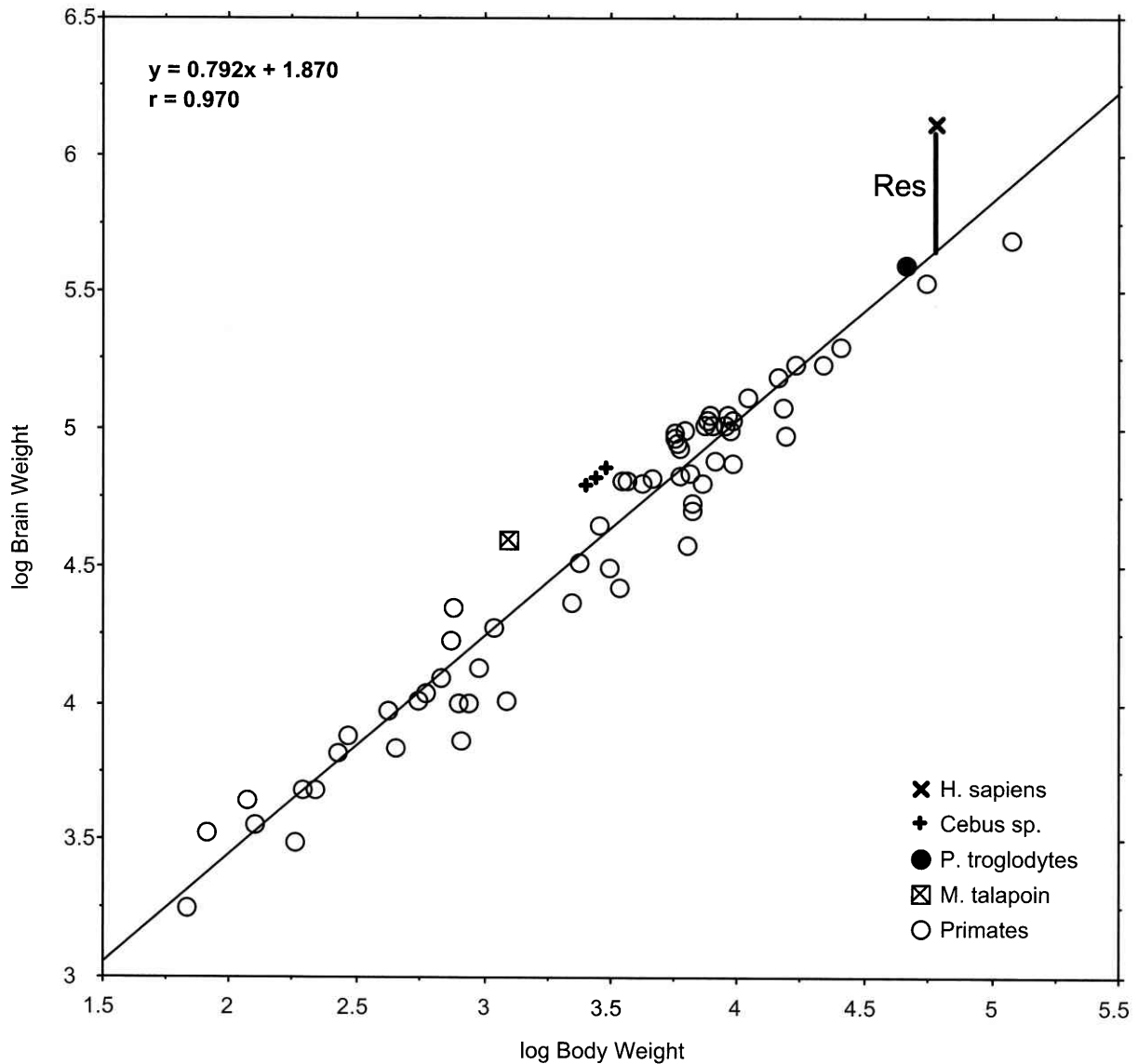


Fig. 1 — Logarithmic plot of brain size against body size for a sample of living primates. The empirical slope of the best-fit line is 0.792 (least-squares regression). Relative brain size can be expressed as the distance (residual value) of a point to the best-fit line (Res = residual value). Modern *Homo sapiens* is the most extreme positive outlier. High positive residual values are also found in *Cebus* sp. and *Miopithecus talapoin*. In general, large primates have a proportionally smaller brain than small primates because of the fact that the empirical slope of the best-fit line for this logarithmically converted dataset is smaller than 1 (negative allometry).

and of Stephan *et al.* (1988), the archives of Adolph H. Schultz, *Anthropologisches Institut und Museum der Universität Zürich-Irchel* (original data), an unpublished dataset assembled by R.D. Martin, The Field Museum, Chicago, in collaboration with A. MacLarnon with the support of a grant from the Medical Research Council (UK) and the original unpublished dataset of the Schoten collection (Royal Belgian Institute of Natural Sciences).

