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Fatty Acid Composition and Energy Density of Foods Available to African Hominids

Evolutionary Implications for Human Brain Development

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With the emergence of species of our own genus *(Homo habilis)* at least 2.3 million years ago [1], a rapid increase in hominid brain mass relative to body mass (encephalization) occurred [2, 3]. Figure 1 shows that the range of cranial capacities for *Homo habilis* significantly exceeded that of earlier *Australopithecus* species, whose brain volumes remained constant for at least 2 million years. Slightly prior to the emergence of *Homo habilis* in the fossil record was the appearance of primitive stone tools [4] whose function was to butcher and disarticulate either scavenged or hunted carcasses of African prey animals [5, 6]. The advent of stone tools as well as the appearance of stone-tool cut marks on the fossilized bones of prey animals suggests that early members of our genus were increasingly exploiting animal foods as a source of sustenance. This dietary shift from a predominantly plant based diet to one in which animal foods became increasingly important allowed for the relaxation of the selection pressures that had formerly constrained encephalization in *Australopithecus* species [7, 8].

In modern humans the brain utilizes 20–25% of the total resting metabolic rate (RMR) whereas in other primates, this value is 8–9% [9]. Because the brain is more metabolically active at rest than the average body RMR, a relative increase in the encephalization index, such as that which occurred in early members of *Homo*, requires that either the total metabolic rate increases on a per weight basis,

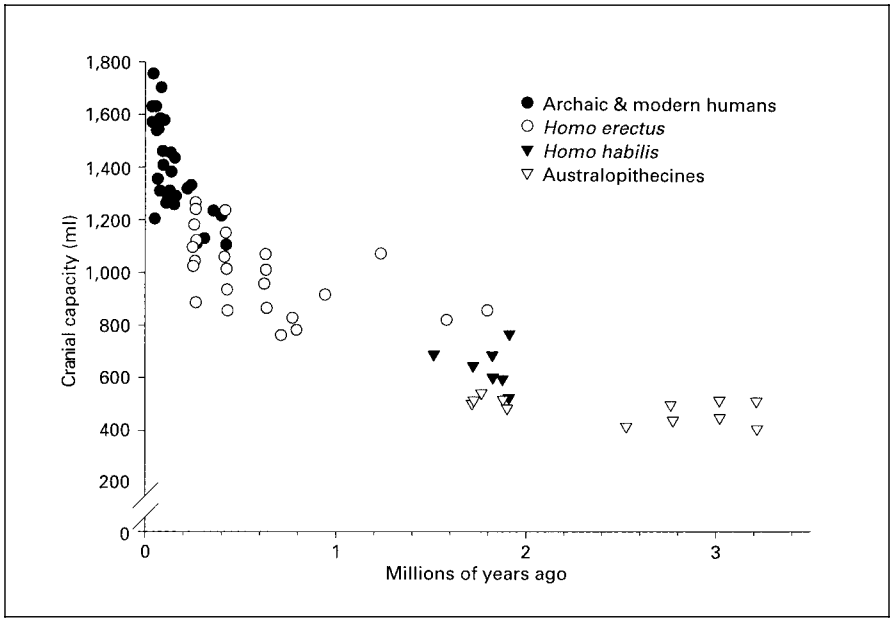

Fig. 1. Increases in absolute hominid cranial capacity over time. Adapted from [8].

or that a concomitant reduction in the size and metabolic rate of another tissue occurs. Figure 2 contrasts the actual RMR of 20 anthropoids (new and old world monkeys and apes) and those predicted from the Klieber [10] equation using body weight. Because the actual human RMR does not deviate from the predicted, nor from other living anthropoids, it can be inferred that RMR did not increase as encephalization progressed in early hominids [7, 8]. Hence, the increased size and metabolic activity that occurred during the encephalization of the hominid brain resulted not from a general increase in RMR, but rather from a reduction in the size and metabolic activity of another organ system. Aiello and Wheeler [8] have shown that the mass of the human gastrointestinal tract is only about 60% of that expected for a similar-sized primate. Consequently, the increase in brain size that occurred in our species was balanced by an almost identical reduction in the size of the gastrointestinal tract [8]. The selective pressure that simultaneously allowed for both a reduction in gut size and an increase in brain size is attributed to an improvement in dietary quality (DQ) that occurred largely as a result of the increased consumption of animal foods that began with the first members of *Homo* [7, 8]. Because a diet with an increased DQ contains less structural plant parts and more animal material [11], the nutrient and energy density of early

