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Comparative Biochemistry and Physiology Part A 136 (2003) 5–15

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Review

Metabolic correlates of hominid brain evolution[☆]

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Received 25 July 2002; received in revised form 22 April 2003; accepted 23 April 2003

Abstract

Large brain sizes in humans have important metabolic consequences as humans expend a relatively larger proportion of their resting energy budget on brain metabolism than other primates or non-primate mammals. The high costs of large human brains are supported, in part, by diets that are relatively rich in energy and other nutrients. Among living primates, the relative proportion of metabolic energy allocated to the brain is positively correlated with dietary quality. Humans fall at the positive end of this relationship, having both a very high quality diet and a large brain size. Greater encephalization also appears to have consequences for aspects of body composition. Comparative primate data indicate that humans are ‘under-muscled’, having relatively lower levels of skeletal muscle than other primate species of similar size. Conversely, levels of body fatness are relatively high in humans, particularly in infancy. These greater levels of body fatness and reduced levels of muscle mass allow human infants to accommodate the growth of their large brains in two important ways: (1) by having a ready supply of stored energy to ‘feed the brain’, when intake is limited and (2) by reducing the total energy costs of the rest of the body. Paleontological evidence indicates that the rapid brain evolution observed with the emergence of *Homo erectus* at approximately 1.8 million years ago was likely associated with important changes in diet and body composition.

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Keywords: Encephalization; Resting metabolism; Diet quality; Body composition; Adiposity; *Homo erectus*

1. Introduction

From the perspective of comparative physiology and nutrition, what is extraordinary about the large brains of humans is their high metabolic cost. Brain tissue has very high energy demands per unit weight, roughly 16 times greater than those of muscle tissue (Kety, 1957; Holliday, 1986). Yet, despite the fact that humans have much larger

brains per body weight than other terrestrial mammals, the total (resting) energy demands for the human body are no more than for any other mammal of the same size (Leonard and Robertson, 1992, 1994). The consequence of this paradox is that humans allocate a much larger share of their daily energy budget to ‘feed their brains’. Brain metabolism accounts for ~20–25% of resting energy demands in an adult human body. This is far more than the 8–10% observed in other primate species, and still more than the 3–5% allocated to the brain by other (non-primate) mammals (Leonard and Robertson, 1994).

The question that remains from all of this is how humans have evolved to support the very high nutritional needs of our large brains. To

[☆] This paper is part of a collection of inter-disciplinary, peer-reviewed articles under the Theme: ‘‘Origin and Diversity of Human Physiological Adaptability’’ invited by K.H. Myburgh and the late P.W. Hochachka.

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address this question, we will use comparative analyses to examine two major domains through which hominids have adapted to the metabolic demands of greater encephalization: (1) improvements in dietary quality, and (2) changes in body composition. Dietary quality refers to the energetic and/or nutrient density of a diet. Increases in diet quality may result from changes in diet composition (i.e. what you eat) or the ways in which foods are modified (processing, cooking, or genetic manipulation) (see Leonard and Robertson, 1994; Wragham et al., 1999). In terms of body composition, we will specifically consider how changes in the relative proportions of adipose and muscle tissue may help accommodate the metabolic demands of larger brains. We will also consider the developmental aspects of these patterns of body composition. These analyses provide a context for understanding the major selective forces that were likely necessary to support the evolution of large hominid brains.

2. Sample and methods

2.1. Primate data: brain size, body size, metabolic rate and diet

Table 1 presents data on body mass (kg), resting metabolic rate (RMR; kcal/day), brain mass (g) and dietary quality for 41 species of primates, including humans. Data on metabolic rates and associated body masses were derived from Leonard and Robertson (1994), McNab and Wright (1987), Thompson et al. (1994) and Kappeler (1996). Data on brain weights and body masses were obtained from Bauchot and Stefan (1969), Stephan et al. (1981) and Jerison (1973). Information on dietary quality was obtained from data presented by Leonard and Robertson (1994), Sailer et al. (1985), Richard (1985) and Rowe (1996). The human data point is an average based on dietary data from 5 human foraging populations: the !Kung, Ache, Hiwi, Ituri Pygmies and Inuit (from Leonard and Robertson, 1994). Diet quality (DQ) was assessed using an index developed by Sailer et al. (1985) that considers the relative energy and nutrient density of dietary items. The DQ index is a weighted average of the proportions of foliage, reproductive plant material, and animal material. DQ is calculated as:

$$DQ = s + 2(r) + 3.5(a)$$

where s = percent of diet derived from structural plant parts (e.g. leaves, stems, and bark), r = percent of diet derived from reproductive plant parts (e.g. fruits, flowers, nectar, and resin) and a = percent of diet derived from animal parts (including both vertebrates and invertebrates). The DQ ranges from a minimum of 100 (100% foliage) to a maximum of 350 (100% animal material).

