Energetics and the Evolution of Brain Size in Early Homo

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Introduction

Anthropologists have increasingly begun to rely on energetic models to understand the patterns and trends in hominin evolution (e.g., Aiello and Wheeler, 1995; Leonard and Robertson, 1994, 1997; Leonard, 2003). The acquisition of food energy, its consumption, and ultimately its allocation for biological processes are all critical aspects of an organism’s ecology (McNab, 2002). In addition, from the perspective of evolution, the goal for all organisms is the same – to allocate sufficient energy to reproduction to ensure their genes are passed on to future generations. Consequently, by looking at the ways in which animals go about acquiring and then allocating energy, we can better understand how natural selection produces important patterns of evolutionary change. This approach is particularly useful in studying human evolution, because it appears that many important transitions in the hominin lineage – the evolution of bipedality, the expansion of brain size and the initial colonization of northern climes – had implications for energy allocation (Leonard, 2002).

In this chapter, we use an energetic approach to gain insights into the evolution of brain size with the emergence of the genus Homo. We begin by looking at the energy demands associated with large brain size in modern humans relative to other primates and other mammals. We then examine the hominin fossil record to gain insights into changes in brain size, foraging strategies and dietary patterns associated with the evolution of early Homo. Both the comparative and fossil evidence suggest that the increased metabolic costs of larger brain sizes in the genus Homo were dependent upon the changes in dietary quality and alterations in body composition. Although we do not know the specific components of the diet of early Homo, it does appear that these hominins consumed a diet of greater energy and nutritional density than their australopithecine ancestors. In addition, it also appears that expansion of the brain size in the hominin lineage was associated with...
potential reductions in musculature and/or gastrointestinal (GI) mass and increases in adiposity (body fatness).

**Metabolic demands of large brain size**

What is remarkable about the large human brain is its high metabolic cost. The energy requirements of brain tissue are about 29 kcal/100 grams/day, roughly 16 times that of skeletal muscle tissue (Kety, 1957; Holliday, 1986). This means that for a 70 kg adult human with a brain weight of about 1400 grams, over 400 kcal per day are allocated to brain metabolism. Yet despite the fact that humans have much larger brains than most other mammals, the total energy demands for our body — our resting energy requirements — are no greater than those of a comparably sized mammal (Kleiber, 1961; Leonard and Robertson, 1992).

![Graph showing log-log plot of resting metabolic rate (RMR; kcal/day) versus body weight (kg) for 51 species of terrestrial mammals, including non-primate mammals, primates, and humans. Humans conform to the general mammalian scaling relationship, as described by Kleiber (1961). The scaling relationship for the entire sample is: RMR = 63(Wt^0.75). Data are from Leonard et al. (2003) and Snodgrass et al. (1999).]

This point is evident in the relationship between metabolic rate (RMR) and body mass (BW) for primates, and humans. The general relationship between energy demands and body mass is:

RMR (kcal/day) = a * BW^b

The implication of this general energy budget to primates and humans is that species which shows the same brain size across the same species...
This point is evident in Figure 1, which shows the relationship between resting metabolic rate (RMR; kcal/day) and body weight (kg) in non-primate mammals, primates, and humans. Humans conform to the general mammalian scaling relationship between RMR and body weight (the "Kleiber relationship"), in which energy demands scale to the $3/4$-power of body weight (Kleiber, 1961):

$$\text{RMR (kcal/day)} = 7 \times w^{0.75}$$

The implication of this is that humans allocate a much larger share of their daily energy budget to brain metabolism than other species. This is evident in Figure 2, which shows the scaling relationship between brain weight (grams) and RMR for the same species noted in Figure 1.

![Figure 2: Log-Log plot of brain weight (BW;g) versus RMR (kcal/day) for 51 species of terrestrial mammals. The primate regression line is systematically and significantly elevated above the non-primate mammal regression. The scaling relationships are: non-primate mammals: $BW = 0.13(RMR^{0.93})$; primates: $BW = 0.38(RMR^{0.93})$. Thus, for a given RMR, primates have brain sizes that are three times those of other mammals, and humans have brain sizes that are three times those of other primates.](image-url)
We find that at a given metabolic rate, primates have systematically larger brain sizes than other mammals, and humans, in turn, have larger brain sizes than other primates. Adult humans allocate 20-25% of their RMR to brain metabolism, approximately three times that of other primates (~7-9% of RMR), and nine times that of non-primate mammals (about 3% of RMR).