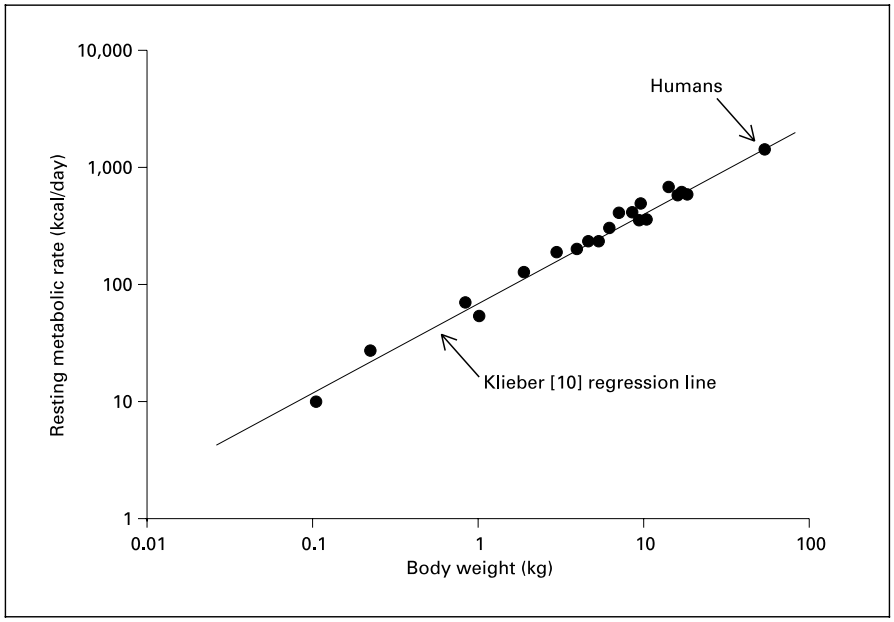

Fig. 2. Log-to-log chart of the resting metabolic rate of 20 anthropoids (new and old world monkey, apes and humans) relative to the predicted relationship based upon the Klieber [10] equation. Adapted from [7].

Homo diets was likely greater than that in Australopithecine precursors, hence the greater DQ permitted the relaxation of the selective pressures that formerly required a large, metabolically active gut which in turn permitted the natural selection of a large metabolically active brain.

A greater DQ fulfills the energetic considerations necessary for the encephalization that occurred in early hominids, however, it does not necessarily fulfill the nutrient requirements needed for the evolution of larger brains. In mammals, the polyunsaturated (PUFA) acid content of brain ethanolamine phosphoglycerols is virtually identical among varying species and is dominated by 22:6ω3 (docosahexaenoic acid, DHA) and 20:4ω6 (arachidonic acid, AA) (fig. 3) [12, 13]. Whether a mammalian species has a high encephalization quotient or a low encephalization quotient, the relative percentage of DHA and AA of the total brain phospholipids remains constant, hence all mammalian brain tissue appears to have an invariant structural requirement for these two fatty acids without which, normal neural function cannot occur [13, 14]. Limitations to the supply of either one of these fatty acids will determine limitations to brain growth [14, 15]. As mammals

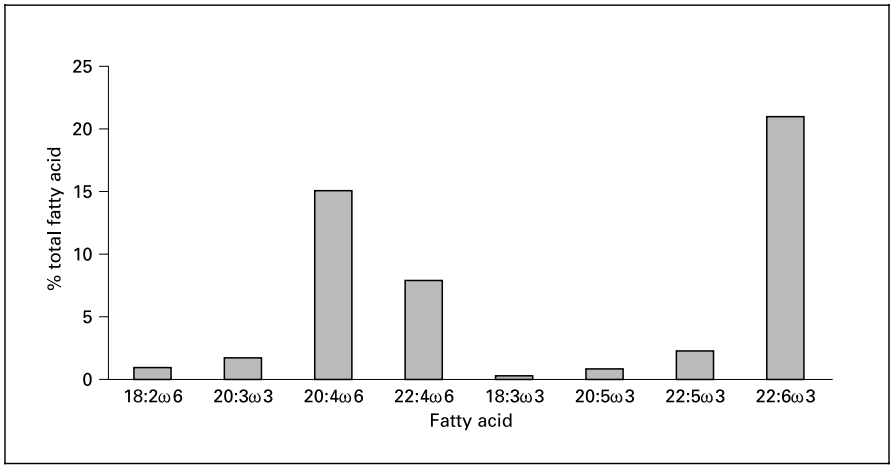

Fig. 3. Average polyunsaturated fatty acid composition of ethanolamine phosphoglycerols (g/100 g) in brain motor cortex gray matter of 32 mammalian species. Adapted from [12].

