Chapter 1
Diet and Brain Evolution: Nutritional Implications of Large Human Brain Size

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Abbreviations

AA	Arachidonic acid
DHA	Docosahexaenoic acid
DQ	Dietary quality
IGF-1	Insulin-like growth factor I
LC-PUFA	Long-chain polyunsaturated fatty acid
MYA	Million years ago
RMR	Resting metabolic rate
RQ	Respiratory quotient

1.1 Introduction

The evolution of the human nutritional requirements is now receiving ever-greater attention among scientists from a variety of different fields, including nutritional science, anthropology and exercise science (Crawford 1992; Leonard et al. 1992, Leonard and Robertson 1994; Aiello and Wheeler 1995; Cordain et al. 2005). We are increasingly coming to realize that many of the key features that distinguish humans from other primates have important implications for our distinctive nutritional needs (Leonard 2002). The most notable of these features is our relatively large brain sizes, which are ~3 times the size our nearest primate relatives, the great apes (Martin 1989; McHenry and Coffing 2000).

Because neural tissue has very high energy demands (~16 times that of muscle tissue; Kety 1957), our large brains exact a high metabolic cost. On average, adult humans spend some 350–400 kcal/day on brain metabolism (Holliday 1986). Yet, despite the fact that humans have much larger brains per body weight than 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 (Leonard and Robertson 1994). As a consequence, humans expend a much larger share of their resting metabolic rate (RMR) to "feed their brains" than other primates or non-primate mammals (Leonard et al. 2003).

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To support the high metabolic demands of our large brains, humans have diets of much higher quality – more dense in calories and nutrients – than other primates (Leonard and Robertson 1994). On average, we consume higher levels of dietary fat than other primates (Popovich et al. 1997), and much higher levels of key long-chain polyunsatured fatty acids (LC-PUFAs) that are critical to brain development (Cordain et al. 2001; Crawford et al. 1999). Moreover, humans also appear to be distinctive in their developmental changes in body composition. We have higher levels of body fatness than other primate species, and these differences are particularly evident in early in life.

This chapter draws on both analyses of living primate species and the human fossil record to explore the influence of brain evolution on human nutritional needs. We begin by examining 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 distinctive aspects of human growth and development that promote increased levels of body fatness from early in life.

1.2 Comparative Perspectives on Primate Dietary Quality

The high energy costs of large human brains are evident in Fig. 1.1 which shows the allometric (scaling) relationship between brain weight (g) and RMR (kcal/day) for humans, 36 other primate species, and 22 non-primate mammalian species. The solid line denotes the best-fit regression for nonhuman

