Effects of Brain Evolution on Human Nutrition and Metabolism

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Key Words

encephalization, hominin, diet quality, body composition, *Homo erectus*

Abstract

The evolution of large human brain size has had important implications for the nutritional biology of our species. Large brains are energetically expensive, and humans expend a larger proportion of their energy budget on brain metabolism than other primates. The high costs of large human brains are supported, in part, by our energy- and nutrient-rich diets. Among primates, relative brain size is positively correlated with dietary quality, and humans fall at the positive end of this relationship. Consistent with an adaptation to a high-quality diet, humans have relatively small gastrointestinal tracts. In addition, humans are relatively "undermuscled" and "over fat" compared with other primates, features that help to offset the high energy demands of our brains. Paleontological evidence indicates that rapid brain evolution occurred with the emergence of *Homo erectus* 1.8 million years ago and was associated with important changes in diet, body size, and foraging behavior.

Contents

INTRODUCTION

Over the past 20 years, the evolution of human nutritional requirements has received ever greater attention among both anthropologists and nutritional scientists (3, 21, 28, 29, 35, 48, 49, 86). Increasingly, we have come to understand that many of the key features that distinguish humans from other primates (e.g., our bipedal form of locomotion and large brain sizes) have important implications for our distinctive nutritional needs (3, 47, 50). The most important of these is our high levels of encephalization (large brain:body mass). The energy demands (kcal/g/min) of brain and other neural tissues are extremely high—approximately 16 times that of skeletal muscle (37, 43). Consequently, the evolution of large brain size in the human lineage came at a very high metabolic cost.

Encephalization: brain size in relation to body size. In general, primates are more encephalized than other mammals

RMR: resting metabolic rate

GI: gastrointestinal

Despite the fact that humans have much larger brains per body weight in comparison with other primates or terrestrial mammals, the resting energy demands for the human body are no more than for any other mammal of the same size (48, 49). 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% to 25% of resting metabolic rate (RMR) in an adult human body. This is far more than the 8% to 10% observed in other primate species and still more than the 3% to 5% allocated to the brain by other (nonprimate) mammals (49).

The disproportionately large allocation of our energy budget to brain metabolism has important implications for our dietary needs. This review draws on both analyses of living primate species and the human fossil record to examine the avenues through which humans have adapted to the metabolic demands of greater encephalization. We begin by considering the energy demands associated with large brain size in modern humans relative to other primates and nonprimate mammals. Next we examine comparative dietary data for modern human groups and other primate species to evaluate the influence that variation in relative brain size has on dietary patterns among modern primates. We then turn to an examination of the human fossil record to examine when and under what conditions in our evolutionary past key changes in brain size and diet likely took place. Finally, we explore how the evolution of large human brains was likely accommodated by differential changes in the relative sizes of other organs [e.g., muscle, fat, and gastrointestinal (GI) tract]. The high metabolic costs of our large brains appear to play a strong hand in shaping distinctive aspects of human growth and development.

COMPARATIVE PERSPECTIVES ON BRAIN SIZE, BODY SIZE, DIET, AND METABOLIC RATE

Table 1 presents comparative data on RMR, brain size, body size, and diet for living humans and nonhuman primates (from 51). Primates, as a group, are similar to other mammals in having RMRs that scale to approximately three-fourths power of body mass (see 44). **Figure 1** (see color insert) presents the relationship RMR (kcal/day) and body

Table 1 Comparative data on resting metabolic rate (RMR; kcal/day), body mass (kg), brain mass (g), and diet quality (DQ) in 41 primate species[a]

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

[a] Data sources: References 8, 40, 42, 49, 58, 69, 70, 72, 79, and 85.

Scaling (allometry): the change in size on biological measure with respect to another biological measure (often body size)

DQ: diet quality

mass (kg) for humans and the 40 other primate species from **Table 1**. It is clear that humans conform to the general primate scaling relationship between RMR and body weight, having RMRs that fall within 2% of the value predicted from the general primate relationship. The implication of this is that humans allocate a much larger share of our daily energy budget for brain metabolism than do other species.

The disproportionately high energy costs of our large brains are evident in **Figure 2** (see color insert), which shows the scaling relationship between brain weight (grams) and RMR for humans and 35 other primate species (from **Table 1**) and 22 nonprimate mammalian species. The solid line denotes the best-fit regression for nonhuman primate species, and the dashed line denotes the best-fit regression for the nonprimate mammals. The slopes of the two regressions are similar (0.94 primates, 0.90 mammals; n.s.), whereas the y-intercepts are significantly different (−0.377 primates, −0.832 mammals; $P < 0.01$). Thus, at a given metabolic rate, primates have systematically larger brain sizes than those of other mammals, and humans, in turn, have larger brain sizes than do other primates. As a group, primates have brains that are approximately three times the size of brains of other mammals. Human brain sizes are some three times those of other primates.