evolve larger bodies, encephalization quotients (brain mass/body mass) generally decrease [16], consequently evolving mammalian brains were not able to maintain their relative mass with greater and greater evolutionary increases in body mass. This limitation occurs because the supply of the fatty acid building blocks for brain tissue (AA and DHA) is constrained by the limited ability of the liver (primarily) and other tissues to synthesize these fatty acids from their dietary precursors [12–15]. Figure 4 shows the elongation and desaturation of the dietary precursor fatty acids that lead to the synthesis of AA and DHA. Numerous studies in mammals, including humans, have shown that the elongation and desaturation of linoleic acid (18:2ω6) to AA and of alpha-linolenic acid (18:3ω3) to DHA are inefficient pathways with low product to substrate ratios [17–19]. Hence, the limited availability of these two fatty acids from endogenous metabolic synthesis may have represented the evolutionary 'bottleneck' impeding the encephalization process in all herbivorous mammals. Encephalization quotients decrease with increasing body size because there literally may be insufficient long chain fatty acid product (AA and DHA) to build more brain tissue [14, 15].

Cats and other obligate carnivores represent a notable departure from the metabolic and evolutionary considerations that limit brain size in herbivorous animals because they obtain virtually all of their AA and DHA as preformed product in the flesh and organs of their prey [20] and are only minimally reliant upon elongation and desaturation of 18 carbon fatty acids as their source of AA