2.2. Comparative body composition: skeletal muscle mass, infant body fatness

Table 2 presents information on skeletal muscle mass and body weight compiled for 15 primates (including humans). The non-human primate data were derived from Grand (1977) and Zihlman (1984). The human data were obtained from Wang et al. (2001). In addition, limited data on percent body fatness at birth for 15 mammalian species (including humans) were derived from Kuzawa (1998) (see Fig. 6).

2.3. Fossil hominid data

Table 3 presents data on geological ages (millions of years ago), brain size (cm³), estimated male and female body weights (kg), and posterior tooth surface areas (mm²) for selected fossil hominid species. All data presented in Table 3 were derived from McHenry and Coffing (2000) other than the information on *Homo erectus*. For early *H. erectus* brain size was calculated from data presented by McHenry (1994b) for the African specimens, Antón and Swisher (2001) for Indonesian specimens, and Gabunia et al. (2000, 2001) for Georgian (Dmanisi) remains. All data for late *H. erectus* were taken from McHenry (1994a).

3. Results

3.1. Variation in brain size, body size and diet quality in modern primates

Among primates, as in other mammals, RMR scales to body mass with an exponent of less than 1. As shown in Fig. 1, the relationship between RMR and body mass among primate species is similar to the Kleiber relationship for mammals in general (Kleiber, 1961).

$$RMR = 55Wt^{0.81} \quad (r = 0.97)$$

Table 1
Metabolic rate (RMR; kcal/day), body mass (kg), brain mass (g) and diet quality (DQ) for 41 primate species

Species	Metabolic data		Brain data		
	RMR (kcal/d)	Body mass (kg)	Brain mass (g)	Body mass (kg)	DQ
Suborder strepsirhini					
<i>Arctocebus calabarensis</i>	15.2	0.206	7.2	0.323	327.5
<i>Cheirogaleus medius</i>	22.7	0.300	3.1	0.177	
<i>Eulemur fulvus</i>	42.0	2.397	25.2	2.397	129
<i>Euticus elegantulus</i>	25.1	0.260	7.2	0.274	230
<i>Galago moholi</i>	13.9	0.155			
<i>Galago senegalensis</i>	18.1	0.215	4.8	0.186	278
<i>Galagoides demidoff</i>	6.3	0.058	3.4	0.081	305
<i>Lemur catta</i>	45.1	2.678	25.6	2.678	166
<i>Lepilemur ruficaudatus</i>	27.6	0.682	7.6	0.682	149
<i>Loris tardigradus</i>	14.8	0.284	6.6	0.322	327.5
<i>Microcebus murinus</i>	4.9	0.054	1.8	0.054	
<i>Nycticebus coucang</i>	32.4	1.380	12.5	0.800	
<i>Otolemur crassicaudatus</i>	47.6	0.950	10.3	0.850	195
<i>Otolemur garnettii</i>	47.8	1.028			275
<i>Perodicticus potto</i>	41.3	1.000	14	1.150	190
<i>Propithecus verreauxi</i>	86.8	3.080	26.7	3.480	200
<i>Varecia variegata</i>	69.9	3.512	34.2	3.512	
Suborder haplorhini					
<i>Alouatta palliata</i>	231.9	4.670	51	6.400	136
<i>Aotus trivirgatus</i>	52.4	1.020	16	0.850	177.5
<i>Callithrix geoffroyi</i>	27.0	0.225	7.6	0.280	235
<i>Callithrix jacchus</i>	22.8	0.356	7.6	0.280	235
<i>Cebuella pygmaea</i>	10.1	0.105	4.5	0.140	249.5
<i>Cercopithecus mitis</i>	407.7	8.500	76	6.500	201.5
<i>Cercocebus torquatus</i>	196.2	4.000	104	7.900	234
<i>Colobus guereza</i>	357.9	10.450	73	7.000	126
<i>Erythrocebus patas</i>	186.9	3.000	118	8.000	
<i>Homo sapiens</i>	1400.0	53.500	1295	53.500	263
<i>Hylobates lar</i>	123.4	1.900	102	6.000	181
<i>Leontopithecus rosalia</i>	51.1	0.718			
<i>Macaca fascicularis</i>	400.9	7.100	74	5.500	200
<i>Macaca fuscata</i>	485.4	9.580	84	5.900	223
<i>Macaca mulatta</i>	231.9	5.380	110	8.000	159
<i>Pan troglodytes</i>	581.9	18.300	420	46.000	178
<i>Papio anubis</i>	342.9	9.500	205	26.000	207
<i>Papio cynacephalus</i>	668.9	14.300	195	19.000	184
<i>Papio papio</i>	297.3	6.230	190	18.000	
<i>Papio ursinus</i>	589.3	16.620	190	18.000	189.5
<i>Pongo pygmaeus</i>	569.1	16.200	370	55.000	172.5
<i>Saguinus geoffroyi</i>	50.5	0.500	10	3.800	263
<i>Saimiri sciureus</i>	68.8	0.850	22	6.800	323
<i>Tarsius syrichta</i>	8.9	0.113			350

Sources: Bauchot and Stefan (1969), Stephan et al. (1981), Jerison (1973), Richard (1985), Sailer et al. (1985), McNab and Wright (1987), Leonard and Robertson (1994), Thompson et al. (1994), Kappeler (1996) and Rowe (1996).