The large allocation of our energy budget to brain metabolism raises the question of how humans are nutritionally able to accommodate the metabolic demands of our large brains. Recent work suggests that important dimensions of human nutritional biology are associated with the high energy demands of our large brains. It appears that humans consume diets that are denser in energy and nutrients in comparison with diets of other primates of similar size. Recent studies have shown that modern human foraging populations typically derive more than half of their dietary energy intake from animal foods, although considerable variation in diets exists (20, 41). In comparison, modern great apes obtain much of their diet from low-quality plant foods. Gorillas derive more than 80% of their diet from fibrous foods such as leaves and bark (69). Even among common chimpanzees (*Pan troglodytes*), only about 5% to 10% of calories are derived from vertebrate animal foods (62, 78, 84). Field studies indicate that meat is a desirable and prized food item for many primate species. The low rates of consumption reflect the limited ability of chimpanzees and other primates to obtain large and consistent quantities of vertebrate foods because of high foraging costs (61). That is, the time and energy associated with pursuing game animals appear to be prohibitively high for most large-bodied primates.

Comparative dietary analyses of living primate species (including humans) are shown in **Figure 3** (see color insert), which plots dietary quality (DQ) as function of body mass (kg) for 33 different primate species (from **Table 1**). The DQ index was developed by Sailer et al. (72) and quantifies the energy and nutrient density of the diet based on the relative proportions of structural plant parts (***s***; e.g., leaves, stem, bark), reproductive plant parts (***r***; e.g., fruits, flowers), and animal foods (***a***; vertebrates and invertebrates):

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

The index ranges from a minimum of 100 (a diet of all leaves and/or structural plant parts) to 350 (a diet of all animal material).

Figure 3 shows that an inverse relationship exists between DQ and body mass ($r = -0.59$ total sample, –0.68 nonhuman primates only; $P < 0.001$). This tendency of larger primates to feed on lower-quality diets is something that is observed in other mammals (10, 39) and appears to be a consequence of the scaling relationship between energy requirements and body mass. As noted in **Figure 1**, the scaling coefficient between RMR and mass is less than one, implying that larger primates have proportionally lower metabolic rates than smaller ones. Large primates such as gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*) have high total energy requirements but relatively low mass-specific needs (e.g., kcal/kg/day). They fulfill their energy needs by feeding on foods that are abundant but low in quality (e.g., leaves and foliage). Conversely, small animals [e.g., the pygmy marmoset (*Cebuella pygmaea*)] have low total energy requirements but very high mass-specific needs. They typically subsist on foods that are rich in calories and nutrients but relatively limited in abundance (e.g., saps, gums, and insects).

Humans, however, have substantially higher-quality diets than would be expected for a primate of our size. Note that the average diet for modern human foragers (based on dietary data from five modern human foraging populations; see 49) falls substantially above the regression line. Overall, the staple 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 a smaller volume of food to get the energy and nutrients we require.

Figure 4 (see color insert) shows relative brain size versus relative dietary quality for the 33 different primate species from **Figure 3**. Relative brain size for each species is measured as the standardized residual (z-score) from the primate brain versus body mass regression, and relative DQ is measured as the residual from the DQ versus body mass regression. There is a strong positive relationship ($r = 0.63$; $P < 0.001$) between the amount of energy allocated to the brain and the caloric and nutrient density of the diet. Across all primates, larger brains require higher-quality diets. Humans fall at the positive extremes for both parameters, having the largest relative brain size ($z = +3.27$) and the highest quality diet ($z = +2.05$). Thus, the large, metabolically expensive human brain is partially offset by the consumption of an energy-dense and nutrient-rich diet. This relationship implies that the evolution of larger hominin brains would have necessitated the adoption of a sufficiently high-quality diet (including meat and energy-rich fruits) to support the increased metabolic demands of greater encephalization.

The relative size and morphology of the human GI tract also reflect our high-quality diet. Most large-bodied primates have expanded large intestines (colons), an adaptation to fibrous, low-quality diets (59). Humans, on the other hand, have small gut volumes for our size, with relatively enlarged small intestines and a smaller colon (3, 53, 75).

The enlarged colons of most large-bodied primates permits fermentation of low-quality plant fibers, allowing for extraction of additional energy in the form of volatile fatty acids (60, 63). In contrast, the GI morphology of humans (small colon and relatively enlarged small intestine) is more similar to a carnivore and reflects an adaptation to an easily digested, nutrient-rich diet (52, 53, 81).

Together, these comparative data suggest that the dramatic expansion of brain size over the course of human evolution likely would have required the consumption of a diet that was more concentrated in energy and nutrients than is typically the case for most large primates. This does not imply that dietary change was the driving force behind major brain expansion during human evolution. Rather, the available evidence indicates that a sufficiently high-quality diet was probably a necessary condition for supporting the metabolic demands associated with evolving larger hominin brains.

Hominin: living humans and our fossil ancestors that lived after the last common ancestor between humans and apes

EVOLUTIONARY CHANGES IN BRAIN SIZE AND DIET

Trends in the Hominin Brain Size, Body Size, and Tooth Size

Over the past four million years, average brain size in the hominin lineage has more than tripled, increasing from approximately 400 cm^3 in the earliest australopithecines to 1300–1400 cm^3 in modern humans (57). However, the rates of evolutionary change in brain size have been highly variable over this

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

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

All data, except for *Homo erectus*, from (57). Early *H. erectus* brain size is the average of African specimens as presented in (56), Indonesian specimens from (5), and Georgian specimens from (31, 32). Data for late *H. erectus* are from (55).

period. Human evolution has been characterized by periods of slow increases in brain size alternating with periods of dramatic change. The human fossil record indicates that the first substantial burst of evolutionary change in hominin brain size occurred about 2.0 to 1.7 million years ago (mya) and was associated with the emergence and evolution of early members of our own genus, *Homo*.