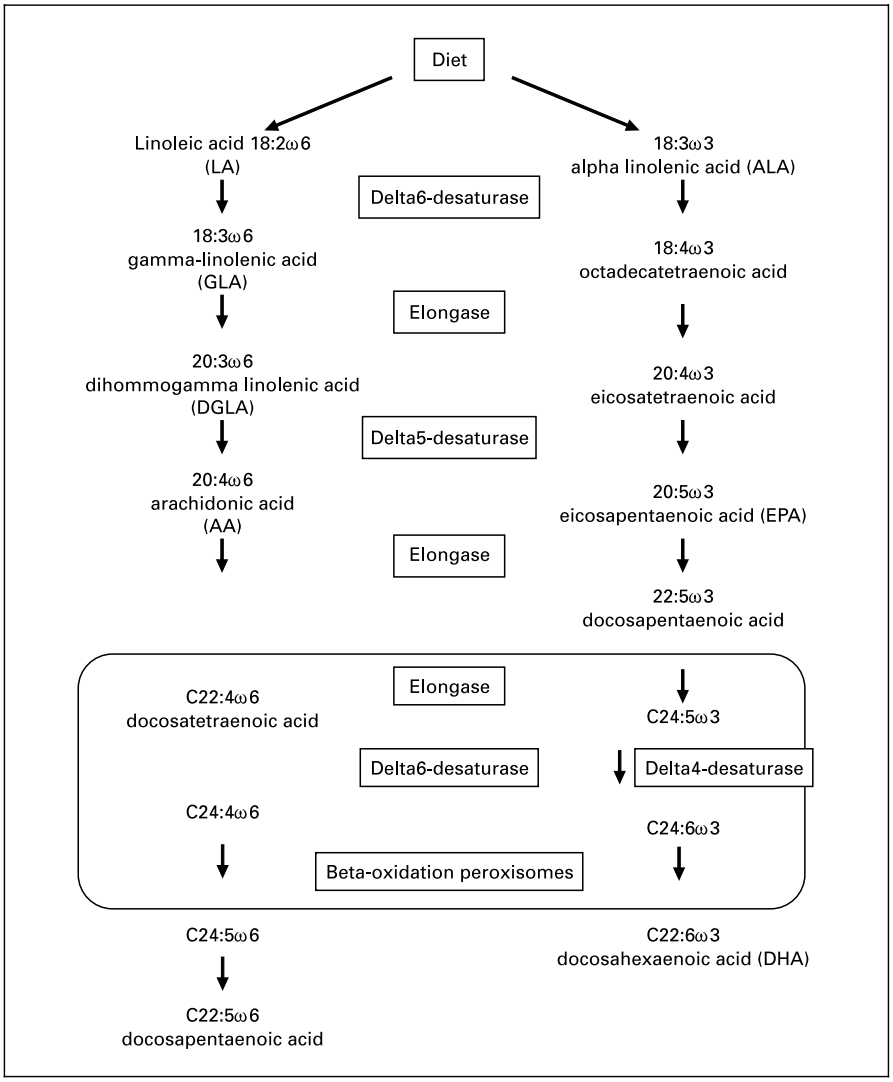

Fig. 4. The essential fatty acids and their long-chain polyunsaturated metabolites.

and DHA [21]. Throughout evolutionary history, carnivorous mammals have always maintained a proportionately larger brain size relative to body size when compared to their herbivorous prey [22]. The dietary availability of preformed AA and DHA is exclusive to meat eaters, since these fatty acids are not present or present only in trace quantities in plant food sources [23]. Consequently, the con-

sumption of animal tissues by carnivores provided the structural components necessary for increased neural development and thereby allowed for the natural selection of a larger brain. In a similar manner, increasing consumption of animal food products also provided early hominids with a dietary source of preformed AA and DHA, substances that may have opened the evolutionary 'window' for encephalization.

Collectively, animal foods represented both the energy source and the fatty acid source necessary for encephalization to proceed. Without the inclusion of energetically dense animal foods, laden with AA and DHA, into the diets of our early hominid ancestors, it is unlikely that increased encephalization would have occurred. However, there is still considerable debate regarding the precise animal foods that would have provided both energy and essential fatty acids necessary for brain expansion. Neither Aiello et al. [8] nor Leonard et al. [7] stipulated the types of animal foods that would have provided the increased energy for encephalization. In contrast, Broadhurst et al. [12] and others [14, 15] have strongly argued that freshwater fish and shellfish would have represented the dominant animal food providing the fatty acids necessary for encephalization, and that the evolution of a large human brain could have only occurred from consumption of animal foods available at a land-water interface [14, 15]. At least one group has even volunteered the idea that plant foods (cooked tubers and underground storage structures), and not animal foods, represented the 'energy dense' food source that allowed for the evolution of complex behavior associated with encephalization [24]. In order to gain insight into the fatty acid (FA) and energy sources that allowed for hominid encephalization, we compiled nutrient values from the literature for African ruminant tissues (brain, muscle, depot fat, marrow, liver), African freshwater fish, and edible, wild plant foods.

Methodology

Literature Compilation and Nutrient Derivation

On-line databases utilized for our literature search included MEDLINE, CARL, Wildlife Worldwide, Anthropological Index Online, and International Bibliography of the Social Sciences. Fatty acid (AA and DHA) and energy density databases were identified for muscle, liver and subcutaneous fat tissues in wild, African ruminants [25–27] and fish [28]. DHA and AA values in the brain of wild African ruminants [13] were used in conjunction with previous FA ruminant brain measurements [29] and with energy density values for ruminant brains [30] to estimate absolute quantities of AA and DHA per unit mass of brain. Estimates for absolute amounts of AA and DHA in marrow were determined using known energy density values for African ruminant marrow [31] in combination with previously published fatty acid profiles of ruminant marrow [29, 32–34]. The total fat content of ruminant marrow is highly variable and is dependent upon the nutritional status of the animal [31], hence we used a mean value of 51 g fat/100 g sample from a sample of 17 African

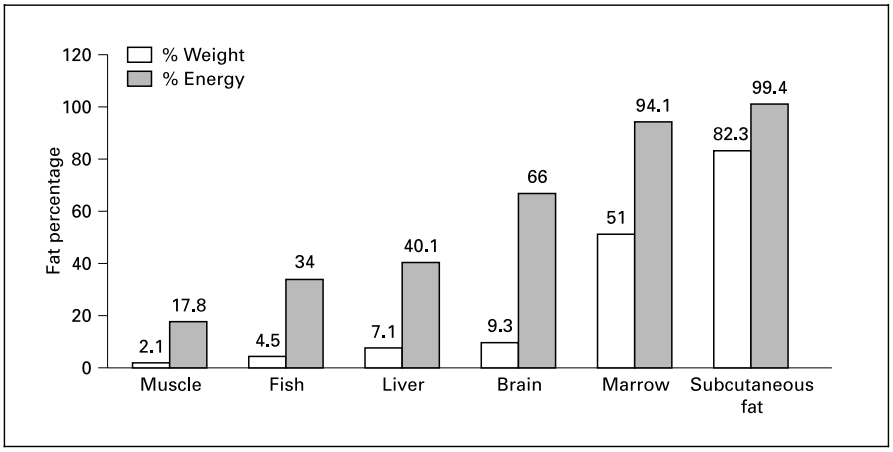

Fig. 5. Total fat percentage by percent weight and by percent energy in African ruminant tissues and in four species of African fish. Adapted from [25–30].