The consequence of this scaling relationship is that small primates have low total energy needs but very high energy demands per unit mass. Conversely, large primates have high total energy needs, but low mass-specific costs. These different metabolic constraints dictate different feeding strategies. Small primates (e.g. the pygmy mar-

moset (*Cebuella pygmaea*)), constrained by very high mass-specific energy costs, meet their dietary needs by consuming foods that are limited in abundance but high in quality (insects, saps, gums). In contrast, the main constraint for large primates is getting enough total energy; hence, large bodied species such as the gorilla (*Gorilla*

Table 2
Body mass (kg) and skeletal muscle mass (kg) of 15 primate species

Species	Body mass (kg)	Muscle mass (kg)
<i>Alouatta caraya</i>	6.08	1.68
<i>Aotus trivirgatus</i>	0.63	0.19
<i>Ateles</i> sp	7.60	3.48
<i>Cebus</i> sp	3.80	1.73
<i>Galago senegalensis</i>	0.25	0.09
<i>Galago crassicaudatus</i>	0.88	0.31
<i>Homo sapiens</i> M	80.50	33.40
F	67.30	20.70
<i>Macaca mulatta</i>	6.04	2.50
<i>Macaca nemestrina</i>	14.50	7.12
<i>Macaca nigra</i>	9.40	3.46
<i>Mandrillus leucophaeus</i>	25.26	11.16
<i>Nycticebus coucang</i>	1.16	0.30
<i>Pan paniscus</i>	29.50	13.51
<i>Pan troglodytes</i>	31.50	11.03
<i>Perodicticus potto</i>	0.99	0.25

Sources: Grand (1977), Zihlman (1984) and Wang et al. (2001).

gorilla) and orangutan (*Pongo pygmaeus*) are large volume feeders, eating foods that are widely available, but low in nutritional density (leaves, bark and low quality plant foods).

This inverse relationship between diet quality and body size is evident in Fig. 2. Across all primates, there is a significant negative correlation between diet quality and body mass ($r = -0.66$; $P < 0.001$). Humans, however, have substantially higher quality diets than expected for a primate of our size. Note that the average diets of the five modern human foraging populations fall substantially above the regression line. Overall, the staple

Table 3

Geological ages (millions of years ago), brain size (cm^3), estimated male and female body weights (kg), and posterior tooth surface areas (mm^2) for selected fossil hominid species

Species	Geological age (mya)	Brain size (cm^3)	Body weight		Posterior tooth surface area (mm^2)
			Male (kg)	Female (kg)	
<i>Australopithecus afarensis</i>	3.9–3.0	438	45	29	460
<i>A. africanus</i>	3.0–2.4	452	41	30	516
<i>A. boisei</i>	2.3–1.4	521	49	34	756
<i>A. robustus</i>	1.9–1.4	530	40	32	588
<i>Homo habilis (sensu strictu)</i>	1.9–1.6	612	37	32	478
<i>H. erectus</i> (early)	1.8–1.5	863	66	54	377
<i>H. erectus</i> (late)	0.5–0.3	980	60	55	390
<i>H. sapiens</i>	0.4–0.0	1350	58	49	334

All data from McHenry and Coffing (2000), except for *H. erectus*. Early *H. erectus* brain size is the average of African specimens as presented in McHenry (1994b), Indonesian specimens from Anton and Swisher (2001) and Georgian specimens from Gabunia et al. (2000, 2001). Data for late *H. erectus* are from McHenry (1994a).

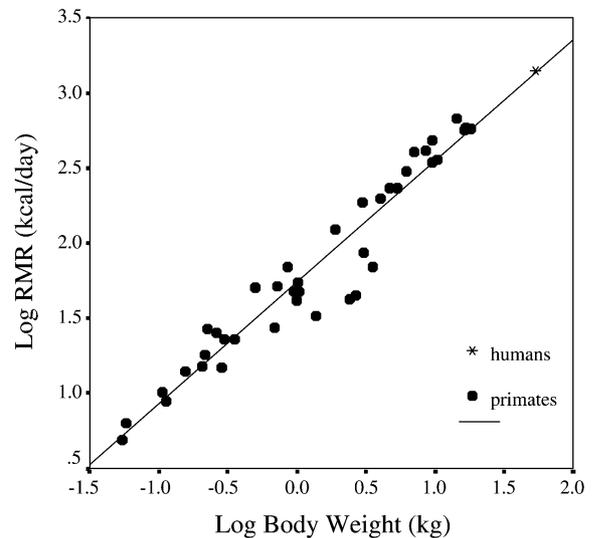


Fig. 1. Log–log plot of resting metabolic rate (RMR; kcal/day) vs. body weight (kg) of 41 primate species. The allometric relationship is: $\text{RMR} = 55\text{Wt}^{0.81}$ ($r = 0.97$). The scaling coefficient of less than 1 implies that smaller primates have higher mass-specific energy costs larger primates.

foods for all human societies are much more nutritionally dense than those of other large-bodied primates. This ‘higher quality’ diet for humans relative to other large-bodied primates means that we need to eat less volume of food to get the energy and nutrients we require.