Important dimensions of human nutritional biology appear to be associated with the high-energy demands of our large brains. Humans consume diets that are more dense in energy and nutrients than other primates of similar size. For example, Cordain et al. (2000) have shown that modern human foraging populations typically derive 45-65% of their dietary energy intake from animal foods. 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 chimpanzees, only about 5% of their calories are derived from animal foods, including insects (Teleki, 1981; Stanford, 1996).

Meat and other animal foods are more concentrated sources of calories and nutrients than most of the plant foods typically eaten by large-bodied primates. This higher-quality diet may reflect our high-quality plant fibers, complex carbohydrates, and volatile fatty acids (VFA) as well as the morphology of human digestive tracts, which are more similar to a carnivore-plant-fruit diet-plant-fruit diet (Sussman, 1985). Together, these changes result in a larger brain size over the course of human evolution. The predominant diet of a diet that was high in meat may have been the case for most large-brained primates, so the driving force behind human brain evolution is the necessary condition of increased large hominin brains.

**Brain evolution in hominins**

The human fossil record suggests that the change in hominin brain size began with the expansion of the cranial vault and then culminated in the expansion of the brain itself, possibly driven by a combination of factors such as increased social complexity, tool use, and cognitive abilities.
higher-quality diet means that humans need to eat a smaller volume of food to get the energy and nutrients they require.

Comparative analyses of living primate species (including humans) support the link between brain size and dietary quality. Figure 3 shows relative brain size versus dietary quality (an index based on the relative proportions of leaves, fruit, and animal foods in the diet) for 31 different primate species (adapted from Leonard et al., 2003). There is a strong positive relationship \( r = 0.63; P < 0.001 \) between the amount of energy allocated to the brain and the calorific 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 and the highest quality diet. This relationship implies that the evolution of larger hominin brains would have necessitated the adoption of a sufficiently high-quality diet to support the increased metabolic demands of greater encephalization.

The relative size and morphology of the human gastrointestinal (GI) tract also reflect our high-quality diet. Most large-bodied primates have expanded large intestines (colon), an adaptation to fibrous, low-quality diets (Milton, 1987). This is evident in Figure 4, which shows the relative sizes of the colon and small intestines in humans and the great apes. In all three ape species, the colon accounts for over half of the GI volume and is greatly expanded over the size of the small intestine. Humans, on the other hand, have relatively enlarged small intestines and a reduced colon.

The enlarged colons of most large-bodied primates permit fermentation of low-quality plant fibers, allowing for extraction of additional energy in the form of volatile fatty acids (Milton and Demment, 1988; Milton, 1993). 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 (Sussman, 1987; Martin, 1989).

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.

**Brain evolution in early Homo**

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, associat-
Fig. 4. Relative proportions of the small intestine and large intestine (colon) in modern humans (Homo sapiens) and the great apes (Pan troglodytes, Pongo pygmaeus, Gorilla gorilla). The colon volume of humans is markedly smaller than that of all three great apes (20% of GI volume vs. >50% in the apes), and is indicative of adaptation to a higher-quality and more easily digested diet. Data derived from Milton (1987).

ed with the emergence and evolution of early members of the genus Homo. Table 1 presents data on evolutionary changes in hominin brain size (cm³), estimated adult male and female body weights (kg) and posterior tooth area (mm²). The australopithecines showed only modest brain size evolution from about 430 to 550 cm³ over more than 2 million years (from about 4 to 1.5 million years ago). However, with the evolution of the genus Homo, there were substantial increases in encephalization, with brain sizes of over 600 cm³ in Homo habilis (at 1.9–1.6 mya) and 800–900 cm³ in early members of Homo erectus (at 1.8–1.5 mya). Although the relative brain size of Homo erectus is smaller than the average for modern humans, it is outside of the range seen among other living primate species (Leonard and Robertson, 1994).