ungulates [31]. Estimates for absolute AA and DHA in subcutaneous fat were determined using known energy density values for ruminant subcutaneous fat [26, 30] in combination with previously published fatty acid profiles of ruminant subcutaneous fat [26, 29, 30]. The fatty acid and energy density values for wild plant foods [23, 35, 36] including nuts, tubers and roots [37, 38] were assembled from the available literature.

Results

Fatty Acid and Energy Comparisons

Figure 5 shows the mean estimated total fat content (by % weight and by % energy) for ruminant tissues (muscle, liver, brain, marrow and subcutaneous fat) and for four species of freshwater fish from Lake Nyas in Tanzania, East Africa. Table 1 contrasts the relative amounts of AA and DHA for these fish as well as for values reported in brain gray matter, liver and muscle tissues of wild African ruminants. All studies of ruminant marrow have shown that it contains no detectable quantities of either AA or DHA [29, 32–34]. Similarly, subcutaneous fat in ruminants has been reported to contain either trace quantities (less than 0.01% of total fatty acids) [26, 29] of AA and DHA or low levels (<0.5% of total fatty acids) [26] of these fatty acids. Hence, neither marrow nor subcutaneous fat is a significant dietary source of DHA.

Except for certain species of oily nuts and seeds [37, 38], other edible wild plant foods contain relatively low concentrations of fat and consequently are of a

Table 1. Comparison of wild African ruminant muscle, brain and liver tissue fatty acid concentrations (arachidonic acid [AA] and docosahexaenoic acid [DHA]) relative to values in four species of East African freshwater fish (values are % total fatty acids): adapted from [13, 25, 28]

	AA	DHA
Ruminant brain gray matter[a]		
Giraffe *(Giraffa camelopardalis)*	14.0	24.0
Eland *(Taurotragus oryx)*	14.0	11.0
Hartebeest *(Acephalus buselaphus)*	11.0	17.0
Cape Buffalo *(Syncerus caffer)*	12.0	16.0
Mean	12.8	17.0
East African freshwater fish		
Kambale (local name)	5.9	13.3
Mfui (local name)	8.0	19.1
Njenu (carp)	5.8	7.8
Mbelele (catfish)	4.3	8.6
Mean	6.0	12.2
Ruminant liver[a]		
Topi *(Damaliscus korrigum)*	9.2	0.8
Giraffe *(Giraffa camelopardalis)*	12.0	0.8
Eland *(Taurotragus oryx)*	14.0	6.4
Hartebeest *(Acephalus buselaphus)*	14.0	0.9
Cape Buffalo *(Syncerus caffer)*	13.0	1.8
Mean	12.4	2.1
Ruminant muscle		
Giraffe *(Giraffa camelopardalis)*	7.4	0.4
Eland *(Taurotragus oryx)*	6.0	0.7
Hartebeest *(Acephalus buselaphus)*	4.0	0.1
Topi *(Damaliscus korrigum)*	7.2	0.3
Cape Buffalo *(Syncerus caffer)*	7.5	0.3
Wildebeest *(Connochaetes taurinus)*	5.0	0.5
Waterbuck *(Kobus defassa)*	6.6	0.1
Mean	6.2	0.3

[a] Fatty acid values for brain and liver derived from ethanolamine phosphoglycerols lipid fraction.