Table 2 presents data on evolutionary changes in hominin brain size (cm^3), estimated adult male and female body mass (kg), and posterior tooth area (mm^2) (data from 5, 31, 32, 55–57). Hominin body masses were estimated from measurements of weight-bearing joint surfaces using predictive equations derived from a diverse skeletal sample of modern humans (see 54). Posterior tooth areas are the summed surface areas of the premolar and molar teeth (57).

The australopithecines showed only modest brain size evolution from about 430 to 530 cm^3 over more than two million years (from about 4 to 1.5 mya). With the evolution of the genus *Homo* there were substantial increases in encephalization, with brain sizes of over 600 cm^3 in *Homo habilis* (at 1.9 to 1.6 mya) and 800 to 900 cm^3 in early members of *Homo erectus* (at 1.8 to 1.5 mya). Although body sizes also increase with *H. erectus*, the changes in brain size are disproportionately greater than those in body mass. Thus, the level of encephalization we find with *H. erectus* is greater than that seen among any living nonhuman primate species today (49).

Australopithecus: genus of early hominins that existed in Africa between 4 and 1.2 mya

The changes in the craniofacial and dental anatomy of *H. erectus* suggest that these forms were consuming different foods from those consumed by its australopithecine relatives. During the evolution of the australopithecines, the total surface area of the grinding teeth increased dramatically from 460 mm^2 in *Australopithecus afarensis* to 756 mm^2 in *A. boisei*. In contrast, with the emergence of early *Homo* at approximately 2 mya, we see marked reductions in the posterior dentition. Postcanine tooth surface area is 478 mm^2 in *H. habilis* and 377 mm^2 in early *H. erectus*.

H. erectus also shows substantial reductions in craniofacial and mandibular robusticity relative to the australopithecines (91). Yet, despite having smaller teeth and jaws, *H. erectus* was a much bigger animal than the australopithecines, being humanlike in its stature, body mass, and body proportions (54, 55, 57, 71). Together, these features indicate that early *H. erectus* was consuming a richer, more calorically dense diet with less low-quality fibrous plant material. How the diet might have changed with the emergence of *H. erectus* is examined in the following section.

Dietary Changes Associated with Brain Evolution in Early *Homo*

Increasing evidence suggests that the evolution of early *Homo*, particularly *H. erectus*, was associated with important changes in foraging patterns and dietary consumption compared with earlier hominin species. Recent analyses of dental microwear and stable carbon isotope levels of tooth enamel indicate that the australopithecines consumed a seasonally variable diet composed of both plant (e.g., fruits, seeds, grasses, and tubers) and some animal foods (76, 77, 83). Earlier interpretations of the so-called "robust" australopithecines (*A. robustus* and *A. boisei*)—with their massive jaws, robust faces, and large molar teeth—viewed these species as being dietary specialists that subsisted largely on seeds, nuts, and other hard objects common to the African savanna. However, the isotopic analyses now show that their diets were likely broader and more varied than previously thought (76, 77, 87). The consumption by australopithecines of limited quantities of animal foods (including invertebrates) is suggested by analogies with living primates (especially chimpanzees) and supported by stable isotope studies and association with putative bone tools likely used for termite extraction (7).

Paleontological and archaeological evidence indicates modest dietary change in earliest *Homo* (i.e., *H. habilis*); this species likely incorporated more animal foods in its diet, although the relative amounts obtained through hunting compared with scavenging is debated (12, 13, 36, 65). Evidence for dietary change in this species can be seen in the reduced masticatory functional complex (e.g., posterior tooth size); dental reduction in *H. habilis* reversed successive increases in cheek tooth size among the australopithecines (57). Technological advancements, such as the development of Oldowan industry tools, allowed easier processing of vertebrate carcasses and increased access to meat as well as energy- and nutrient-rich marrow and brains (74).

The evolution of *H. erectus* appears to be a major adaptive shift in human evolution. With the emergence of *H. erectus* in East Africa 1.8 mya we find (*a*) marked increases in brain and body size, (*b*) reductions of posterior tooth size and craniofacial robusticity, (*c*) the evolution of humanlike limb proportions, and (*d*) important changes in foraging/subsistence behavior (2, 4, 91, 92). These changes occurred within the context of large-scale climatic shifts (88, 95). The environment was becoming much drier, resulting in declines in forested areas and an expansion of open woodlands and grasslands (14, 26, 68, 95). Such a transformation of the African landscape would have strongly influenced the distribution of food resources for our hominin ancestors, making animal foods more abundant and thus an increasingly attractive food resource (9, 65). Using modern tropical ecosystems as our reference, we have found that although savanna/grasslands have much lower net primary (energetic) productivity than woodlands (4050 versus 7200 kcal/m^2/yr), the level of herbivore productivity in savannas is almost three times that of the woodlands (10.2 versus 3.6 kcal/m^2/yr) (50). Thus, fundamental changes in ecosystem structure 2.0 to 1.8 mya appear to have resulted in a net increase in the energetic abundance of grazing mammals (e.g., ungulates) on the E. African landscape. Such an increase would have offered an opportunity for hominins with sufficient behavioral and technological capability to exploit those resources.