Changes in the craniofacial and dental anatomy of Homo erectus suggest that these forms were consuming different foods than their australopithecine ancestors. During the evolution of the australopithecines, the total surface area of the grinding teeth (molars and premolars) increased dramatically from 460 mm² in A. afarensis to 750 mm² in A. afarensis and A. afarensis to approximately 900 mm² in A. afarensis. Postcranial robusticity also suggests that H. erectus, H. erectus also showed a more robusticity relative to their much smaller teeth than the australopithecines, but not as great as chimpanzees (McHenry, 2000). This pattern of increasing a robusticity in postcranial material. How this relates to the diet remains in the future.

Dietary changes in Homo erectus

The marked increase in brain size and posterior tooth surface area suggest changes in the composition of the diet.
Table 1. Geological ages (millions of years ago), brain size (cm³), estimated male and female body weights (kg), and postcanine tooth surface areas (mm²) for selected fossil hominid species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Geological age (mya)</th>
<th>Brain size (cm³)</th>
<th>Male (kg)</th>
<th>Female (kg)</th>
<th>Postcanine tooth surface (mm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. afarensis</td>
<td>3.9-3.0</td>
<td>438</td>
<td>45</td>
<td>29</td>
<td>460</td>
</tr>
<tr>
<td>A. africanus</td>
<td>3.0-2.4</td>
<td>452</td>
<td>47</td>
<td>30</td>
<td>516</td>
</tr>
<tr>
<td>A. boisei</td>
<td>2.3-1.4</td>
<td>521</td>
<td>49</td>
<td>34</td>
<td>756</td>
</tr>
<tr>
<td>A. robustus</td>
<td>1.9-1.4</td>
<td>530</td>
<td>40</td>
<td>32</td>
<td>588</td>
</tr>
<tr>
<td>Homo habilis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(sensu stricto)</td>
<td>1.9-1.6</td>
<td>612</td>
<td>37</td>
<td>32</td>
<td>478</td>
</tr>
<tr>
<td>H. erectus (early)</td>
<td>1.8-1.5</td>
<td>863</td>
<td>66</td>
<td>54</td>
<td>377</td>
</tr>
<tr>
<td>H. erectus (late)</td>
<td>0.5-0.3</td>
<td>980</td>
<td>60</td>
<td>55</td>
<td>390</td>
</tr>
<tr>
<td>H. sapiens</td>
<td>0.4-0.0</td>
<td>1350</td>
<td>58</td>
<td>49</td>
<td>334</td>
</tr>
</tbody>
</table>


A. afarensis to 756 mm² in A. boisei. In contrast, with the emergence of early Homo at approximately 2 million years ago, we see marked reductions in the posterior dentition. Postcanine tooth surface area is 478 mm² in H. habilis and 377 mm² in early H. erectus.

H. erectus also shows substantial reductions in craniofacial and mandibular robusticity relative to the australopithecines (Wolpoff, 1999). Yet, despite having smaller teeth and jaws, H. erectus was a much bigger animal than the australopithecines, being human-like in its stature, body mass and body proportions (McHenry, 1992, 1994a; Ruff and Walker, 1993; Ruff et al., 1997; McHenry and Coffing, 2000). Together these features indicate that early Homo 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**

The marked increases in brain and body size coupled with the reductions of posterior tooth size and craniofacial robusticity all suggest that there was a shift in the composition and quality of the diet consumed by H. erectus. However, there re-
mains considerable debate over what kinds of dietary changes likely occurred during this period of human evolution. The most widely held view is that the diet of early *Homo* included more animal foods (Stanford and Bunn, 2001). The environment at the Plio-Pleistocene boundary (2.0 – 1.8 mya) was becoming increasingly drier, creating more arid grasslands (Vrba, 1995; Reed, 1997; Owen-Smith, 1999). These changes in the African landscape made animal foods more abundant and, thus, an increasingly attractive food resource (Behrensmeyer et al., 1997). Specifically, when we examine modern ecosystems, we find that although savanna/grasslands have much lower net primary productivity than woodlands (4050 vs. 7200 kcal/m²/yr), the level of herbivore productivity in savannas is almost three times that of the woodlands (102 vs. 3.6 kcal/m²/yr) (Leonard and Robertson, 1997). Thus, fundamental changes in the ecosystem structure during the Plio-Pleistocene transition likely resulted in a net increase in the energetic abundance of game animals in the African landscape. Such an increase would have offered an opportunity for hominins with sufficient capability to exploit the animal resources.