The 4% upper limit for the brain weight vs. body weight ratio probably indicates an upper limit of brain metabolism that mammals

can support. Within mammals, several groups have species with brain weight to body weight ratio approaching the 4% value. Such species are found within primates, didelphid and dasyurid marsupials, vespertilionid bats, squirrels, rodents, and weasels. A similar limit was described for birds by Lapique and Dastre (1908). The actual value of this ratio in adult humans is 2.1% and has remained at that level for about 100,000 years (Sacher, 1975). In *Cebus albifrons*, the value of this ratio is 2.2%. The expected values of this ratio are respectively 0.7% in adult humans and 1.6% in *Cebus albifrons*

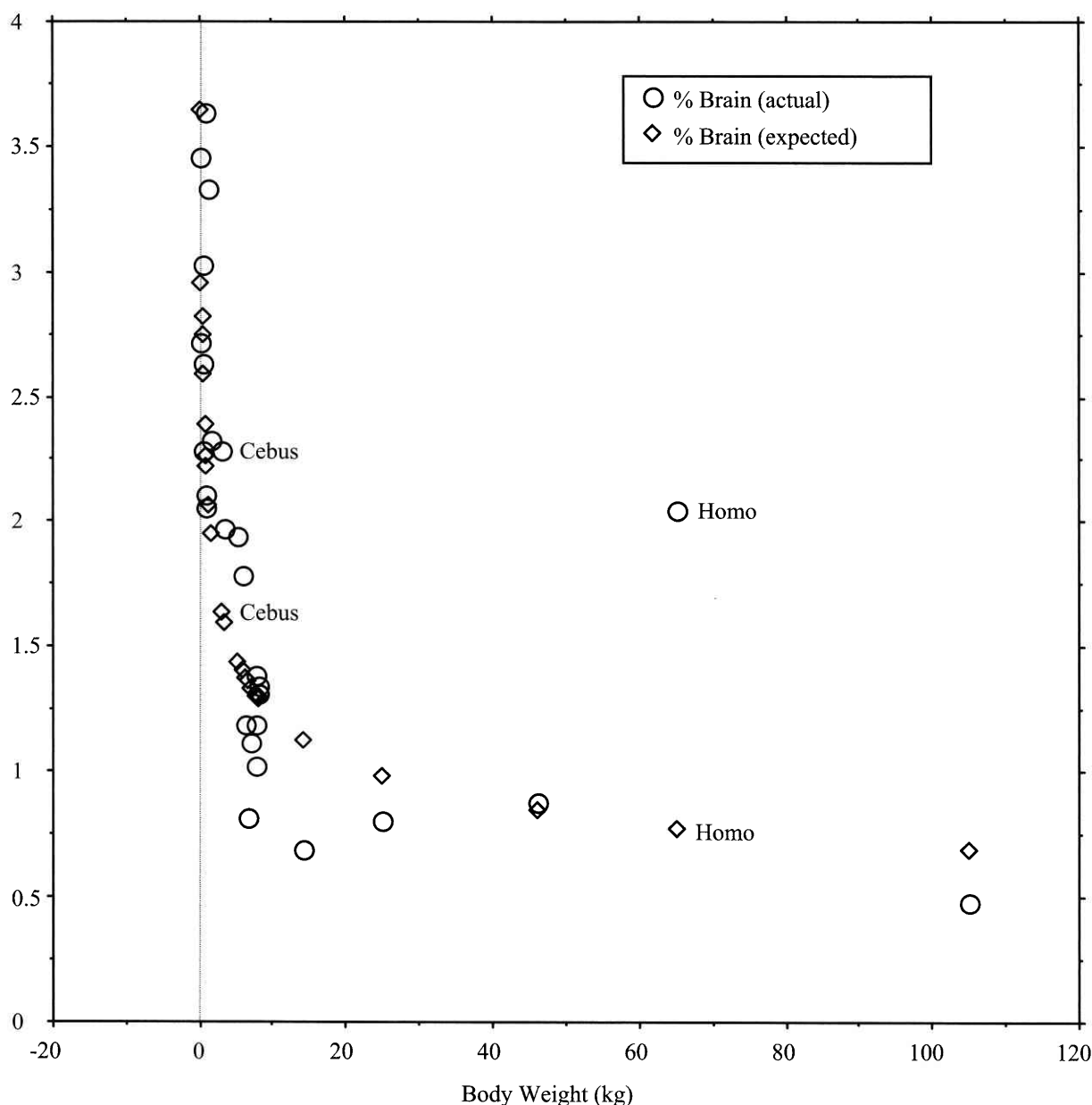


Fig. 2 — Relationship between percentage of brain tissue and body weight for 28 primate species. “% Brain (actual)” represents the actual observed value. “% Brain (expected)” represents the value expected from the reduced major axis (Model II regression) between brain weight and body weight (log transformed values).