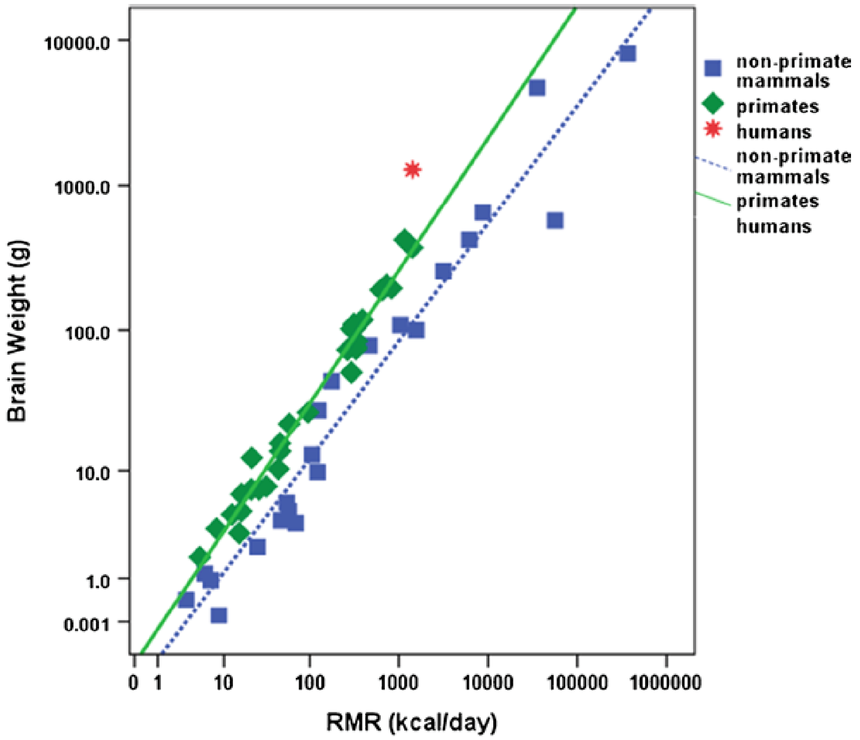

Fig. 1.1 Log-log plot of brain weight (*BW*;g) versus resting metabolic rate (*RMR*; kcal/day) for humans, 36 other primate species, and 22 non-primate mammalian species. The primate regression line is systematically and significantly elevated above the non-primate mammal regression. For a given RMR, primates have brain sizes that are three times those of other mammals, and humans have brains that are three times those of other primates

primate species, and the dashed line denotes the best-fit regression for the non-primate mammals. The data point for humans is denoted with a star.

The slopes of the primate and non-primate mammalian log-log regressions are comparable (0.93 vs 0.90, respectively), whereas the Y-intercept of the primate regression is significantly greater than that of the non-primate mammals (–0.38 vs –0.83; $P<0.001$). These differences imply that for a given RMR, primates have systematically larger brains than other mammals. Humans, in turn, are outliers on the primate regression, having markedly larger brains than expected for their RMRs. In caloric terms, this means that brain metabolism accounts for ~20–25% of RMR in adult humans, as compared to about 8–10% in other primate species, and roughly 3–5% for non-primate mammals.

To accommodate the metabolic demands of our large brains, humans consume diets that are more dense in energy and nutrients than other primates of similar size.

Figure 1.2 shows the association between dietary quality and body weight in living primates, including modern human foragers. The diet quality (DQ) index is derived from Sailer et al. (1985), and reflects the relative proportions (percentage by volume) of (1) structural plant parts (*s*; e.g., leaves, stems, bark), (2) reproductive plant parts (*r;* e.g., fruits, flowers), and (3) animal foods (*a*; including invertebrates):

$$\text{DQ index} = s + 2(r) + 35(a)$$

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).

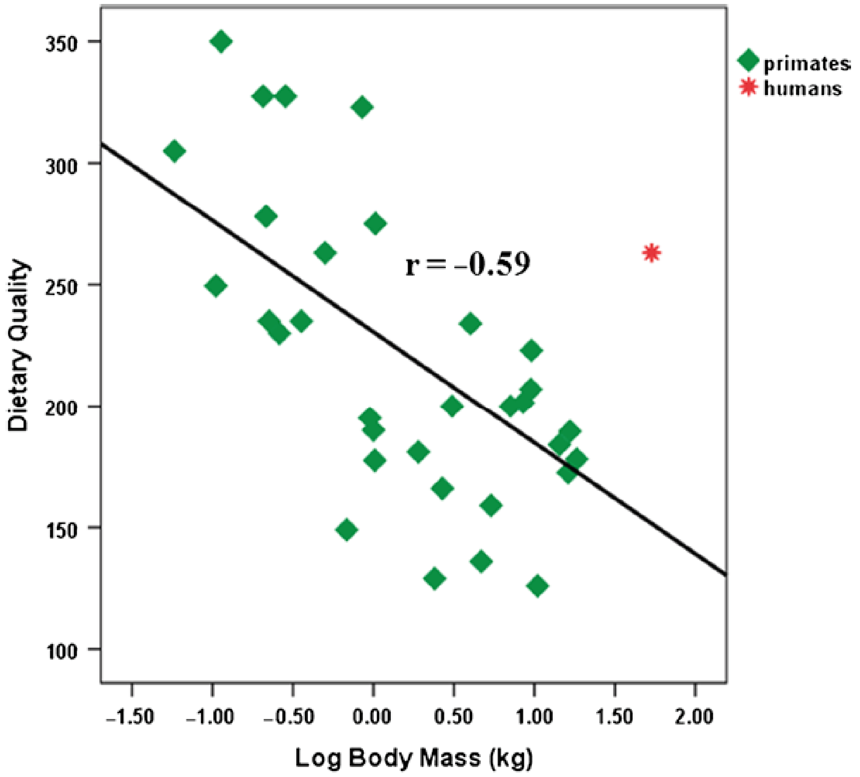

Fig. 1.2 Plot of diet quality (*DQ*) versus log-body mass for 33 primate species. DQ is inversely related to body mass ($r=-0.59$ [total sample]; -0.68 [nonhuman primates only]; $P<0.001$), indicating that smaller primates consume relatively higher quality diets. Humans have systematically higher quality diets than predicted for their size (Adapted from Leonard et al. 2003)