The archaeological record provides evidence that this occurred with *Homo erectus* – the development of the first rudimentary hunting and gathering economy in which game animals became a significant part of the diet and resources were shared within foraging groups (Potts, 1988; Harris and Capaldo, 1993; Roche et al., 1999). These changes in diet and foraging behaviour 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 hominin diets.

Greater consumption of animal foods also would have provided increased levels of key fatty acids that would have been necessary for supporting the rapid brain evolution seen with the emergence of *Homo erectus*. Mammalian brain growth is dependent upon sufficient amounts of two long-chain polyunsaturated fatty acids (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 mammalian lineages (Crawford, 1992; Crawford et al., 1999).

Cordain and colleagues (2000) have shown that the 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

<table>
<thead>
<tr>
<th>Food item</th>
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</thead>
<tbody>
<tr>
<td>African ruminant</td>
</tr>
<tr>
<td>African ruminant</td>
</tr>
<tr>
<td>African ruminant</td>
</tr>
<tr>
<td>African ruminant</td>
</tr>
<tr>
<td>African fish</td>
</tr>
<tr>
<td>Wild tuber/roots</td>
</tr>
<tr>
<td>Mixed wild plants</td>
</tr>
</tbody>
</table>

moderate to high levels of PUFAs, indicating that a rich source of DHA and AA are unlikely. As a result, Cordain et al., (2000) propose that the use of aquatic resources, particularly fish, is critical to the diet. An alternative scenario considered by Wrangham et al. (2000) is that wild plants, such as tubers and nuts, were not an abundant or available form of DHA and AA.

Although cooked foods appear to have been included in the diet from the beginning of the Pleistocene, it is not known when or how cooking began. Although cooking has been suggested to have important implications for human evolution (Brain and Short, 1994), the precise nature of these implications remains a subject of debate.
changes likely occurred during the Pleistocene. The commonly held view is that the diet of Homo erectus and Homo habilis (e.g., Bunn, 2001). The environment likely was becoming increasingly seasonal and more complex (e.g., 1997; Owen-Smith, 1999). Speciation of grass species made it possible for savanna and woodland foods more abundant and, thus, easier to exploit than woodlands (4050 vs. 400 kcal per d). A diet high in savannas is almost three times more energetic (26 k/1.9 Torre, 1995).) (Leonard and Robertson, 1993) (note 9). The increased structure during the Plio-Pleistocene in the energetic abundance and diversity of the environment would have offered greater opportunities to exploit the animal resources.

Despite the improvements that occurred with Homo erectus hominins, the hunting and gathering economy in the savannas, although more diverse in diet and resources were relatively small (Bunn, 1992; Capaldo, 1993; Roche et al., 1996). A more effective economy would not have turned to cooking until the addition of even modest quantities of energy, combined with the sharing of foods (e.g., 1995), would have significantly increased the energetic returns.

Fire likely provided increased levels of energy, thus supporting the rapid brain growth during the Pleistocene. Australian brain growth is driven by increased availability of polyunsaturated fatty acids (PUFAs) such as arachidonic acid (AA) (Crawford et al., 1993). A high level of all mammalian brain fatty acids is associated with higher levels of intelligence (Hunt, 1990). The low levels of AA (Crawford et al., 1993) and a limited capacity to synthesize these fatty acids from other sources of DHA and AA are associated with the production of larger brain size in modern humans (Bloom, 1999).

Among the plant foods available on the savanna were tubers and roots, which provide large amounts of AA and DHA. The plants from which these tubers were derived, such as African ruminants provide moderate to high levels of these fatty acids. As shown in Table 2, 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 (Broadhurst et al., 1998; Crawford et al., 1999; Coddin et al., 2001). Cunnane and colleagues (Cunnane and Crawford, 2003; Broadhurst et al., 1998) have suggested that the major increases in hominin encephalization were associated with systematic use of aquatic or marine or lacustrine resources. However, there is little archaeological evidence for the systematic use of aquatic resources until later in human evolution (Klein, 1999).

