1 Evolutionary Perspectives on Fat Ingestion and Metabolism in Humans

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1.1 INTRODUCTION

Increasingly, biomedical researchers are coming to recognize the importance of an evolutionary perspective for understanding the origin and nature of modern human health problems. This is particularly true when examining "nutritional/metabolic" disorders such as obesity and cardiovascular disease. Research in human evolutionary biology over the last 20 years has shown 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 (Aiello and Wheeler, 1995; Leonard and Robertson, 1997; Leonard, 2002). The most important of these features 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 (Kety, 1957; Holliday, 1986). Consequently, the evolution of large brain size in the human lineage came at a very high metabolic cost.

Compared to other primates and mammals of our size, humans allocate a much larger share of their daily energy budget to "feed their brains." The disproportionately large allocation of our energy budget to brain metabolism has important implications for our dietary needs. To accommodate the high energy demands of our large brains, humans consume diets that are of much higher quality (i.e., more dense in

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energy and fat) than those of our primate kin (Leonard and Robertson, 1992, 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 polyunsaturated fatty acids (LC-PUFAs) that are critical to brain development (Crawford et al., 1999; Cordain et al., 2001). 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 early in life.

The need for an energy-rich diet also appears to have shaped our ability to detect and metabolize high-fat foods. Humans show strong preferences for lipid-rich foods. Recent work in neuroscience has shown that these preferences are based on the smell, texture, and taste of fatty foods (Sclafani, 2001; Gaillard et al., 2008; Le Coutre and Schmitt, 2008), and that our brains have the ability to assess the energy content of foods with remarkable speed and accuracy (Toepel et al., 2009). Additionally, compared to large-bodied apes, humans have an enhanced capacity to digest and metabolize higher fat diets. Our gastrointestinal (GI) tract, with its expanded small intestine and reduced colon, is quite different from those of chimpanzees and gorillas and is consistent with the consumption of a high-quality diet with large amounts of animal food (Milton, 1987, 2003). Finch and Stanford (2004) have recently shown that the evolution of key "meat-adaptive" genes in hominid evolution were critical to promoting enhanced lipid metabolism necessary for subsisting on diets with greater levels of animal material.

This chapter draws on both analyses of living primate species and the human fossil record to explore the evolutionary importance of fat in the nutritional biology of our species. 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 consider 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 Figure 1.1 which shows the scaling relationship between brain weight (grams) and resting metabolic rate (RMR) (kcal/day) for humans, 35 other primate species, 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 data point for humans is denoted with a star.

As a group, primates have brains that are approximately three times the size of other mammals (relative to body size). Human brain sizes, in turn, are some 2.5–3 times those of other primates (Martin, 1989). In caloric terms, this means that brain metabolism accounts for ~20%–25% of RMR in an adult human body, as compared to about 8%–10% in other primate species, and roughly 3%–5% for nonprimate mammals (Leonard et al., 2003).

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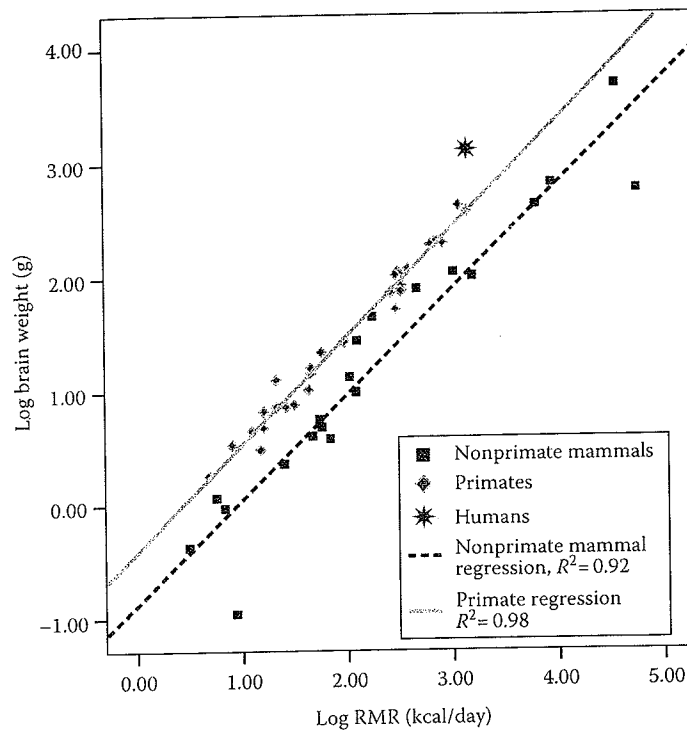ı body, as compared
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FIGURE 1.1　Log–log plot of brain weight (BW, g) versus RMR (kcal/day) for humans, 35 other primate species, and 22 nonprimate mammalian species. The primate regression line is systematically and significantly elevated above the nonprimate 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.