Table 1.1 Macronutrient composition of the diets of humans and modern apes

Species/group	Fat	Protein	CHO	References
Humans (*Homo sapiens*):				
United States (2000)	33	14	53	Briefel and Johnson (2004)
Modern foragers	28–58	19–35	22–40	Cordain et al. (2000)
Chimpanzees (*Pan troglodytes*)	6	21	73[a]	Richard (1985) Tutin and Fernandez (1992, 1993) Popovich et al. (1997)
Gorilla (*Gorilla gorilla*)	3	24	73[a]	Popovich et al. (1997)

Percent (%) of dietary energy intake derived from fat, protein, and carbohydrates (CHO) in selected human populations, chimpanzees (*Pan troglodytes*), and gorillas (*Gorilla gorilla*)

[a] Includes estimated energy derived from fermentation of dietary fiber

There is a strong inverse relationship between DQ and body mass across primates, with smaller primates relying on energy rich food such as insects, saps, and gums, whereas large-bodied primates rely on low-quality plant foods, such as foliage. Note that the diets of modern human foragers fall substantially above the regression line in Fig. 1.2, implying that humans have systematically higher DQs than expected for a primate of our size. In fact, the staple foods for all human societies are much more nutritionally dense than those of other large-bodied primates. Although there is considerable variation in the diets of modern human foraging groups, recent analyses by Cordain and colleagues (2000) have shown that modern human foragers derive fully 45–65% of their dietary energy intake from animal foods. In comparison, modern great apes obtain the bulk of their diet from low-quality plant foods. Gorillas derive over 80% of their diet from fibrous foods such as leaves and bark (Richard 1985). Even among common chimpanzees (*Pan troglodytes*), only about 5–10% of their calories are derived from animal foods, including insects (Stanford 1996). This higher quality diet means that we need to eat less volume of food to get the energy and nutrients we require.

Table 1.1 presents comparative data on macronutrient intakes of selected human groups, compared to those of chimpanzees and gorillas living in the wild. The dietary information for human populations were derived from the US NHANES data (Briefel and Johnson 2004) and from a recent review of the diets of contemporary hunter-gatherers (foragers) by Cordain et al. (2000). Data for chimpanzees and gorillas were derived from foraging studies in the wild (Tutin and Fernandez 1992, 1993; Richards 1985; Popovich et al. 1997) and compositional analysis of commonly consumed food items (Popovich et al. 1997). Contemporary foraging societies derive between 28% and 58% of their daily energy intakes from dietary fat. Those groups living in more northern climes (e.g., the Inuit) derive a larger share of their diet from animal foods, and thus have higher daily fat intakes. Conversely, tropical foraging populations generally have lower fat intakes because they obtain more of their diet from plant foods. In comparison, Americans and other populations of the industrialized world fall within the range seen for hunter-gatherers, deriving about a third of their daily energy intake from fat (Briefel and Johnson 2004).

In contrast to the levels seen in human populations, the great apes obtain only a small share of calories from dietary fat. Popovich and colleagues (1997) estimate that Western lowland gorillas derive approximately 3% of their energy from dietary fats. Chimpanzees appear to have higher fat intakes than gorillas (about 6% of dietary energy), but they are still well below the low end of the modern forager range. Thus, the higher consumption of meat and other animal foods among human hunter-gatherers is associated with diets that are higher in fat and more dense in energy.