The significance of this higher quality diet is explored in Fig. 3, which shows the relationship between relative brain size and relative dietary quality among living primate species. There is a strong positive relationship ($r = 0.63$; $P < 0.001$)

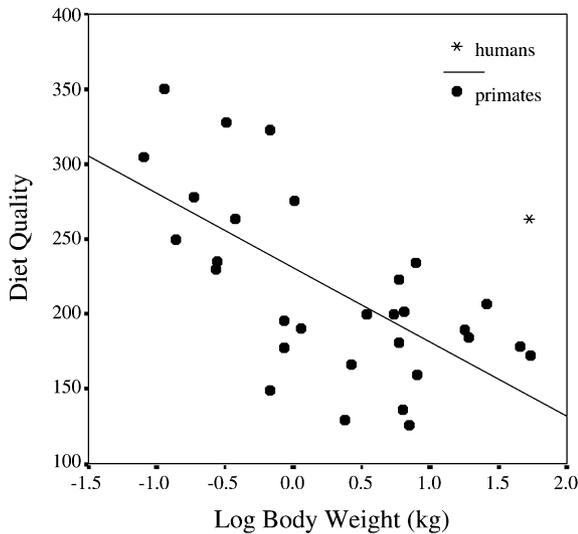


Fig. 2. Plot of Diet Quality (DQ) Index (from Sailer et al. 1985) vs. log body weight for 33 primate species. DQ is inversely related to body weight ($r = -0.66$; $P < 0.001$), reflecting the fact that smaller primates require higher quality more nutrient dense diets to support the high mass-specific energy needs. Humans (average for 5 foraging populations) have markedly higher quality diets than expected for their body size.

between the amount of energy allocated to the brain and the caloric and nutrient density of the diet. Across all primates, bigger brains require better quality diets, and humans are the extreme example of this, having the largest relative brain size and the highest quality diet relative to body weight. This relationship implies that the dramatic expansion of brain size over the course of human evolution would have necessitated the adoption of a sufficiently high quality diet to support the elevated energy demands.

3.2. Evolution of brain size and diet quality: evidence from the fossil record

When we look at the human fossil record, the first major burst of evolutionary change in hominid brain size occurs at approximately 2.0–1.7 million years ago, associated with the emergence and evolution of early members of the genus *Homo* (see Fig. 4). Prior to this, our earlier hominid ancestors, the australopithecines (shown as closed circles), showed only modest brain size evolution from 400 to 510 cm³ over a 2 million year span from 4 to 2 million years ago. With the evolution of the genus *Homo* there is rapid change, with

brain sizes of approximately 600 cm³ in *Homo habilis* (at 2.4–1.6 mya) and 800–900 cm³ in early members of *H. erectus* (at 1.8–1.5 mya). While the relative brain size of *H. erectus* is smaller than that of modern humans, it is nonetheless outside of the range seen among other living primate species.

The factors responsible for the rapid evolution of brain size at this stage of human evolution include environmental changes that promoted shifts in diet, foraging behavior and changes in tool technology. The environment at the Plio-Pleistocene boundary (2.0–1.8 mya) was continuing to become drier, creating more arid grasslands (Vrba, 1995; Owen-Smith, 1999). Changes in the African landscape made animal foods more abundant and thus, an increasingly attractive food resource (Behrensmeyer et al., 1997).

The increasing abundance of game animals in grassland environments is evident in Table 4, which shows the levels of primary, secondary (herbivore) and tertiary (carnivore) productivity in modern day woodland and savanna ecosystems of the tropics. Whereas the overall level of primary productivity in the savanna is only about half that of the woodland, secondary productivity (the abundance of herbivores) is almost three times greater