An alternative strategy for increasing dietary quality in early Homo has been proposed by Wrangham and colleagues (1999, 2003). 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/nutritional 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 (Tagliafure et al., 1995; 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 more accessible to breakdown by digestive enzymes (Garcia-Alonso and Goni, 2000). Thus, cooking increases the nutritional quality of tubers by making more of the carbohydrate energy available for biological processes.

Although cooking is clearly an important innovation in hominin evolution, which 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; Brain and Sillen, 1988; Pennisi, 1999). The more widely held view is that

<table>
<thead>
<tr>
<th>Food item</th>
<th>Energy (kcal)</th>
<th>Fat (g)</th>
<th>Protein (g)</th>
<th>AA (mg)</th>
<th>DHA (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>African ruminant (brain)</td>
<td>126</td>
<td>9.3</td>
<td>9.8</td>
<td>533</td>
<td>861</td>
</tr>
<tr>
<td>African ruminant (liver)</td>
<td>159</td>
<td>7.1</td>
<td>22.6</td>
<td>192</td>
<td>41</td>
</tr>
<tr>
<td>African ruminant (muscle)</td>
<td>113</td>
<td>2.1</td>
<td>22.7</td>
<td>152</td>
<td>10</td>
</tr>
<tr>
<td>African ruminant (fat)</td>
<td>745</td>
<td>82.3</td>
<td>1.0</td>
<td>20-180</td>
<td>trace</td>
</tr>
<tr>
<td>African fish</td>
<td>119</td>
<td>4.5</td>
<td>18.8</td>
<td>270</td>
<td>549</td>
</tr>
<tr>
<td>Wild tuber/roots</td>
<td>96</td>
<td>0.5</td>
<td>2.0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Mixed wild plants</td>
<td>129</td>
<td>2.8</td>
<td>4.1</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
the use of fire and cooking did not occur until later in human evolution, at 200-250,000 years ago (Straus, 1989; Weiner et al., 1998). In addition, nutritional analyses of wild tubers used by modern foraging populations (e.g., Wehmeyer et al., 1969; Brand-Miller and Holt, 1998; Schoeninger et al., 2001) suggest that the energy content of these resources is markedly lower than that of animal foods, even after cooking (Cordain et al., 2001). Unlike animal foods, tubers are also deficient in both DHA and AA (Cordain et al., 2001; see Table 1). 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. Ungar and colleagues (2006) have 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 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 (Leonard and Robertson, 1994; Cordain et al., 2001) and partly through social and behavioral changes like food sharing and perhaps division of foraging tasks (Isaac, 1978; Kaplan et al., 2000). This greater nutritional stability provided a critical foundation for fueling the energy demands of larger brain sizes.

**Implications of changes in body composition for brain evolution**

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. Because humans allocate a substantially larger share of their daily energy budget to their brains than do other primates or other mammals, this 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 (1997; this volume) and Aiello and Wheeler (1995) have argued that the increased energy demands during the reduction in size of the large intestine and its content, having very high energy demand, were associated with the necessary metabolism for obtaining the brain size. However, recent studies have demonstrated the significant role of the various other species of mammals that are more closely related to humans that remain about the same size. In this context, Leonard and colleagues (2006) have accounted for the various metabolic rates and other measures of body composition (Adiposity) in human evolution. First, replacing muscle with fat has been linked to the brain, which can be drawn upon when the body has higher levels of body fat. This may be providing stored energy for additional resources.

<table>
<thead>
<tr>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>New born</td>
</tr>
<tr>
<td>3 months</td>
</tr>
<tr>
<td>18 months</td>
</tr>
<tr>
<td>5 years</td>
</tr>
<tr>
<td>10 years</td>
</tr>
<tr>
<td>Adult male</td>
</tr>
<tr>
<td>Adult female</td>
</tr>
</tbody>
</table>

1) All data are from American and younger, who...
human evolution, at 200-
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 and Wheeler (1995) 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. (1999) have failed to demonstrate the significant differences in GI size between primates and non-primate mammals that are predicted from the “expensive tissue hypothesis.” Thus, questions remain about the extent to which reductions in GI size may have accommodated the dramatic expansion of brain size during the course of human evolution. Leonard and colleagues (2003) and Kuzawa (1998) have suggested that differences in muscle and fat mass between humans and other primates may also account for the variation in budgeting of metabolic energy. Relative to other primates and other mammals, humans have lower levels of muscle mass and higher levels of body fatness (Leonard et al., 2003). The relatively high levels of body fatness (adiposity) in humans have two important metabolic implications for brain metabolism. First, because fat has lower energy requirements than 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 a larger brain size by providing stored energy to buffer against environmental fluctuations in nutritional resources.