The link between brain size and dietary quality is evident in Fig. 1.3, which shows relative brain size versus relative dietary quality for the 33 different primate species for which we have metabolic, brain size and dietary data. 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

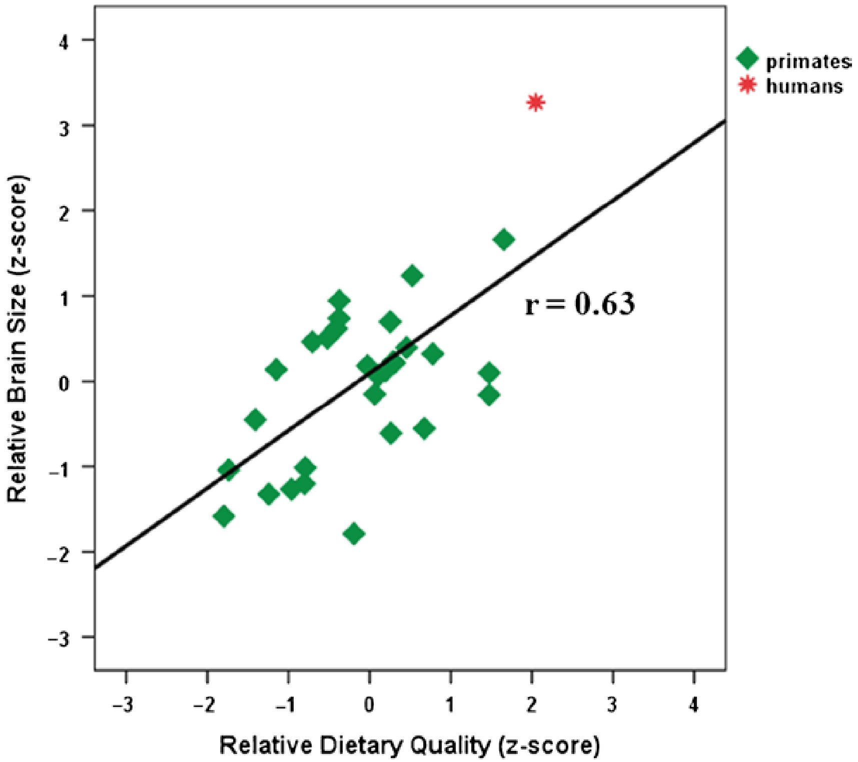

Fig. 1.3 Plot of relative brain size versus relative diet quality for 31 primate species (including humans). Primates with higher quality diets for their size have relatively larger brain size ($r=0.63$; $P<0.001$). Humans represent the positive extremes for both measures, having large brain to body size ratio and a substantially higher quality diet than expected for their size (Adapted from Leonard et al. 2003)

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 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 and the highest quality diet.

Thus, the high costs of the large, metabolically expensive human brain is partially offset by the consumption of a diet that is more dense in energy and fat than those of other primates of similar size. 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.

1.3 Evolutionary Trends in Diet, Brain Size, and Body Size

When we look at the human fossil record, we find that the first major burst of evolutionary change in hominin brain size occurs at about 2.0–1.7 million years ago, associated with the emergence and evolution of early members of the genus *Homo* (see Table 1.2). Prior to this, our earlier hominin ancestors, the australopithecines, showed only modest brain size evolution from an average of 400–510 cm^3 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, on average, ~600 cm^3 in *Homo habilis* (at 2.4–1.6 mya) and 800–900 cm^3 in early members of *H. erectus* (at 1.8–1.5 mya). Although the relative

Table 1.2 Brain size, body weight, and tooth size for selected prehistoric hominin species

Species	Geological age (mya)	Brain size (cm^3)	Body weight Male (kg)	 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
Homo erectus (late)	0.5–0.3	980	60	55	390
H. sapiens	0.4–0.0	1,350	58	49	334

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 hominin species (Data are derived from Leonard et al. 2003)

brain size of *H. erectus* has not yet reached the size of modern humans, it is outside of the range seen among other living primate species.

The evolution of *H. erectus* in Africa is widely viewed as a *major adaptive shift* in human evolution (Antón et al. 2002; Wolpoff 1999). Indeed, what is remarkable about the emergence of *H. erectus* in East Africa at 1.8 million years is that we find marked increases in both brain and body size, and the evolution of human-like body proportions at the same time that we see major reductions of posterior tooth size and craniofacial robusticity (McHenry and Coffing 2000; Ruff et al. 1997). These trends clearly suggest major energetic and dietary shifts: (a) the large body sizes necessitating greater daily energy needs; (b) bigger brains suggesting the need for a higher quality diet; and (c) the craniofacial changes suggesting that they were consuming a different mix of foods than their australopithecine ancestors.