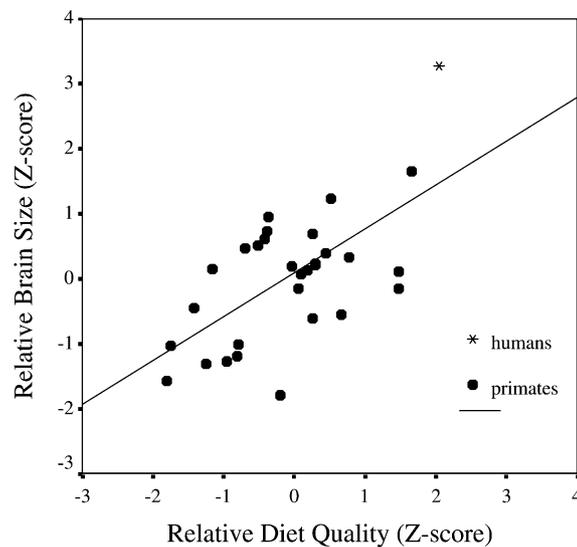


Fig. 3. Plot of relative brain size vs. relative diet quality for 31 primate species. Primates with higher quality diets for their size have relatively larger brain size ($r = 0.63$; $P < 0.001$). Humans represent the positive extremes for both measures, having large brain:body size and a substantially higher quality diet than expected for their size.

in the savanna. Consequently, the expansion of the savanna in Plio-Pleistocene Africa would have limited the amount and variety of edible plant foods for hominids, but also resulted in an increase in the relative abundance of grazing mammals such as antelope and gazelle. These changes in the relative abundance of different food resources offered an opportunity for hominids with sufficient capability to exploit the animal resources. The archeological record suggests that this is what occurred with *H. erectus*—the development of the first rudimentary hunting and gathering economy in which game animals became a significant part of the diet and resources were shared within foraging groups (Potts, 1988; Harris and Capaldo, 1993; Roche et al., 1999).

Additionally, changes in the skeletal and dental anatomy of *H. erectus* relative to the late australopithecines indicate that these forms were consuming different foods. As shown in Table 3, molar tooth sizes are greatly reduced in *H. erectus* compared to the robust australopithecines (377 mm² in early *H. erectus* compared to 588 mm² in *Australopithecus robustus* and 756 mm² in *Australopithecus boisei*). Additionally, *H. erectus*

Table 4

Productivity of modern tropical forest/woodland and savanna ecosystems. From Leonard and Robertson (1997, 2000)

Ecosystem	Primary productivity (kJ/m ² /yr)	Herbivore (2°) productivity (kJ/m ² /yr)	Carnivore (3°) productivity (kJ/m ² /yr)
Forest/Woodland	7200	3.6	0.03
Savanna	4050	10.1	0.08

shows substantial reductions in craniofacial and mandibular robusticity relative to the australopithecines (Wolpoff, 1999). Yet, despite the smaller teeth and jaws, *H. erectus* was a much bigger animal than the australopithecines, being human-like in its stature, body mass and body proportions (McHenry, 1992, 1994a; McHenry and Coffing, 2000; Ruff and Walker, 1993; Ruff et al., 1997). Together these features indicate that early *H. erectus* was consuming a richer, more calorically-dense diet with less low quality plant material and more animal foods.

These changes in diet and foraging behavior did not turn our hominid ancestors into carnivores;

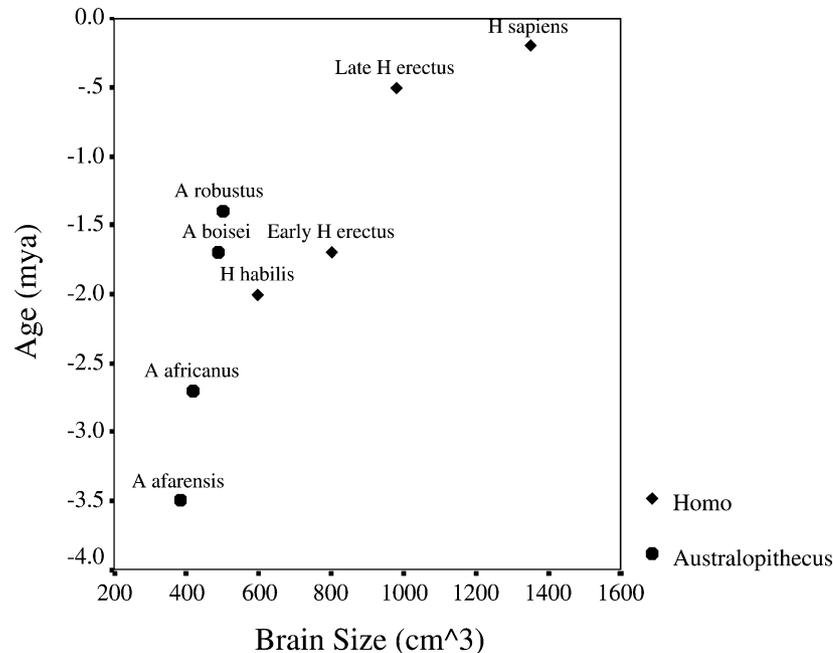


Fig. 4. Evolution of hominid brain size (cm³) over the last 4 million years. Between 4.0 and 2.0 million years ago (mya), the australopithecines show only modest changes in brain size, from ~400–530 cm³. With the emergence and early evolution of the genus *Homo* (i.e. *H. habilis* and early *H. erectus*) at 2.0–1.7 mya we find a rapid burst of evolutionary change in brain size such that brain sizes of early *H. erectus* at 1.7 mya are 800–900 cm³.