To accommodate the metabolic demands of our large brains, humans consume diets that are denser 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 the work of Sailer et al. (1985), and reflects the relative proportions (percentage by volume) of (a) structural plant parts (s; e.g., leaves, stems, bark), (b) reproductive plant parts (r; e.g., fruits, flowers), and (c) animal foods (a; including invertebrates):

$$DQ \text{ index} = s + 2(r) + 3.5(a)$$

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).

There is a strong inverse relationship between DQ and body mass across primates; however, note that the diets of modern human foragers fall substantially above the regression line in Figure 1.2. Indeed, the staple foods for all human societies are
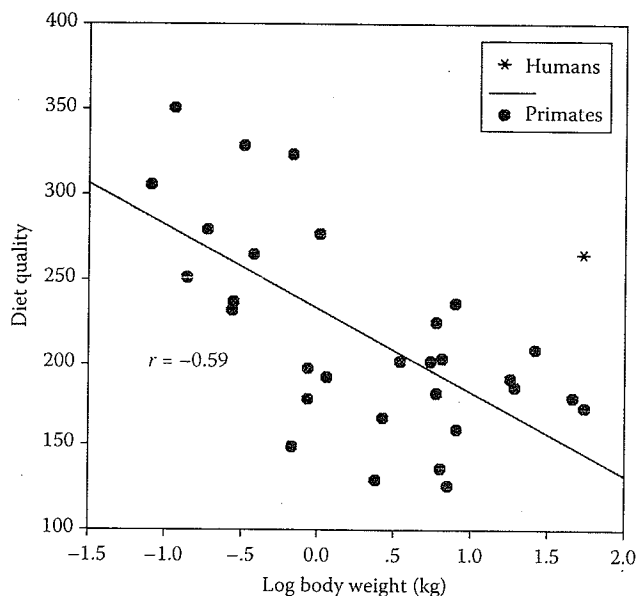
FIGURE 1.2 Plot of DQ versus log body mass for 33 primate species. DQ is inversely related to body mass ($r = -0.59$ [total sample]; -0.68 [nonhuman primates only]; $P < 0.001$), indicating that smaller primates consume relatively higher quality diets. Humans have systematically higher quality diets than predicted for their size. (Adapted from Leonard, W.R. et al., *Comp. Biochem. Physiol., Part A*, 136, 5, 2003.)

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 studies have shown that modern human foragers typically derive over half of their dietary energy intake from animal foods (Cordain et al., 2000). In comparison, modern great apes obtain much 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 (Teleki, 1981; 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 was derived from the U.S. 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 obtained from foraging studies in the wild (Richards, 1985; Tutin and Fernandez, 1992, 1993; Popovich et al., 1997) and compositional analysis of commonly consumed food items (Dufour, 1987; Popovich et al., 1997). Contemporary foraging societies derive between 28% and 58% of their daily energy intake from dietary fat. Those groups living in more northern climes (e.g., the Inuit) derive a
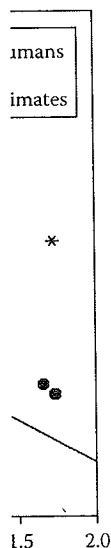
TABLE 1.1
Percent (%) of Dietary Energy Intake Derived from Fat, Protein, and Carbohydrates (CHO) in Selected Human Populations, Chimpanzees (*Pan troglodytes*), and Gorillas (*Gorilla gorilla*)

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 (*P. troglodytes*)	6	21	73[a]	Richard (1985)
				Tutin and Fernandez (1992, 1993)
				Popovich et al. (1997)
Gorilla (*G. gorilla*)	3	24	73[a]	Popovich et al. (1997)

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

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 (Millstone and Lang, 2003; 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 et al. (1997) estimated 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 denser in energy.