Oldowan: the first stone tool technology in the human fossil record, characterized by simple flakes and choppers. First evident approximately 2.5 mya

The archeological record provides evidence that this occurred with *H. erectus*, as this species is associated with stone tools and the development of the first rudimentary hunting and gathering economy. Meat does appear to have been more common in the diet of *H. erectus* than it was in the australopithecines. H. erectus likely acquired mammalian carcasses through both hunting and confrontational scavenging (i.e., allowing other animal hunters to make the kill and then chasing them away from the carcass) (18, 65). In addition, the archaeological evidence

Acheulean: stone tool industry of the early and middle Pleistocene characterized by hand axes and cleavers. First evident 1.6 to 1.4 mya, associated with early *Homo*

DHA: docosahexaenoic acid

AA: arachidonic acid

indicates that butchered animals were transported back to a central location (home base) where the resources were shared within foraging groups (18, 36, 66, 67). Increasingly sophisticated stone tools (i.e., the Acheulean industry) emerged approximately 1.6 to 1.4 mya, improving the ability of these hominins to process animal and plant materials (6). These changes in diet and foraging behavior would not have turned our hominin ancestors into carnivores; however, the addition of even modest amounts of meat to the diet (10% to 20% of dietary energy) combined with the sharing of resources that is typical of hunter-gatherer groups would have significantly increased the quality and stability of the diet of *H. erectus*.

Cordain and colleagues (22) have noted that beyond the energetic benefits, greater consumption of animal foods would have provided increased levels of key fatty acids that would have been necessary for supporting the rapid hominin brain evolution. Mammalian brain growth is dependent upon sufficient amounts of two long-chain polyunsaturated fatty acids: docosahexaenoic acid (DHA) and arachidonic acid (AA) (22, 24). Because the composition of all mammalian brain tissue is similar with respect to these two fatty acids, species with higher levels of encephalization have greater requirements for DHA and AA (24). It also appears that mammals have a limited capacity to synthesize these fatty acids from dietary precursors. Consequently, dietary sources of DHA and AA were likely limiting nutrients that constrained the evolution of larger brain size in many mammalian lineages (23, 24).

Cordain and colleagues (22) have demonstrated that wild plant foods available on the African savanna (e.g., tubers, nuts) contain, at most, trace amounts of AA and DHA, whereas muscle tissue and organ meat of wild African ruminants provide moderate to high levels of these key fatty acids. As shown in **Table 3**, brain tissue is a rich source of both AA and DHA, whereas liver and muscle tissues are good sources of AA and moderate sources of DHA. Other good sources of AA and DHA are freshwater fish and shellfish (17, 22, 24). Cunnane and colleagues (17, 25) have suggested that the major increases in hominin encephalization were associated with systematic use of aquatic (marine, riverine, or lacustrian) resources. However, there is little archeological evidence for the systematic use of aquatic resources until much later in human evolution (45).

An alternative strategy for increasing dietary quality in early *Homo* has been proposed by Wrangham and colleagues (93, 94). These authors argue that the controlled use of fire for cooking allowed early *Homo* to improve the nutritional density of their diet. They note that the cooking of savanna tubers and other plant foods would have served to both soften them and increase their energy/nutrient bioavailability. In their raw form, the starch in roots and tubers is not absorbed in the small intestine and is passed through the body as nondigestible carbohydrate (30, 82). However, when heated, the

Table 3 Energy (kcal), fat (g), protein (g), arachidonic acid (AA), and docosahexaenoic acid (DHA) contents of African ruminant, fish, and wild plant foods per 100 grams. Data derived from (22)

Food item	Energy (kcal)	Fat (g)	Protein (g)	AA (mg)	DHA (mg)
African ruminant (brain)	126	9.3	9.8	533	861
African ruminant (liver)	159	7.1	22.6	192	41
African ruminant (muscle)	113	2.1	22.7	152	10
African ruminant (fat)	745	82.3	1.0	20–180	trace
African fish	119	4.5	18.8	270	549
Wild tuber/roots	96	0.5	2.0	0	0
Mixed wild plants	129	2.8	4.1	0	0

starch granules swell and are disrupted from the cell walls. This process, known as gelatinization, makes the starch much more accessible to breakdown by digestive enzymes (34). Thus, cooking increases the nutritional quality of tubers by making more of the carbohydrate energy available for biological processes.

Although cooking, which served to increase dietary digestibility and quality, is clearly an important innovation in hominin evolution, there is very limited evidence for the controlled use of fire by hominins before 1.5 mya (11, 15, 64). The more widely held view is that the use of fire and cooking did not occur until later in human evolution, at 200,000 to 250,000 years ago (80, 90). Moreover, nutritional analyses of wild tubers used by modern foraging populations (e.g., 16, 73, 89) suggest that the energy content of these resources is markedly lower than that of animal foods, even after cooking (22). Unlike animal foods, tubers are also devoid of both DHA and AA (22; see **Table 3**). Consequently, major questions remain about whether cooking and the heavy reliance on roots and tubers were important forces for promoting rapid brain evolution with the emergence of early *Homo*.