The ultimate driving factors responsible for the rapid evolution of brain size, body size, and craniodental anatomy at this stage of human evolution appear to have been major environmental changes that promoted shifts in diet and foraging behavior. The environment in East Africa at the Plio-Peistocene boundary (2.0–1.8 mya) was becoming much drier, resulting in declines in forested areas and an expansion of open woodlands and grasslands (Bobe and Behrensmeyer 2002; Wynn 2004). Such changes in the African landscape likely made animal foods an increasingly attractive resource for our hominin ancestors (Behrensmeyer et al. 1997; Harris and Capaldo 1993; Plummer 2004).

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, with mammalian carcasses likely being acquired through both hunting and confrontational scavenging (Bunn 2006; Plummer 2004). In addition, the archeological evidence indicates that butchered animals were transported back to a central location (home base) where the resources were shared within foraging groups (Bunn 2006; Harris and Capaldo 1993; Potts 1998). Increasingly sophisticated stone tools (i.e., the Acheulean industry) emerged around 1.6–1.4 million years ago, improving the ability of these hominins to process animal and plant materials (Asfaw et al. 1992). 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 (10–20% 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*.

Beyond the energetic benefits associated with greater meat consumption, it appears that such a dietary shift would have also provided increased levels of key fatty acids that would have been necessary for supporting the rapid hominin brain evolution (Cordain et al. 2001). Mammalian brain growth is dependent upon sufficient amounts of two long-chain polyunsaturated fatty acids (PUFAs): docosahexaenoic acid (DHA) and arachidonic acid (AA) (Cordain et al. 2001; Crawford et al. 1999). Species with relatively larger brain sizes have greater requirements for DHA and AA (Crawford et al. 1999). Since mammals have a limited capacity to synthesize these fatty acids, dietary sources of DHA and AA appear to be limiting nutrients that constrained the evolution of larger brain size in many mammalian lineages (Crawford 1992; Crawford et al. 1999).

Cordain and colleagues (2001) have shown that wild plant foods available on the African savanna (e.g., tubers, nuts) contain little or no AA and DHA, whereas muscle tissue and organ meat of wild African ruminants provide moderate to high levels of these fatty acids. As shown in Table 1.3, 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.

In addition to changes in diet composition, Wrangham and colleagues (1999; Wrangham 2009) have suggested that the development of cooking also helped to increase diet quality and promote brain evolution in early *Homo*. 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 content. In their raw form, the starch in roots and tubers is not absorbed in the small intestine and is passed through the body as non-digestible carbohydrate (Englyst and Englyst 2005). However, when heated, the 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 (García-Al.onso and Goñi 2000). Thus, cooking increases the nutritional quality of tubers by making more of the carbohydrate energy available for biological processes.

While it is clear that cooking is an innovation in hominin evolution that served to increase dietary digestibility and quality, there is very limited evidence for the controlled use of fire by hominins before 1.5 million years ago (Bellomo 1994; Pennisi 1999). The more widely held view is that the use of fire and cooking did not occur until later in human evolution, at 200–250,000 years ago (Weiner et al. 1998). In addition, compositional analyses of wild tubers consumed by contemporary hunting and gathering populations indicates that the energy content of these resources is markedly lower than that of animal foods, even after cooking (e.g., Schoeninger et al. 2001). In contrast to animal foods, tubers are also devoid of both DHA and AA (see Table 1.3). Consequently, there remain major questions 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 than with the australopithecines. Greater

Table 1.3 Nutritional composition of selected wild plant and animal foods from Africa (Data are derived from Cordain et al. 2000)

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

Energy (kcal), fat (g) protein (g), arachidonic acid (AA) and docosahexaenoic acid (DHA) contents of African ruminant, fish and wild plant foods per 100 g consumption of animal foods would have increased total dietary fat consumption in early *Homo*, and markedly increased the levels of key fatty acids (AA and DHA) necessary for brain development. Together, the nutritional stability provided a critical foundation for fueling the energy demands of larger brain sizes.