The link between brain size and dietary quality is evident in Figure 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 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 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 hominid brains would have necessitated the adoption of a sufficiently high-quality diet
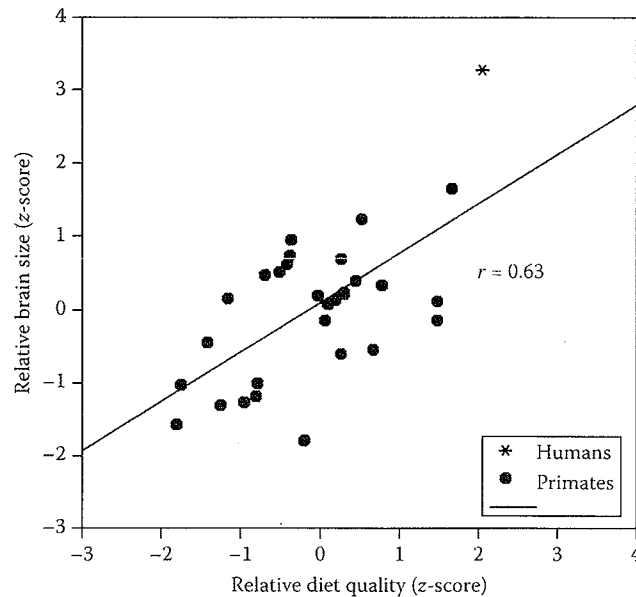
FIGURE 1.3 Plot of relative brain size versus relative DQ for 31 primate species (including humans). Primates with higher quality diets for their size have relatively larger brain size ($r = 0.63$; $P < 0.001$). Humans represent the positive extremes for both measures, having large brain:body size and a substantially higher quality diet than expected for their size. (Adapted from Leonard, W.R. et al., *Comp. Biochem. Physiol., Part A*, 136, 5, 2003.)

(including meat and energy-rich fruits) to support the increased metabolic demands of greater encephalization.

Relative to other large-bodied apes, humans show important differences in the size and morphology of their GI tracts that are tied to the consumption of a more energy-rich diet. Compared to chimpanzees and gorillas, humans have small total gut volumes, reduced colons, and expanded small intestines (Milton, 1987, 2003). In many respects, the human gut is more similar to that of a carnivore and reflects an adaptation to an easily digestible diet that is higher in energy and fat.

In addition, recent work in human evolutionary genetics suggests that the selection for key "meat-adaptive" genes were critical for allowing our hominid ancestors to more effectively exploit diets with higher levels of animal fat. Finch and Stanford (2004) argued that the evolution of the unique E3 allele in *Homo* at the apolipoprotein E (apoE) locus was important for allowing our ancestors to exploit diets with greater animal material. ApoE plays a critical role in regulating the uptake of cholesterol and lipids throughout the body (Davignon et al., 1988). The E3 allele is evident in humans, but not in chimpanzees and gorilla, and is associated with reduced metabolic and cardiovascular risks with the consumption of higher fat diets (Finch and Stanford, 2004).

In light of these important morphological and genetic adaptations to enhanced DQ, it is not surprising that humans also show preferences for foods that are rich in

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fat and energy. Until recently, it was thought that human preference for "fatty foods" was based largely on smell and texture (Sclafani, 2001); however, we now know that taste plays a critical role (Gaillard et al., 2008). Neuroimaging studies also suggest that the human brain has a remarkable ability to assess the energy content of potential food items with speed and accuracy (Toepel et al., 2009).

Across human populations, variation in the degree of preference for both sweet and fatty foods has been well documented (e.g., Messer, 1986; Johns, 1996; Salbe et al., 2004). Recent work by Lussana et al. (2008) has shown that nutritional status during development may play an important role in shaping taste preferences. Drawing on analyses from the Dutch Famine Birth Cohort, these authors show that prenatal exposure to famine conditions is associated with greater preference for fatty foods and increased risk of poor serum lipid profiles in adulthood.

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 hominid brain size occurred at about 2.0–1.7 million years ago (mya), associated with the emergence and evolution of early members of the genus *Homo* (see Table 1.2). Prior to this, our earlier hominid ancestors, the

TABLE 1.2
Geological Ages (mya), Brain Size (cm³), Estimated Male and Female Body Weights (kg), and Postcanine Tooth Surface Areas (mm²) for Selected Fossil Hominid Species

Species	Geological Age (mya)	Brain Size (cm³)	Body Weight Male (kg)	Body Weight Female (kg)	Postcanine Tooth Surface Area (mm²)
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
H. 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	1.350	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 Antón and Swisher (2001) and Georgian specimens from Gabunia et al. (2000, 2001). Data for late *H. erectus* are from McHenry (1994a).