Overall, the available evidence seems to best support a mixed dietary strategy in early *Homo* that involved the consumption of larger amounts of animal foods in comparison with the australopithecines. Ungar and colleagues (87) recently suggested that early *Homo* likely pursued a flexible and versatile subsistence strategy that would have allowed them to adapt to the patchy and seasonally variable distribution of food resources on the African savanna. They note that such a model is more plausible than are ones proposing heavy reliance on one particular type of resource (e.g., meat or tubers). This is indeed true; however, what appears to be happening with early *Homo*—especially with *H. erectus*—is the development of a more stable and effective way of extracting resources from the environment. The increase in dietary quality and stability was likely achieved partly through changes in diet composition (22, 49) and partly through social and behavioral changes like food sharing and perhaps division of foraging tasks (36, 38, 41). This greater nutritional stability provided a critical foundation for fueling the energy demands of larger brain sizes.

BRAIN EVOLUTION AND HUMAN BODY COMPOSITION

In addition to improvements in dietary quality, the increased metabolic cost of larger brain size in human evolution also appears to have been supported by changes in body composition. Humans allocate a substantially larger share of their daily energy budget to their brains than do other primates or other mammals, which implies that the size and metabolic demands of certain other organs/organ systems may be relatively reduced in humans compared with other species. Thus, the critical question is, which organs have been reduced or altered in their relative size over the course of human evolution to compensate for the expansion of brain size?

Analyses of human and primate body composition offer possible answers to this question. Aiello (1) and Aiello & Wheeler (3) have argued that the increased energy demands of the human brain were accommodated by the reduction in size of the GI tract. Since the intestines are similar to the brain in having very high energy demands (so-called expensive tissues), the reduction in size of the large intestines of humans relative to other primates is thought to provide the necessary energy "savings" required to support elevated brain metabolism. Aiello & Wheeler (3) have shown that among a sample of 18 primate species (including humans), increased brain size was associated with reduced gut size. However, recent analyses by Snodgrass et al. (75) have failed to demonstrate significant differences in GI size between primates and nonprimate mammals that are predicted from the expensive tissue hypothesis. Thus, while it is clear that humans have relatively small GI sizes for their body mass, questions remain about the extent to which reductions in GI size helped to balance the increased metabolic costs associated with expansion of brain size during the course of human evolution. The reduced GI size in humans instead may be the direct consequence of improvements in DQ over the course of human evolution.

Leonard and colleagues (51) and Kuzawa (46) have suggested that differences in muscle and fat mass between humans and other primates may also account for variation in the budgeting of metabolic energy. Relative to other primates and other mammals, humans have lower levels of muscle mass and higher levels of body fatness (46, 51, 65). The relatively high levels of adiposity in humans have two important metabolic implications for brain metabolism. First, because fat has lower energy requirements than that of muscle tissue, replacing muscle mass with fat mass results in energy savings that can be allocated to the brain. Additionally, fat provides a ready source of stored energy that can be drawn upon during periods of limited food availability. Consequently, the higher levels of body fat in humans may also help to support larger brain size by providing stored energy to buffer against environmental fluctuations in nutritional resources.

The importance of body fat is particularly notable in human infants, which have both high brain-to-body weight ratios and high levels of body fatness (46). **Table 4** shows age-related changes in body weight (kg), brain weight (g), fatness (%), RMR (kcal/day), and percent of RMR allocated to the brain for humans from birth to adulthood. We see that in infants, brain metabolism accounts for upward of 60% of RMR. Human infants are also considerably fatter than infants of other mammalian species (46). Body fatness in human infants is approximately 15% to 16% at birth, and continues to increase to 25% to 26% during the first 12 to 18 months of postnatal growth. Fatness then declines to about 15% by early childhood (27). Thus, during early human growth and development, it appears that body fatness is highest during the periods of the greatest metabolic demand of the brain.

It is likely that fundamental changes in body composition (i.e., the relative sizes of different organ systems) during the course of hominin evolution allowed for the expansion of brain size without substantial increases in the total energy demands for the body. At present, we do not know which alterations were the most critical for accommodating brain expansion. Variation in body composition both within and between primate species is still not well understood. Our knowledge of variation in body composition among humans is based largely on data from populations of the industrialized world. Consequently, more and better data on interspecific and ontogenetic variation in primate and human body composition are necessary to further resolve these issues.

Table 4 Body weight (kg), brain weight (g), percent body fat (%), resting metabolic rate (RMR; kcal/day), and percent of RMR allocated to brain metabolism (BrMet, %) for humans from birth to adulthood[a]

Age	Body weight (kg)	Brain weight (g)	Body fat (%)	RMR (kcal/day)	BrMet (%)
Newborn	3.5	475	16	161	87
3 months	5.5	650	22	300	64
18 months	11.0	1045	25	590	53
5 years	19.0	1235	15	830	44
10 years	31.0	1350	15	1160	34
Adult male	70.0	1400	11	1800	23
Adult female	50.0	1360	20	1480	27

[a] All data are from (37), except for percent body fat data for children 18 months and younger, which are from (27).