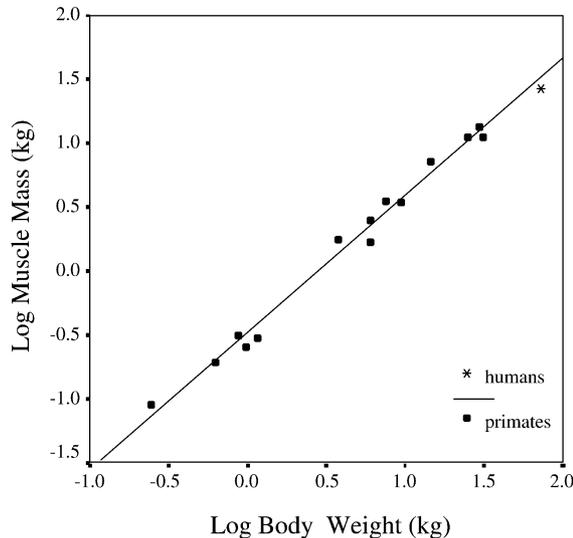


Fig. 5. Log–log plot of muscle weight (kg) vs. body weight (kg) of 15 primate species (including humans). Across all primates, skeletal muscle mass scales isometrically with body weight ($SM=0.33Wt^{1.06}$; $r=0.994$). Humans fall below the primate regression line (standardize residual = -0.86), indicating that they are ‘under-muscled’ relative to other primates.

however, the addition of modest amounts of meat to the diet combined with the sharing of resources that is typical of hunter-gatherer groups would have significantly increased the quality and stability of hominid diets. These changes in dietary quality appear to have been critical in promoting the rapid brain evolution seen with the evolution of *H. erectus*. While dietary change alone cannot explain the evolution of large hominid brains, a sufficiently high quality diet was probably necessary for supporting the increased energy demands of larger brains.

3.3. Human body composition in evolutionary perspective

Distinctive differences in human body composition also may be linked to the metabolic costs of our large brains. Relative to other primates, humans are ‘under-muscled’, having relatively low levels of skeletal muscle for a primate of our size. Fig. 5 shows the scaling relationship between muscle mass and body weight in living primate species from Table 2. Across all primates, there is an isometric relationship between muscle mass and body mass:

$$\text{Skeletal Muscle Mass} = 0.33Wt^{1.06} \quad (r=0.994)$$

Humans fall substantially below the primate regression, deviating by 0.86 SD units. This indicates that at the same body weight, humans have systematically lower levels of muscle mass than other primates. Further, recent work by Snodgrass et al. (1999) has shown that primates, as a group, are relatively ‘under-muscled’ compared to other mammals.

Unlike many bodily tissues and organs, brain metabolism is stable and may not be down-regulated to conserve resources during periods of starvation or negative energy balance. In light of this constraint, the human brain may have posed a special challenge during infancy, when the brain accounts for a substantial percentage of total metabolic expenditure. The challenge of sustaining cerebral metabolism during infancy is compounded by the problem of nutritional stress related to weaning and the common infectious diseases of infancy and early childhood. One partial solution to this problem may have been to maintain a larger energy reserve (Kuzawa, 1998). Indeed, humans appear to be relatively fatter than other mammals – a feature particularly notable at birth and during infancy.

Fig. 6 compares percent body fat at birth among mammals (adapted from Kuzawa, 1998). At ~15–16% human infants have the highest body fat levels of the 15 species shown here. Not only

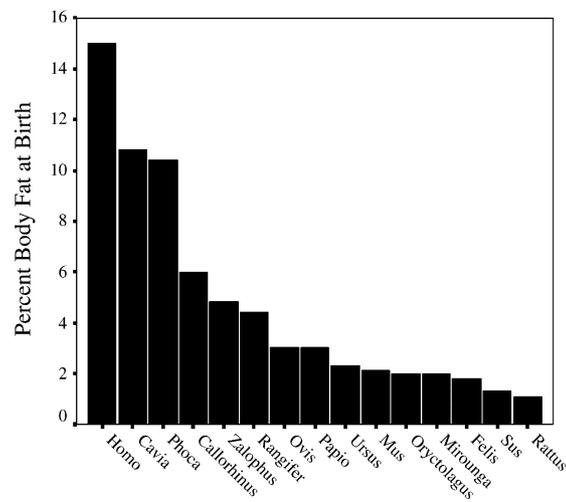


Fig. 6. Percent body fat at birth of 15 mammalian species (adapted from Kuzawa, 1998). At 15–16% human infants have the highest level of adiposity.