australopithecines, showed only modest brain size evolution from an average of 400–510 cm³ over a span of 2 million years from 4 to 2 mya. With the evolution of the genus *Homo* there is rapid change, with brain sizes of, on average, ~600 cm³ in *Homo habilis* (at 2.4–1.6 mya) and 800–900 cm³ in early members of *Homo erectus* (at 1.8–1.5 mya). Furthermore, while the relative 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 (Wolpoff, 1999; Antón et al., 2002; Antón, 2003). Indeed, what is remarkable about the emergence of *H. erectus* in East Africa at 1.8 mya is that we find (a) marked increases in both brain and body size, (b) the evolution of human-like body proportions, and (c) major reductions of posterior tooth size and craniofacial robusticity (McHenry, 1992, 1994a,b; Ruff et al., 1997; McHenry and Coffing, 2000). 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 cranio-dental 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-Pleistocene boundary (2.0–1.8 mya) was becoming much drier, resulting in declines in forested areas and an expansion of open woodlands and grasslands (Vrba, 1995; Reed, 1997; Bobe and Behrensmeyer, 2002; deMenocal, 2004; Wynn, 2004). Such changes in the African landscape likely made animal foods an increasingly attractive resource for our hominid ancestors (Harris and Capaldo, 1993; Behrensmeyer et al., 1997; Plummer, 2004).

This can be seen by looking at the differences in ecological productivity between modern-day woodland and savanna ecosystems of the tropics. Despite the fact that tropical savanna environments produce only about half as much plant energy per year as tropical woodlands (4050 versus 7200 kcal/m²/year), the abundance of herbivores (secondary productivity) is almost three times greater than in the savanna (10.1 versus 3.6 kcal/m²/year) (Leonard and Robertson, 1997). Consequently, the expansion of the savanna in Plio-Pleistocene Africa would have limited the amount and variety of edible plant foods (to things like tubers, etc.) 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 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 (Plummer, 2004; Bunn, 2006). In addition, the archaeological evidence indicates that butchered animals were transported back to a central location (home base) where the resources were shared within foraging groups (Potts, 1988a,b; Harris and Capaldo,

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African fish
Wild tuber/roots
Mixed wild plants

Source: Data derived f

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1993; Bunn, 2006). Increasingly sophisticated stone tools (i.e., the Acheulean indus-try) emerged around 1.6–1.4 mya, improving the ability of these hominids to process animal and plant materials (Asfaw et al., 1992). These changes in diet and foraging behavior would not have turned our hominid 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*.

In addition to 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 necessary for supporting the rapid hominid brain evolution (Cordain et al., 2001). Mammalian brain growth is dependent upon sufficient amounts of two LC-PUFAs: docosahexaenoic acid (DHA), and arachidonic acid (AA) (Crawford et al., 1999; Cordain et al., 2001). 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 (Crawford et al., 1999). 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 mam-malian lineages (Crawford, 1992; Crawford et al., 1999).

Cordain et al. (2001) have demonstrated that wild plant foods available on the African savanna (e.g., tubers, nuts) contain only tiny 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 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. Other good sources of AA and DHA are fresh-water fish and shellfish (Broadhurst et al., 1998; Crawford et al., 1999). Cunnane and Crawford (2003) have suggested that the major increases in hominid encephaliza-tion 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 (see Klein, 1999).

TABLE 1.3

Energy, Fat, Protein, AA, and DHA Contents of African Ruminant, Fish, and Wild Plant Foods per 100 g

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

Source: Data derived from Cordain, L. et al., *World Rev. Nutr. Diet.* 90, 144, 2001.

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 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 BRAIN METABOLISM AND HUMAN BODY COMPOSITION: THE IMPORTANCE OF FAT

In addition to improvements in dietary quality and greater fat intakes, the increased metabolic cost of larger brain size in human evolution also appears to have been supported by developmental changes in body composition. During the human life course, the metabolic demands of our large brains are most dramatic in infancy and early childhood, when brain: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 uses upwards 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 an ample supply of body fat (Kuzawa, 1998; Leonard et al., 2003). At ~15%–16% body fat, human infants have the highest body fat levels of any mammalian species (cf., Dewey et al., 1993; Kuzawa, 1998). Further, human infants continue to gain body fat during their early postnatal life. During the first year, healthy infants typically increase in fatness from about 16% to about 25% (see Table 1.4). Thus, the very high levels of adiposity seen in early human growth and development coincide with the periods of greatest metabolic demand of the brain.

TABLE 1.4

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

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	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

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).

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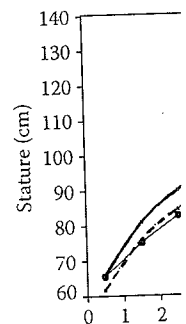**FIGURE 1.4** Patte and subscapular ski: is characterized by l ably to U.S. norms.

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ic demand of the brain.

(%), Resting Metabolic
to Brain Metabolism

MR (kcal/day)	BrMet (%)
161	87
300	64
590	53
830	44
1160	34
1800	23
1480	27

ildren 18 months and younger.