Table 2. Comparison of energy density, protein content and arachidonic acid (AA) and docosahexaenoic acid (DHA) in food sources (100 g samples) available to early hominids

Food	Energy kcal	Fat g	Protein g	AA mg	DHA mg	DHA/ energy mg/kcal	DHA/ protein mg/g
African ruminant brain[a]	126	9.3	9.8	533	861	6.83	87.86
African freshwater fish[b]	119	4.5	18.8	270	549	4.61	29.20
African ruminant liver[c]	159	7.1	22.6	192	41	0.27	1.81
African ruminant muscle[d]	113	2.1	22.7	152	10	0.09	0.45
Ruminant marrow[e]	488	51.0	7.0	n.d.[i]	n.d.	–	–
African ruminant subcutaneous fat[f]	745	82.3	1	20–180	trace[j]	–	–
Wild tubers/roots[g]	96	0.5	2.0	n.d.	n.d.	–	–
Wild nuts[g]	306	29.0	13.0	n.d.	n.d.	–	–
Mixed, edible wild plant foods[h]	129	2.8	4.1	n.d.	n.d.	–	–

[a] Derived from [13, 29, 30], [b] derived from [28], [c] derived from [27], [d] derived from [27], [e] derived from [29–31], [f] derived from [26], [g] derived from [37, 38], [h] derived from [35], [i] n.d. (not detectable), [j] trace (less than 0.01% of total fatty acids).

uniformly low caloric density [35–37]. Eaton et al. [35] showed the mean caloric density of 44 wild plants consumed by hunter-gatherers to be 129 kcal/100 g. The mean caloric density of 151 species of wild, edible roots and tubers is even lower (96 kcal/100 g), whereas the mean caloric density of 74 species of wild nuts is higher (306 kcal/100 g) [37]. Additionally, long chain PUFA such as AA and DHA have rarely been reported in plant foods and then only in low or trace quantities [23]. The existence of long chain PUFA in plant foods is disputed, and some investigators contend that apparent values actually represent technical artifacts of measurement [36].

From figure 5 and table 1, it becomes evident that the absolute amount of dietary AA and DHA that are available in any food is a function of the total amount of fat and the relative concentrations of these specific fatty acids contained within that amount of fat. Table 2 provides estimates of the absolute amounts (per 100-gram sample) of both AA and DHA that are present in a variety of foods that may have been available to early hominids. Additionally, the relative concentrations of DHA per kcal and DHA per g protein are provided, as these variables will influence dietary DHA intake.

Discussion

The encephalization that occurred in hominid species coincident with or slightly following the appearance of crude stone tools in the fossil record has most frequently been attributed to an increase in dietary quality (DQ), primarily via the inclusion of more and more animal foods into the diet [7, 8]. In order for encephalization to occur, both a concentrated energy source [7, 8] and a source of preformed DHA and AA must be available [14, 15]. Aiello et al. [8] and Leonard et al. [7] suggested that the candidate animal food must have an increased DQ, however, neither of these authors mentioned the simultaneous dietary need for the essential fatty acid building blocks (AA and DHA) of neuronal tissue. Hence, they did not specify which animal foods would have been the most likely candidates that allowed for the natural selection of a larger brain in hominids. In contrast, Crawford et al. [12–15] suggested that fish and invertebrates available at land/water interfaces would have provided both the energy and fatty acid sources necessary for encephalization.

Table 2 shows the likely candidate foods that may have permitted hominid encephalization to occur and their fatty acid and macronutrient characteristics. Obviously, foods with high energy densities, fulfill the need for an increased DQ as proposed by both Aiello et al. [8] and Leonard et al. [7], whereas foods with high concentrations of both DHA and AA fulfill the long chain PUFA requirement for encephalization as proposed by Crawford et al. [14, 15]. Unfortunately, as can be determined from table 2, no single food simultaneously fulfills both of these requirements. High energy foods such as subcutaneous depot fat, marrow and nuts are virtually devoid of DHA, whereas high DHA and AA containing foods such as brain and fish have low to moderate caloric densities that are similar to the average value in a mixture of wild edible plants [35]. Hence, if increased DQ is a requirement for hominid encephalization as previously proposed [7, 8], then only three of the candidate foods (marrow, subcutaneous or depot fat, and nuts) qualify by virtue of having energy densities significantly greater than values found in non-oily, wild plants. However, none of these foods contain significant quantities of AA and DHA. Consequently, a combination of high energy density foods and foods containing concentrated sources of long chain PUFA (AA and DHA) represents the only avenue to simultaneously accomplish both physiological requirements for the natural selection of a larger, metabolically active brain.

In all likelihood, early hominids were opportunistic and would have consumed any and all of the foods listed in table 2, however, the combinations of foods that allowed for encephalization by necessity would have been more energy dense and would have contained more AA and DHA than the diets of earlier, nonencephalized hominids. The various food combinations from table 2 that can accomplish this goal would not have occurred randomly but

would have been dependent upon food accessibility and its energetic cost of procurement.