1.4 Applications to Other Areas of Health

The high metabolic costs of our large brains also appear to have important implications for patterns of growth and development of human infants. During the human life course, the energy demands of our large brains are highest during infancy and early childhood, when brain to body weight ratios are largest and when brain growth is most rapid. Whereas brain metabolism accounts for 20–25% of resting needs in adults, in an infant of under 10 kg, it is using upward of 60% (Holliday 1986)! Table 1.4 shows changes in the percent of RMR allocated to the brain over the course of human growth and development.

To accommodate the extraordinary energy demands of the developing infant brain, human infants are born with high levels of body fat (Kuzawa 1998; Leonard et al. 2003). Human infants have the highest body fat levels of any mammalian species, and continue to gain fat during their early postnatal life (c.f., Dewey et al. 1993; Kuzawa 1998; Table 1.4). These high levels of adiposity in early life thus coincide with the periods of greatest metabolic demand of the brain.

For young children growing up in impoverished conditions in the developing world, getting sufficient energy and nutrients to sustain rapid rates of growth in both the brain and body can be challenging. This is particularly true during the weaning period, when children are exposed to both higher infectious disease loads and reduced dietary quality. To adapt to these stressors, human infants and toddlers show metabolic responses to preserve body fat reserves.

Research on children of the developing world suggests that chronic, mild-moderate undernutrition has a relatively small impact on a child's fatness. Instead of taking away the fat reserves, nutritional needs appear to be downregulated by substantially reducing rates of growth in height/length – producing the common problem of infant/childhood "growth stunting" or growth failure that is ubiquitous among impoverished populations of the developing world (Martorell and Habitch 1986).

Figure 1.4 shows an example of this process based on growth data collected from young girls of the indigenous Tsimane' farming and foraging population of lowland Bolivia (from Foster et al. 2005).

Table 1.4 Changes in brain size, body weight, percent body fat, resting metabolic rate, and percent of energy allocated to the brain from birth to adulthood (All data are from Holliday (1986), except for percent body fat data for children 18 months and younger, which are from Dewey et al. (1993))

Age	Body weight (kg)	Brain weight (g)	Body fat (%)	RMR (kcal/day)	BrMet (%)
New born	3.5	475	16	161	87
3 months	5.5	650	22	300	64
18 months	11.0	1,045	25	590	53
5 years	19.0	1,235	15	830	44
10 years	31.0	1,350	15	1,160	34
Adult male	70.0	1,400	11	1,800	23
Adult female	50.0	1,360	20	1,480	27

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

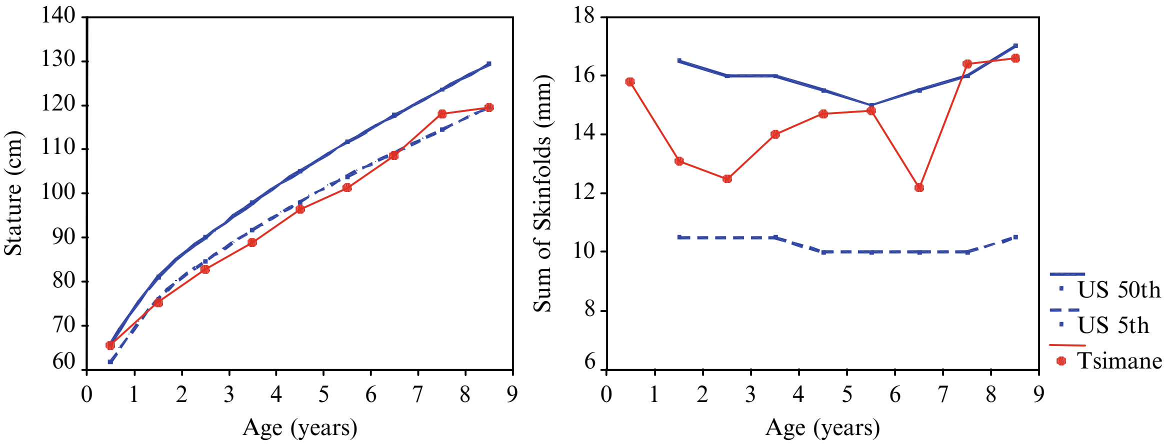

Fig. 1.4 Patterns of physical growth in stature (cm) and body fatness (as sum of triceps and subscapular skinfolds, mm) in girls of the Tsimane' of lowland Bolivia. Growth of Tsimane' girls is characterized by marked linear growth stunting, whereas body fatness compares more favorably to US norms (Data from Foster et al. 2005)