Human infants and toddlers also appear to show metabolic adaptations to preserve body fatness in face of nutritional and disease stressors. Research on children of the developing world suggests that chronic, mild to 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 Habicht, 1986).

Figure 1.4 shows an example of this process based on growth data collected from the Tsimane' farmers and foragers of lowland Bolivia (from Foster et al., 2005). Note that stature early in life closely approximates the U.S. median, but by age 3–4 years it has dropped below the 5th percentile, 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 U.S. norms, tracking between the 15th and 50th U.S. percentiles. The problem of early childhood growth failure is the product of both increased infectious disease loads and reduced dietary quality.

Recent work among impoverished children in Brazil provides insights into the physiological mechanisms associated with the preservation of body fatness under conditions of growth stunting. In a study of children (8–11 years) living in the shantytowns of São Paulo, Hoffman et al. (2000) found that children who were growth stunted had significantly lower rates of fat oxidation than those of their "nonstunted" group. The observed difference in fat oxidation levels under fasting conditions suggested that the stunted children derived about 25% of the resting energy needs from fat, as compared to 34% in the nonstunted group. It appears that the reductions in insulin-like growth factor I (IGF-I) commonly observed with early childhood growth stunting may promote impaired fat oxidation and increased fat storage (Sawaya et al., 1998, 2004; Hoffman et al., 2000). Indeed, because IGF-I has been shown to increase
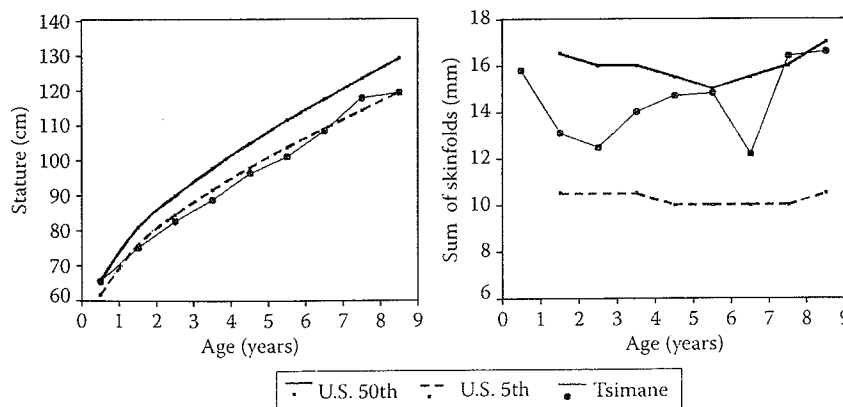

FIGURE 1.4 Patterns of physical growth in stature (cm) and body fatness (as sum of triceps and subscapular skinfolds, mm) in Tsimane' girls of lowland Bolivia. Growth of Tsimane' girls is characterized by marked linear growth stunting, whereas body fatness compares more favorably to U.S. norms. (Data from Foster. Z. et al., *Am. J. Phys. Anthropol.*, 126, 343, 2005.)

lipolysis (Hussain et al., 1994), significant reductions in IGF-I 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 to preserve brain metabolism by (a) "downregulating" linear growth, (b) reducing fat oxidation, and (c) 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; Grillo et al., 2005; Hoffman et al., 2007).

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 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 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.

Greater encephalization also appears to have consequences for human body composition, particularly in early life. Human infants have higher levels of adiposity than the infants of other mammals. These greater levels of body fatness allow human infants to accommodate the growth of their large brains by having 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 mya in Africa. With the evolution of early *H. erectus* at 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 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

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reduced size of the face and grinding teeth of *H. erectus*, coupled with its more sophisticated tool technology suggest that these hominids 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.

Associated with the evolution of our high-quality diet, humans developed distinct molecular pathways for detecting and metabolizing high-fat foods. We show preferences for foods that are rich in fat and energy. Key genetic mutations during later hominid evolution were critical to promoting the enhanced lipid metabolism necessary for subsisting on diets with greater levels of animal material. Moreover, accumulating evidence highlights the remarkable capacity of the human brain and sensory system for accurately assessing the energy content of potential food items. In sum, the ability to effectively detect, metabolize, and store fats likely provided tremendous selective advantages to our hominid ancestors, allowing them to expand into diverse ecosystems around the world. Further research is needed to better understand the nature of the dietary changes that took place with the emergence of early human ancestors and how they are associated with distinctive aspects of our own nutritional biology.

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FAT DETECTION
TASTE, TEXTURE, AND POST INGESTIVE EFFECTS

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