New imaging techniques such as magnetic resonance imaging and positron emission tomography scans offer the potential to directly explore variation in organ weight and organ-specific energy demands in living humans and primates. For example, Gallagher et al. (33) recently used magnetic resonance imaging technology to measure how differences in organ weights contribute to ethnic differences in RMRs among living humans. These authors demonstrated that the significant differences in RMR between their African American and Euro-American samples could be accounted for by differences in the summed weight of the most metabolically expensive organs (liver, heart, spleen, kidneys, and brain). Similarly, Chugani (19) utilized positron emission tomography scans to quantify changes in glucose utilization in the human brain from birth to adulthood. His findings suggest that the extremely high metabolic costs of brain metabolism characteristic of early human life (as outlined in **Table 4**) may extend further into childhood than previously realized. Together, these studies highlight the potential use of new imaging techniques for better understanding how interspecific variation in body composition contributes to differences in metabolic rate.

CONCLUSIONS

The evolution of large human brain size has had important implications for the nutritional biology of our species. Our large brains are energetically expensive, yet, paradoxically, our overall metabolic requirements are similar to those of any comparably sized mammal. As a consequence, humans expend a relatively larger proportion of their resting energy budget on brain metabolism than do other primates or nonprimate mammals.

Comparative analyses of primate dietary patterns indicate that 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.

Greater encephalization also appears to have consequences for other aspects of body composition, most notably the GI mass, muscularity, and adiposity. Relative to other primates, human have smaller GI tracts and a relatively reduced colon. This type of gut is consistent with adaptation to a diet that is relatively high in energy and nutrients and is easy to digest.

In addition, humans appear to be relatively undermuscled (i.e., less skeletal muscle) and over fat compared with other primates of similar size. The relatively high levels of adiposity in humans are particularly notable 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: (*a*) by having a ready supply of stored energy to feed the brain and (*b*) by reducing the total energy costs of the rest of the body.

The human fossil record indicates that major changes in both brain size and diet occurred in association with the emergence of early members of the genus *Homo* between 2.0 and 1.7 mya in Africa. With the evolution of early *H. erectus* 1.8 mya, we find evidence of an important adaptive shift—the evolution of the first hunting and gathering economy, characterized by greater consumption of animal foods, transport of food resources to home bases, and sharing of food within social groups. *H. erectus* was humanlike in body size and proportions and had a brain size beyond that seen in nonhuman primates, approaching the range of modern humans. In addition, the reduced size of the face and grinding teeth of *H. erectus*, coupled with its more sophisticated tool technology, suggest that these hominins were consuming a higher quality and more stable diet that would have helped to fuel the increases in brain size. Consequently, although dietary change was not the prime force responsible for the evolution of large human brain size, improvements in dietary quality appear to have been a necessary condition for promoting encephalization in the human lineage.

Further research is needed to better understand the nature of the dietary changes that took place with emergence of *Homo*. In addition, the application of new biomedical imaging techniques offers the potential to directly explore how intra- and interspecific variation in body composition may contribute to variation in metabolic rates.

SUMMARY POINTS

1. Our large brains are energetically expensive, yet paradoxically our overall metabolic requirements are similar to those of any comparably sized mammal. Consequently, humans expend a relatively larger proportion of their resting energy budget on brain metabolism than do other primates or nonprimate mammals.
2. Comparative analyses of living primate species show that 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. This suggests that large human brains are supported, in part, by diets that are relatively rich in energy and other nutrients.
3. Compared with other primates, humans have smaller overall gastrointestinal tracts with a relatively reduced colon. This type of gut is consistent with adaptation to a diet that is relatively high in energy and nutrients and is easy to digest.
4. Humans have relatively lower levels of muscularity and higher levels of adiposity than do other primates of similar size. High levels of adiposity in humans are particularly notable in infancy. Greater body fatness and lower muscle mass allow human infants to accommodate the growth of their large brains by having a ready supply of stored energy, reducing the total energy costs of the rest of the body.
5. The human fossil record indicates that major changes in both brain size and diet occurred in association with the emergence of early members of the genus *Homo* between 2.0 and 1.7 mya in Africa. With the evolution of early *H. erectus* 1.8 mya, we find evidence of an important adaptive shift—the evolution of the first hunting and gathering economy, characterized by greater consumption of animal foods, transport of food resources to home bases, and sharing of food within social groups. Improvements in diet quality with *H. erectus* appear to have been important for fueling rapids rates of encephalization.
6. Consumption of more animal foods with early *Homo* was likely important for providing high levels of key long-chain polyunsaturated fatty acids (docosahexaenoic acid and arachidonic acid) that are necessary for brain growth.