Table 1.5 Body size and metabolic measures for "stunted" and non-stunted children from São Paulo, Brazil (All values are presented as mean ± SEM)

Measure	Non-tunted ($n=30$)	Stunted ($n=28$)
Age (mo)	120 ± 3	122 ± 3
Stature (cm)	136 ± 3	126 ± 2**
Weight (kg)	32 ± 1	26 ± 1**
RMR (kcal/day)	1,179 ± 28	1,044 ± 22**
CHO oxidation (% of RMR)	66 ± 2	75 ± 2*
Fat oxidation (% of RMR)	34 ± 2	25 ± 2*

Age, stature (cm), weight (kg), resting metabolic rate (RMR; kcal/day), carbohydrate (CHO) and fat oxidation (% of RMR) in stunted and non-stunted children (8–11 years) from São Paulo, Brazil. Results are derived from Hoffman et al. (2000)

Differences between stunted and non-stunted groups are significant at: *$P<0.01$; **$P<0.001$

Note that early in life the stature of Tsimane' girls closely approximates the US median, but by age 3–4 it has dropped below the 5th centile, where it will track for the rest of life. In contrast, body fatness (as measured by the sum of the triceps and subscapular skinfolds) compares more favorably to US norms, tracking between the 15th and 50th US centiles. The problem of early childhood growth failure is the product of both increased infectious disease loads and reduced dietary quality.

Research on impoverished children in Brazil provides insights into the mechanisms for preserving body fatness under conditions of growth stunting. Hoffman and colleagues (2000) found that children who were growth stunted had significantly lower rates of fat oxidation than those of their "non-stunted" group. Table 1.5 presents a summary of the results of this study. The authors measured RMR on a sample of 28 stunted and 30 non-stunted (control) children between the ages of 8 and 11 years from the slums of Sao Paulo, Brazil. They used the respiratory quotient (RQ) assess levels of fat and carbohydrate oxidation form.

As shown in Table 1.5, the stunted children have significantly lower RMRs and lower levels of fat oxidation compared to their non-stunted counterparts. Under fasting conditions, the stunted children derived only 25% of the resting energy needs from fat, as compared to 34% in the non-stunted group. These researchers hypothesize that the impaired fat oxidation of the stunted children is associated with reductions in insulin-like growth factor I (IGF-I) that is commonly observed with poor childhood growth (Sawaya et al. 2004; Hoffman et al. 2000). IGF-I has been shown to increase lipolysis

(Hussain et al. 1994); hence, significant reductions in IGF-1 during growth can be expected to result in decreased fat oxidation.

Overall, key aspects of human growth and development of body composition are shaped by the very high metabolic demands of brain metabolism early in life. Human infants are born altricially (relatively underdeveloped for their age), and unlike other primates, continue rapid brain growth into early postnatal life (Martin 1989; Rosenberg 1992). To provide energy reserves for the high metabolic demands of large, rapidly growing brains, human infants are born with high body fat levels, and continue to gain fat during the first year of postnatal life. Further, under conditions of chronic nutritional stress, human infants show the capacity preserve brain metabolism by (1) "downregulating" linear growth, (2) reducing fat oxidation, and (3) increasing fat storage. These adaptive responses are evidenced in the preservation of body fatness among "growth stunted" children, and in the tendency of stunted children to gain weight and body fatness later in life (see Frisancho 2003).

1.5 Conclusions

The evolution of large human brain size has had important implications for the nutritional biology of our species. Humans expend a much larger share of their resting energy budget on brain metabolism than other primates or non-primate 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 fat. Relative to other large bodied apes, modern humans derive a much larger share of their dietary energy from fat. 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.