(fig. 2). If adult *Cebus albifrons* would have the same level of encephalisation as adult humans, the brain weight vs. body weight ratio would be 4.4% in this species and thus would be above the upper limit for adult mammals (fig. 3). A body weight of about 10 kg is a prerequisite to eventually reach a degree of encephalisation comparable to that observed in modern adult humans. It is therefore to some extent misleading to say that after modern humans, the next largest relative brain sizes among primates are found in capuchin monkey

species. They are simply too small to reach the human level of encephalisation (average adult body weight: 2.5–3.0 kg).

In small primates where the percentage of brain tissue is proportionally larger than in large primates (fig. 1), changes in brain mass could have more important consequences with regard to the 4% brain tissue empirical limit observed by Sacher (1975). However, lower body mass variability in small primates could constitute an additional constraint on changes in brain size body size ratio. In general, small mammals as

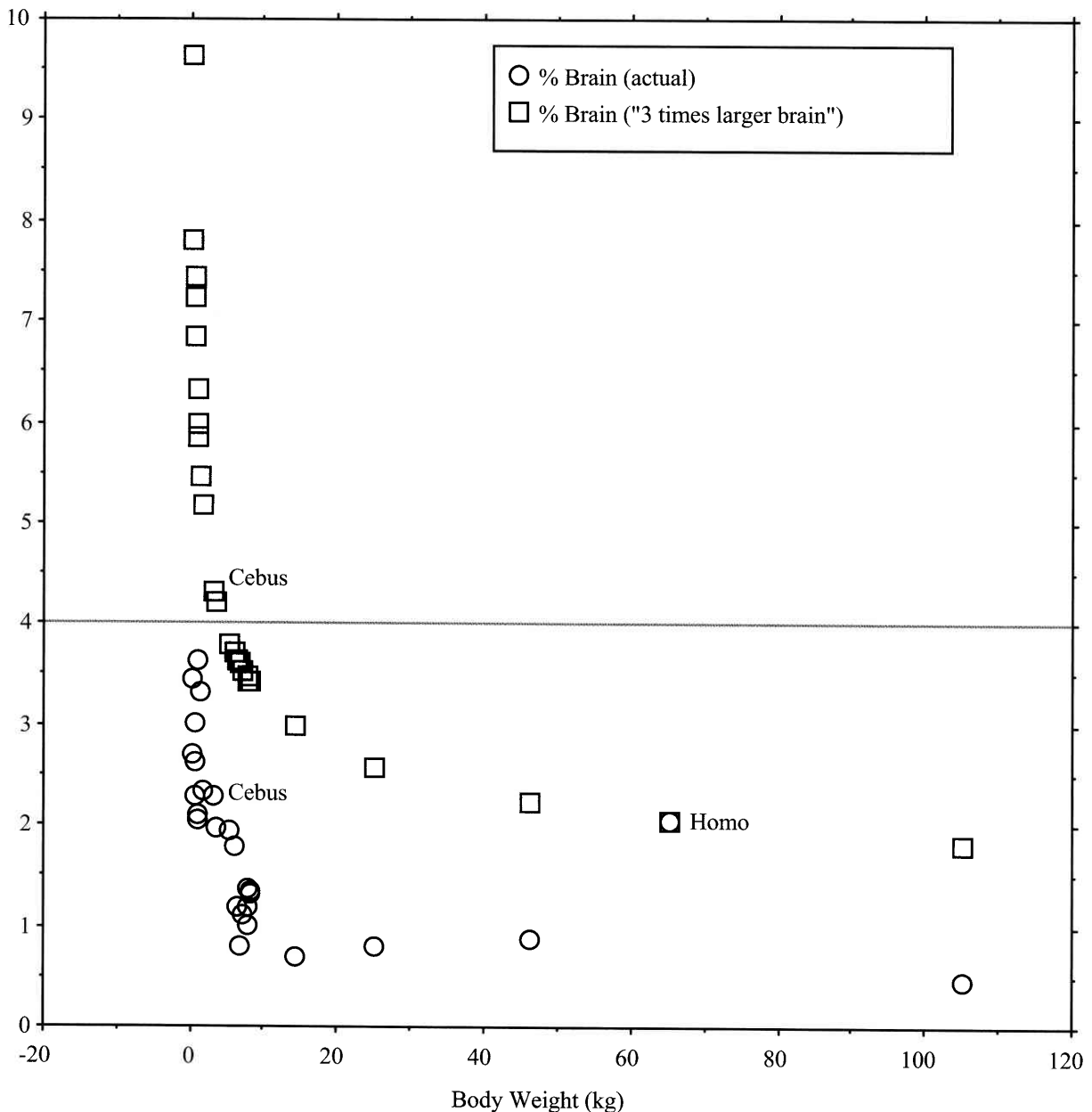


Fig. 3 — Relationship between percentage of brain tissue and body weight for 28 primate species. “% Brain (3 times larger brain)” represents the percentage of brain tissue that would be found in these various primate species if they would have the human level of encephalisation, that is, a brain size approximately three times larger than expected for their body size. In that case, it appears that the adult brain tissue percentage of several small primates (especially New World monkeys) would represent more than 4% of the total body mass. Note that the “% Brain (actual)” value and the “% Brain (3 times larger brain)” value are the same for *Homo*.

well as small birds have a low body mass variability because they are composed of a large proportion of components in which size variation is more highly constrained by energetic and functional factors (viscera and nervous system). In contrast, large mammals and birds show an important body mass variability because their body mass contains a larger proportion of components with higher intrinsic variability (bone, fat, and muscle) [Hallgrímsson, 2000].