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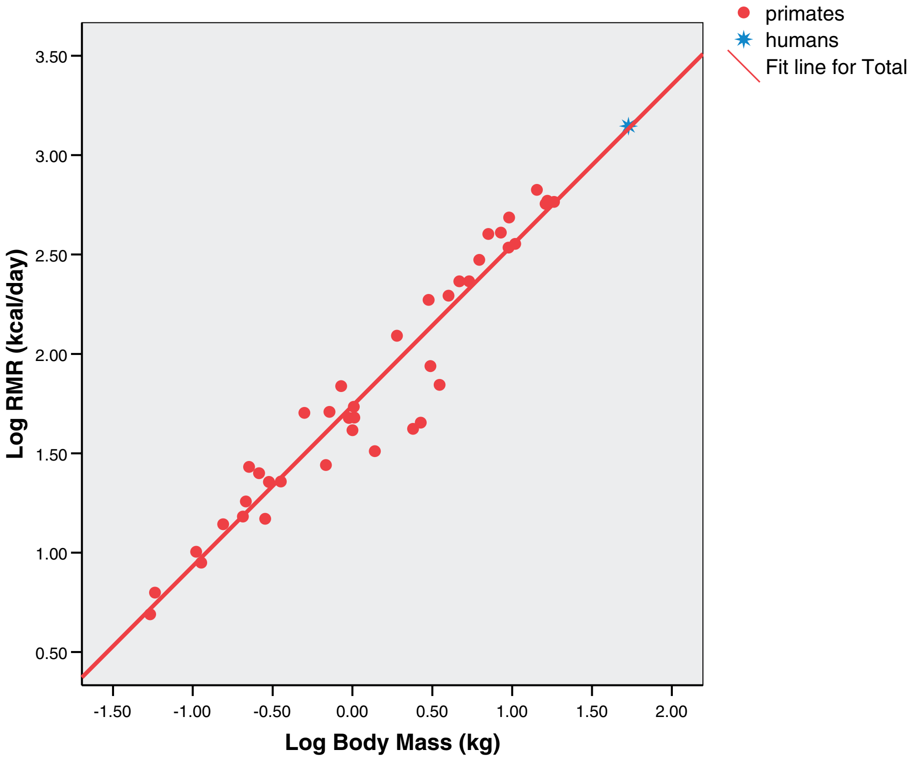

Figure 1

Log-Log plot of resting metabolic rate (RMR; kcal/day) versus body mass (kg) for 41 species of primates (including humans). Humans conform to the general primate scaling relationship [RMR = 55(Wt$^{0.81}$)]. Adapted from Reference 51.

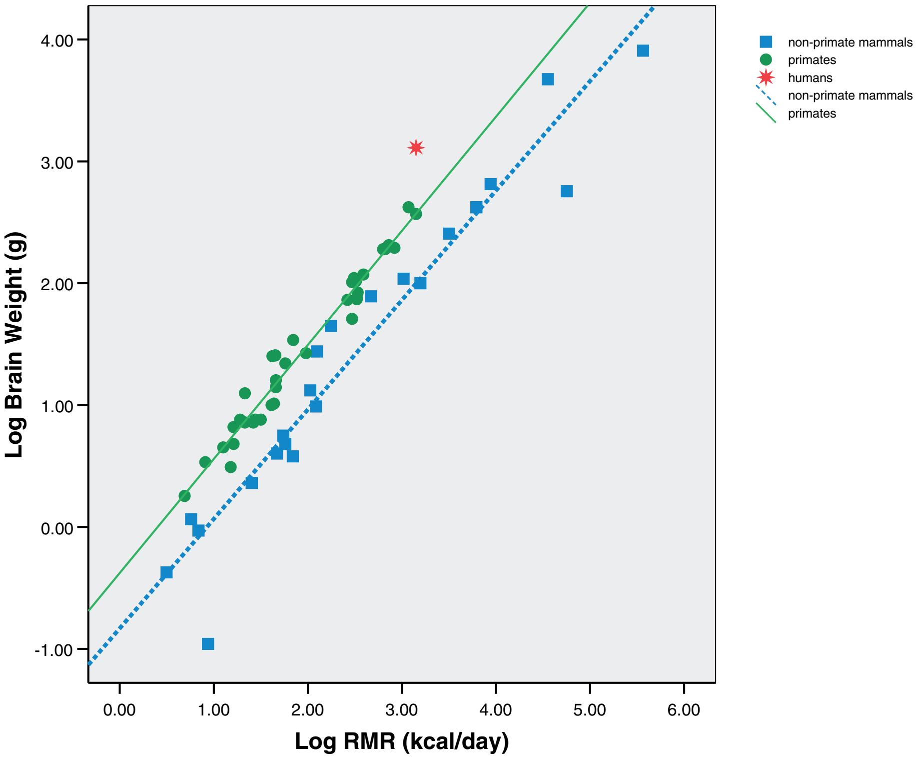

Figure 2

Log-Log plot of brain weight (BW; g) versus resting metabolic rate (RMR) (kcal/day) for humans, 35 other primate species, and 22 species of nonprimate mammals. The primate regression line (*solid*) is elevated systematically and significantly above the nonprimate mammal regression (*dashed*) (y-intercepts = −0.377primates, −0.832mammals; $P < 0.01$). The scaling relationships for nonprimate mammals are $BW = 0.14 (RMR^{0.90})$; primates, $BW = 0.42 (RMR^{0.94})$. Thus, for a given RMR, primates have brain sizes that are approximately three times those of other mammals, and humans have brains that are three times those of other primates.