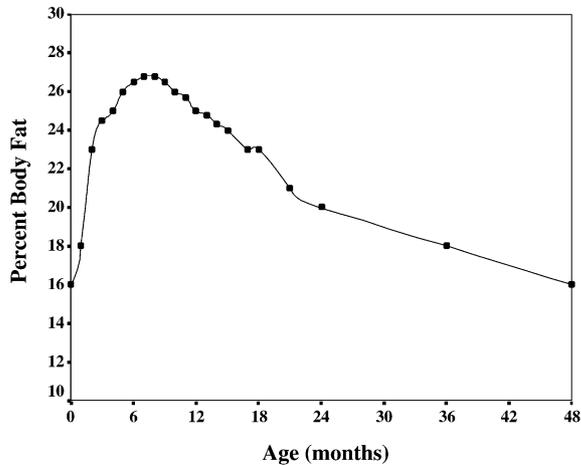


Fig. 7. Changes in percent body fat of human infants during the first 48 months of life (from Dewey et al., 1993). Body fatness rises from 16% to 26% during the first 12–18 months of life, and then declines to ~16% by 4 years of age.

is the large-brained human newborn especially fat, but there appears to be a link between relative body fatness at birth and levels of encephalization across mammals generally. For the species shown in Fig. 6, the correlation between relative adult brain size and relative body fatness at birth is 0.61 ($P < 0.05$). Although the number of data points is small the results are consistent with our expectations – species devoting a larger percentage of metabolism to meeting the obligatory demands of a large brain also increase the size of the energy buffer, as represented by fat stores.

The need to maintain a sizeable energy buffer to support cerebral metabolism may also help explain developmental changes in human body composition. Although born fat, human infants continue to gain body fat during their early post-natal life. Fig. 7 shows changes in percent body fat among infants during the first 48 months of life based on longitudinal research by Dewey et al. (1993). During the first half year of life, well-fed infants increase in percentage body fat from about 16% to about 26%. This pattern is likely not accidental: adiposity peaks at the age when weaning is common in many societies, and when the likelihood of having to rely upon energy reserves is thus greatest.

These high levels of body fatness during infancy are likely linked to the extreme metabolic demands of the brain (see Kuzawa, 1998). Fig. 8 shows the percent of RMR that is allocated to the brain

plotted as a function of body weight over the course of human growth and development (from data presented in Holliday, 1986). Whereas a 70 kg adult expends ~20–25% of RMR for the brain, an infant of less than 10 kg is using upwards of 60%! These enormous relative energy demands for infants primarily reflect both their high brain:body weight ratios.

Overall, key aspects of human growth and development of body composition are shaped by the metabolic demands of our brains. As has been widely noted, human gestation length is relatively short for a species of our body and brain size. Our infants are born altricially (relatively under-developed), and, unlike other primates, rapid brain growth continues into early post-natal life (Martin, 1990; Rosenberg, 1992). To provide energy stores for the metabolic demands of relatively large brains during infancy, humans have high levels of body fat at birth and continue to gain fatness during the first year of life. Additionally, the development of higher levels of body fat and lower levels of muscularity in humans compared to other mammals, serves to reduce the total metabolic costs of the rest of the body aside from the brain.

Even with these alterations of body composition, mass-specific energy and nutrient requirements during infancy are much higher than at any point later in life (Kuzawa, 1998). Energy requirements

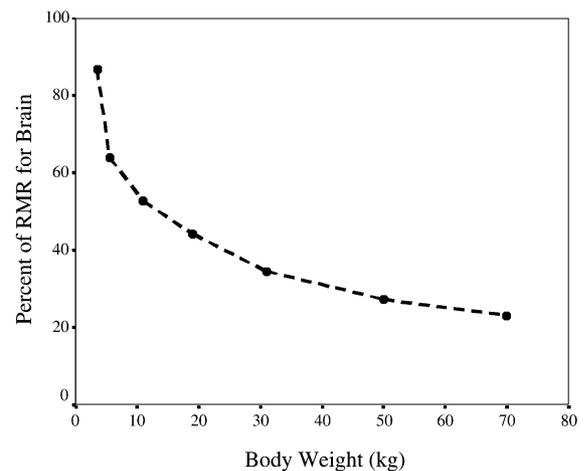


Fig. 8. Percent of resting metabolic rate (RMR) allocated to the brain during human growth and development (data from Holliday, 1986). During infancy (body weight < 10 kg), brain metabolism accounts for upwards of 60% of RMR. At adulthood (weight = 70 kg), brain metabolism represents ~20% of RMR.