High levels of encephalization in humans also appear to have important consequences for early childhood growth and development. Human infants have much higher levels of body fatness than the infants of other mammals. These greater levels of adiposity help to accommodate the high metabolic demands of rapid brain growth by providing a ready supply of stored energy. Under conditions of nutritional stress, human infants and toddlers preserve body fat reserves for brain metabolism by reducing rates of linear growth. This process of "'linear growth stunting" is also associated with reduced rates of fat oxidation and increased rates of fat storage. Thus, humans appear to show important adaptations in fat metabolism to accommodate the high energy demands of the brain early in life.

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 million years ago in Africa. With the evolution of early *H. erectus* at 1.8 million years ago, 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 human-like 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, while dietary change was not the prime force responsible for the evolution of large human brain size, improvements in dietary quality and increased consumption of dietary fat 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 the emergence of early human ancestors.

1.6 Table of Key Points on Diet and Human Brain Evolution

The energy demands of brain tissue are ~16 times those of skeletal muscle.
Human adults spend 20–25% of their resting energy budget on brain metabolism, as compared to 8–10% in other primates, and 3–5% in non-primate mammals
Humans fuel the high energy costs of our brains by consuming diets that are much richer in energy and fat than other primates. Human hunter-gatherers derive about half of their daily energy intake from animal foods, much more than chimpanzees, who obtain less than 10%
Over the last 4–5 million years of human evolution, brain size has more than tripled, going from ~400 cc in our australopithecine ancestors to 1,300–1,500 cc in modern humans.
The rate of human brain evolution has been highly variable over the last 4 million years. From 4 to 2 million years ago, brain evolution was relatively slow. With the evolution of the genus *Homo* at ~2 million years ago, brain sizes evolved quite rapidly, in association with changes in foraging and dietary patterns.
Human infants have distinct nutritional needs and growth patterns that are shaped, in part, by the extraordinary energy costs of large, rapidly growing brains.
Human infants have higher levels of body fatness than those of any other mammal. This high level of adiposity helps to accommodate the energy demands of the brain.
Under conditions of chronic, mild-moderate nutritional stress, human infants substantially reduce rates of growth in length/stature, while preserving levels of body fatness. This pattern of growth stunting – characterized by "low height-for-age" – is commonly observed among impoverished populations of the developing world.

Definitions

Altricial: Being relatively "underdeveloped" for one's chronological age.

Australopithecus: Genus of early hominins that existed in Africa between 4 and 1.2 million years ago.

Acheulean: Stone tool industry of the early and middle Pleistocene characterized by hand axes and cleavers. First evident 1.4–1.6 million years ago, associated with early *Homo*.

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

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

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

1.7 Summary Points on Diet and Human Brain Evolution

- Humans expend a much larger share of their resting energy budget on brain metabolism than other species. Adult humans spend 20–25% of the RMR on the brain, as compared to 8–10% in other primates, and 3–5% in non-primate mammals.
- To support the high energy costs of brain metabolism, humans consume diets that are easier to digest and much more dense in energy and fat than other primate species.
- The first major increase in brain size in the human lineage occurred with the evolution of the genus *Homo* at 2.0–1.7 million years ago. During this time, we also have evidence from the fossil and archaeological record for greater consumption of animal foods. This increased dietary quality was likely important for supporting brain evolution.

- The addition of animal foods to the diet of early *Homo* would also have increased the availability of key long-chain polyunsaturated fatty acids that are essential for brain growth and development: DHA and AA.
- For human infants, the energy costs of brain metabolism are extraordinarily high (<60% of RMR) due to high brain to body weight ratios and rapid brain growth. These costs are supported, in part, by very high levels of body fatness. At 15–16% fat, humans have the fattest infants of any mammal.
- Under conditions of chronic nutritional and disease stress, human infants "downregulate" growth in length/stature, while preserving body fatness. This pattern of "linear growth stunting" is widely observed among impoverished populations of the developing world, and appears to be associated with reduced fat oxidation and increased fat storage.
- Ongoing research is attempting to better characterize the dietary patterns of our earliest human ancestors through chemical analyses of hominin bones and analyses of microscopic wear patterns of hominin teeth.

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