Table 3. 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.²

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

² 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).
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. Table 3 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 upwards of 60% of RMR. Human infants are also considerably fatter than those of other mammalian species (Kuzawa, 1998). Body fatness in human infants is about 15-18% at birth, and continues to increase to 25-26% during the first 12 to 18 months of postnatal growth. Fatness then declines to about 15% by early childhood (Dewey et al., 1993). 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. Among humans, our knowledge of variation in body composition 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.

New imaging techniques such as magnetic resonance imaging (MRI) and positron emission tomography (PET 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. (2006) recently used MRI 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 Euroamerican 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 (1998) has recently utilized PET 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 3) may extend further into childhood than previously realized. Together these studies highlight the potential use of new imaging techniques to improve our understanding of how interspecific variation in body composition contributes to differences in metabolic rate.

Conclusions

An energetic perspective on brain size in the hominid line demonstrates profound consequences for energy budgets among mammals. The higher metabolic rates that are relatively necessary for the relative proportion of energy distributed with dietary quantities among species of similar body mass (muscle mass and brains in two important cases, in 1 and 2, respectively). With the emergence of bipedalism, we find the first remarkable changes in body composition, with evidence from archeological and biomolecular studies suggesting that the increases in brain size among the hominids was associated with increases in brain size and the metabolic costs of brain metabolism. Further research on the role of dietary factors and their impact on brain size and metabolic rates is necessary.
Conclusions

An energetic perspective is particularly useful for understanding the evolution of brain size in the hominin lineage. Large human brain sizes have important metabolic consequences as humans expend a relatively larger proportion of their resting energy budget on brain metabolism than other primates or non-primate mammals. The high costs of large human brains are supported, in part, by diets that are relatively rich in energy and other nutrients. Among living primates, the relative proportion of metabolic energy allocated to the brain is positively correlated with dietary quality. Humans fall at the positive end of this relationship, having both a very high-quality diet and a large brain size.

Greater encephalization also appears to have consequences for other aspects of body composition. Comparative primate data indicate that humans are "under-muscled", having relatively lower levels of skeletal muscle than other primate species of similar size. Conversely, levels of body fatness are relatively high in humans, particularly in infancy. These greater levels of body fatness and reduced levels of muscle mass allow human infants to accommodate the growth of their large brains in two important ways: (1) by having a ready supply of stored energy to "feed the brain" and (2) by reducing the total energy costs of the rest of the body.

With the emergence and evolution of the genus Homo between 2.0 and 1.7 mya, we find the first major pulse of brain evolution in the hominin lineage. The corresponding changes in craniofacial anatomy and postcanine tooth size, coupled with evidence from the archaeological record, suggest that these hominins were consuming a higher-quality and more stable diet that would have helped to fuel the increases in brain size.

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


Evidence for unique function of docosahexaenoic acid during the evolution of the modern human brain. Lipids 34, 539-547.


Energetics and the Evolution of Brain Size in Early Homo


Introduction

This paper presents both the primates and the human diet. To address the simultaneity of diet change across the species, it extends the evidence for the evolution of dietary behavior (Kaplan et al., 1994; Kaplan, 1994; Capaldo et al., 1991; Capaldo, 1991; Robson, 2001b), investing in the evolution of human diet over time. The chapter begins by addressing the primates and then applies it to understanding of the evolution of human diet and its role in the evolution of the human species. The human diet is then examined in detail, focusing on the evolution of the human diet and its role in the evolution of human development and its implications for understanding the issues raised at the beginning of the chapter.

The embodied individual

According to the theory of embodied cognition, the human mind is the result of a process of evolution and development that is shaped by the environment and context.
Guts and Brains: An Integrative Approach to the Hominin Record

Wil Roebroeks (ed.)

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