for children under 2 years of age are greater than 100 kcal/kg, whereas moderately active adults require only approximately 40 kcal/kg ((Food and Agriculture Organization/World Health Organization/United Nations University), 1985; James and Schofield, 1990). Because of these elevated energy demands during infancy, nutrient dense breast milk and weaning foods are essential for sustaining the high rates of brain and body growth that are characteristic of early life. Indeed, among many populations of the developing world today, high levels of physical and cognitive growth retardation are linked to low-quality weaning foods that are not sufficiently nutritionally dense (Allen et al., 1992; Berti et al., 1998; Leonard et al., 2000; Pollitt et al., 2000)

When the distinct developmental pattern of body composition emerged in human evolution is difficult to discern. However, with *H. erectus* we do find the first evidence of 'human-like' patterns of sexual dimorphism in body weight (Aiello and Key, 2002). The sex-specific estimates of fossil body weights in Table 3 show that with *H. erectus*, not only is there a marked increase in average size, but the increase is disproportionately large in females. That is, with the first major pulse of brain evolution in hominids (*H. erectus*) is associated with a dramatic increase in female body size, from approximately 30–34 kg in the australopithecines to ~52 kg with early *H. erectus*. This pattern is consistent with a metabolic model for brain evolution, since the high costs of 'growing' large brains is largely born by females (mothers) through the energy demands of pregnancy and lactation (Martin, 1989). Thus, the increased female body size (and the resulting reduction in sexual dimorphism) seen in *H. erectus* may be another signal that sufficient nutritional resources were available to support the development of larger brain size.

Recent comparative analyses on human populations further support the link between high reproductive costs and reductions in sexual dimorphism. Guégan et al. (2000) showed that sexual dimorphism in stature was lowest among human populations with the highest fecundity levels and greatest risks of maternal mortality. In other words, in populations where fertility is high and the cumulative risk of death during pregnancy is elevated for mothers, there is selection for relatively larger body size in females in order to reduce problems during childbirth. This type of selective

regime may have been responsible for promoting relatively larger body size among *H. erectus* females.

4. Discussion

The high energy demands of human brain size appeared to have necessitated both improvements in dietary quality and changes in body composition over the course of hominid evolution. Indeed many of the important changes and evolutionary innovations in human evolutionary history have been about improvements in dietary quality. Such changes were critical to the evolution of our large brains and to the broad expansion of humans throughout the world (Leonard, 2002). With *H. erectus*, we see improvements in dietary quality likely resulting from (1) the incorporation of more animal foods into the diet, (2) improved tool technology, and (3) the development of a food sharing associated with a hunting and gathering lifeway (Potts, 1988; Harris and Capaldo, 1993; Blumenschine et al., 1994). Other improvements in DQ later in human evolution include the use of fire and the development of cooking as means of making food more digestible, providing more usable calories than if the same food had been consumed raw (Wragham et al., 1999). Even the much later advent of agriculture had important implications for DQ, as human populations began to manipulate relatively marginal plant species so as to increase their productivity, digestibility and nutritional content (Flannery, 1973).

Along with changes in DQ, human evolution also resulted in important changes in the developmental aspect of human body composition. By increasing the relative levels of body fatness, particularly early in life, and reducing levels of muscle mass, humans are able to accommodate the growth of their large brains in two important ways: (1) by having a ready supply of stored energy to 'feed the brain', and (2) by reducing the total energy costs of the rest of the body, replacing metabolically more expensive muscle with adipose tissue.

The reductions in muscle mass are also evident for primates in general, compared to other mammalian species. Such reductions in muscularity relative to body size may be a consequence of the arboreal heritage of the primate order (Snodgrass et al., 1999). Additionally, such reductions in muscularity help to explain the paradox of primate

species having large (metabolically costly) brains, without showing substantial elevations in RMR. In terms of a 'metabolic budget', the high energy costs of relatively large primate brains may be partly offset by reductions in muscularity (Snodgrass et al., 1999). Aiello and Wheeler (1995) have suggested that reduction in gut size may account for the lack increase in RMR among humans and other primates. However, recent analyses suggest that primates do not have systematically smaller gastrointestinal sizes that other non-primate mammals (Snodgrass et al., 1999).

From the perspective of modern humans, what is extraordinary is the variety of different strategies used to accommodate our distinctive metabolic and nutritional needs among populations living in radically different environments. Humans have evolved creative ways of developing nutritionally rich diets in virtually all environments, from Inuit hunters of the arctic, subsisting largely on meat and fat to Amazonian horticulturalists, consuming a diet of rice, cassava, and wild game. Indeed, the hallmark of human evolution has been the diversity of different strategies that have been used to create diets that meet our distinctive metabolic requirements.

Acknowledgments

We are grateful to Drs. Peter Hochachka and Kathy Myburgh for the opportunity to contribute to this special issue. The comments and suggestions from Dr Susan Antón and two anonymous reviewers helped to substantially improve this paper. This research was supported, in part, by grants to WRL by the Natural Sciences and Engineering Council (NSERC) of Canada (OGP-0116785) and the Wenner-Gren Foundation for Anthropological Research (#295).

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