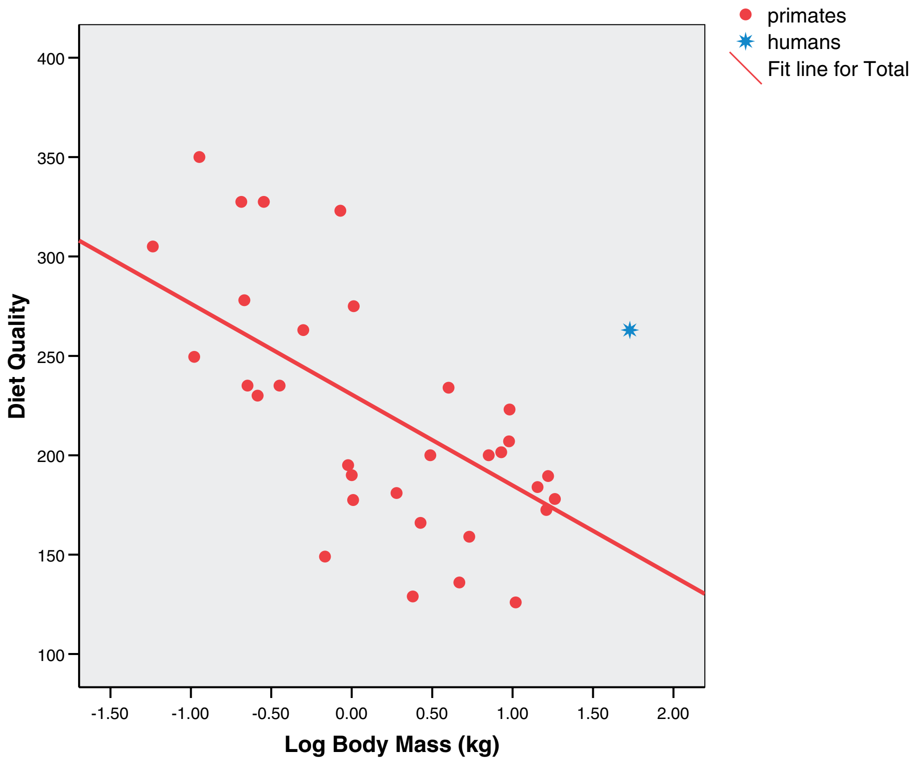

Figure 3

Plot of diet quality (DQ) versus log-body mass for 33 primate species. DQ is inversely related to body mass (r = −0.59 total sample, −0.68 nonhuman primates only; $P < 0.001$), indicating that smaller primates consume relatively higher-quality diets. Humans have systematically higher-quality diets than predicted for their size.

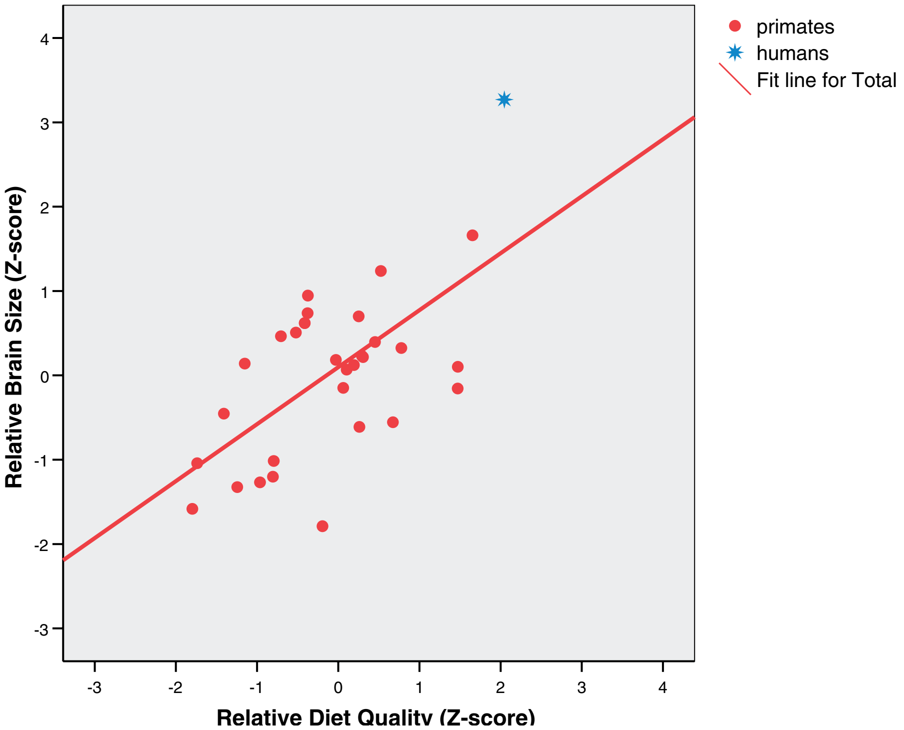

Figure 4

Plot of relative brain size versus relative diet quality for 33 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 would be expected for their size.