Given the high percentage of brain tissue and the low body mass variability in small bodied mammals, it would be interesting to control if the coefficient of variation of brain mass is lower in small mammals including primates when compared to large bodied ones. We therefore analysed samples of cranial capacities to determine if the intraspecific variability is similar when considering large or small primate brain sizes. It appears that small and large

cranial capacities have comparable patterns of variability (table 1). Very small primate species such as callitrichids are nevertheless required to draw firm conclusions. This result should therefore be considered as preliminary. It is however possible that variability of human brain size is more important than what can be observed in other primates (see for instance the Schoten sample, table 1). This issue requires further investigation (Howells, 1973). Because of its position well below the 4% brain tissue empirical limit (figs. 2 and 3), possible increased variability of modern *Homo sapiens* brain size should have little consequence with regard to this limit.

	N	Mean	CV
Schoten (F)	18	1291.1	10.2
Schoten (M)	24	1540.4	7.9
Schoten (M+F)	51	1434.3	12.0
North West Greenland (F)	18	1491.8	7.5
North West Greenland (M)	24	1533.0	6.3
North West Greenland (M+F)	51	1504.9	6.7
<i>Hylobates lar</i> (F)	18	104.0	7.5
<i>Hylobates lar</i> (M)	24	104.2	6.7
<i>Hylobates lar</i> (M+F)	51	103.9	6.7
<i>Ateles geoffroyi</i> (F)	18	105.5	6.7
<i>Ateles geoffroyi</i> (M)	24	108.2	5.5
<i>Ateles geoffroyi</i> (M+F)	51	107.0	6.1

Table 1 — Mean (cm³) and coefficient of variation of cranial capacity for human and non human primate samples. Males (M) and females (F) are treated both as two different samples and as a unique sample (M+F). “Schoten” represents a sample of Belgian human subjects, “North West Greenland” represents a sample of human subjects from Upernivik and Umanak (Fürst & Hansen, 1915). The data for *H. lar* and *A. geoffroyi* were obtained in the archives of Adolph H. Schultz. The coefficients of variation of cranial capacity are comparable. However, the sample of Schoten shows a pattern of high variability that requires further analysis.

It is commonly assumed that, in contrast with percentages, residual values are a measure of brain size independent of body size (fig. 4). It however appears that body size is a constraint on relative brain size and residual values of individual species relative to a best-fit line between brain size and body size values are not independent of body size itself.

This result is important when considering the encephalisation level of miniaturized primates such as the callitrichids. Implications of small body size have been reviewed by Bourlière (1975) and by Ford and Corruccini (1985). Primary problems posed by small body size are thermoregulation and the high metabolic cost

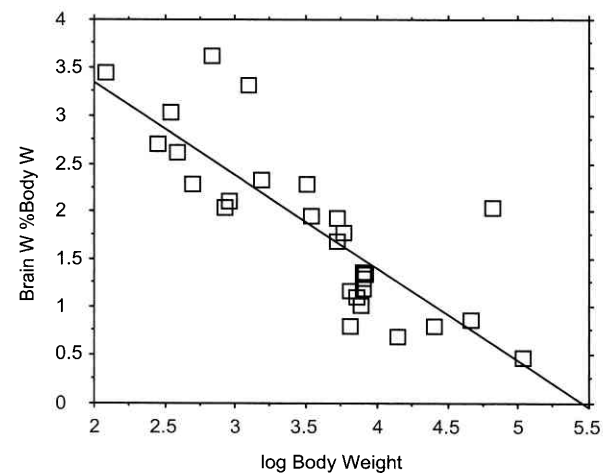
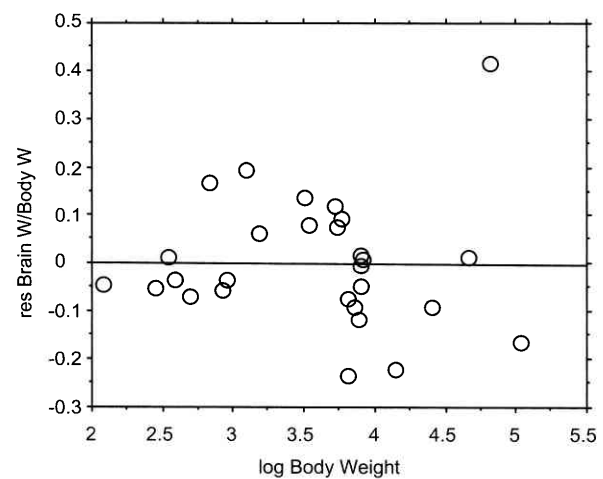


Fig. 4 — Top: relationship between relative brain size (residuals) and body weight (log) for 28 primate species ($r = 0.016$; $p = 0.9$). Residual values are a measure of encephalisation. They represent deviations from the best-fit line between brain size and body size and are classically considered as independent of body size. Bottom: relationship between percentage of brain tissue and body weight (log) for 28 primate species ($r = 0.785$; $p = 0.0001$). Because of the negative allometry that characterises the relationship between brain size and body size (empirical slope of the best-fit line smaller than 1), large primates have a proportionally smaller brain than small primates and percentages are considered as dependent of body size.

of maintaining a constant body temperature. It is therefore understandable that small mammals such as callitrichids are under much less stress in tropical environments. Large body size probably evolved to retard heat loss in colder environments. Adaptation to cold ecological systems can be achieved by larger primates. In this view, the migrations of humans and their ancestors can be seen primarily as a consequence of their increased body size. It is also possible that the cost of body temperature maintenance in small bodied primates also represents an

energetic constraint against energy consuming brain size increase.

3. AFTERTHOUGHTS

Factors and strategies related to increase in absolute and relative brain size are most probably the keys to understand human place among other primates. It has been hypothesised that various levels of self-knowledge exist in animals and that self-knowledge serves as a standard to assess the qualities of co specific compared to those of the self. This adaptive function is of particular importance for deciding between alternative reproductive and subsistence strategies (Parker, 1997). Self-recognition, a level of self-knowledge, appears to be unique to humans and great apes. Monkeys and other mammals cannot recognise themselves in a mirror. There are nevertheless notable exceptions such as large brained dolphins, whose capability of self-recognition is a striking example of psychological evolutionary convergence with great apes and humans (Reiss & Marino, 2001). Recent studies demonstrated that cognitive abilities might be important in self-recognition (Bard, 1997). An index of cognitive ability available for a wide range of primates is the frequency in using manipulation of other group members. This ability (tactical deception) occurs when an individual is able to use an act from his normal repertoire in a different context to mislead other group members and appears to correlate with brain size (Whiten & Byrne, 1988; Byrne, 1993). Tactical deception implicates self-knowledge as well as the ability to transfer learned information across tasks and stimulus conditions. This learning capacity which enables animals to reuse information in new contexts, has been shown to correlate with brain size but not encephalisation (i.e., amount of brain mass above the mass expected for a given body size) (Rumbaugh *et al.*, 1996). Humans combine both the largest absolute brain size and the highest level of encephalisation among primates. It is possible that the supposed human uniqueness emerges from this combination. Other primates such as the capuchin monkey show a high degree of encephalisation and therefore an absolute brain size comparable to larger primates. Comparative studies should help to understand behavioural correlates of brain size and encephalisation, and

their respective contribution in the emergence of new cognitive processes.

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