Subcutaneous Fat, Marrow and Energetic Considerations

Consumption of subcutaneous and other depot fat represents an excellent strategy for increasing DQ, however, it is likely that our early hominid ancestors would have had limited access to this food source. Early hominids may have been able to capture and kill small mammals similar to the hunting techniques observed in chimpanzees [39], on the other hand it is unlikely that they would have been successful hunters of large African ruminants because of their small size (*Homo habilis* male: height = 132 cm, weight = 37 kg), lack of effective weapons and limited behavioral sophistication [40–42]. Consequently, successful hunting activities would likely have been limited to small animals. Small mammals are not good sources of fat because both the absolute and relative amounts of fat are lower than in a larger animal.

Within a mammalian species, body fat varies with age, gender, season and the health of the animal, however, between species body fat is largely a function of body size or the fat free mass (FFM), and in wild mammals interspecies body fat percentage correlates ($r = 0.86$) highly with FFM [43]. For instance, a small rodent with a FFM of 190 g would have 4% body fat by weight (total fat = 7.9 g), whereas a medium sized antelope with a FFM 30.6 kg would have 12% body fat by weight (total fat = 4.1 kg). Accordingly, small animals that early hominids could have easily hunted and killed would have provided them with insignificant quantities of fat needed for the encephalization process to occur.

Because of their lack of sophisticated hunting skills, early hominids likely would have had access to large African ruminants and their greater stores of body fat only through scavenging of carcasses killed by accident, disease or by predators [40–42]. However, to adopt this ecological niche (scavenging) they had to compete with established scavengers such as hyenas that were larger, more powerful and who could drive them from carcasses. Further, it is unlikely that early hominids would have been successful in confrontational scavenging by driving large carnivores such as lions and leopards from their kills [44]. The most likely scenario for early hominid scavenging would have been passive encounters with defleshed carcasses from lion and other felid kills [41, 44, 45]. A field study examining the carcass consumption sequence in which large carnivores consumed the edible parts of 260 large herbivore carcasses in the Serengeti region of Tanzania demonstrated that the marrow and head contents were the last items consumed and that defleshed marrowbones with intact marrow and defleshed heads with intact brains were the items most likely to be abandoned [45]. Hence, head contents and defleshed marrowbones would have been the most frequently available body parts to prehistoric scavengers, as they are today [41, 44–47]. In a study

evaluating the types of animal foods that would have been available to early hominids with minimal hunting skills, Schaller and Lowther [47] wandered about a 200 km^2 area in Tanzania and found 'four freshly abandoned lion kills, three of zebra and one of wildebeest. The marrow and the brains were the only edible portions left'. Taken together, these studies indicate that of the two energy dense animal foods (marrow and subcutaneous or depot fat) listed in table 2, only marrow would have been regularly available in substantial quantities to early hominids.

Ruminant Muscle and Liver Tissues and Fatty Acid Considerations

From table 2, it is apparent that the lean muscle tissue of wild ruminants is slightly less energetically dense than a variety of mixed, edible wild plants. Therefore, increasing consumption of 'meat' by early hominids would have conferred little selective advantage in terms of the increased DQ needed for encephalization. Additionally, there is a physiologic limit to the amount of lean protein that can be consumed that is determined by the ability of the liver to up-regulate enzymes required for urea synthesis [48]. In modern humans, this amounts to about 40% of total energy intake or between 200 and 300 g of protein per day, assuming a eucaloric energy intake [49]. The total energy expenditure for early hominids *(Homo habilis)* has been estimated to be 2,388 kcal/day [50], therefore maximal protein intake would be 227 g, assuming that early hominids had a metabolic limit to protein ingestion similar to modern humans. The physiologic protein ceiling effectively limits the amount of lean muscle tissue that can be consumed without producing toxic effects [49]. From table 2, it can be shown that the (protein/energy) ratio for muscle tissue in African ruminants is 22.7 g protein/100 g. Consequently, the maximal amount of lean muscle tissue that could be consumed on a regular daily basis, without causing hyperammonemia and hyperaminoacidemia [49] would be approximately 1.0 kg. The total AA ingested along with the consumption of 1.0 kg of lean muscle would be 1,520 mg and the total DHA would be 100 mg. It has been estimated that 100 mg of daily DHA are required in pregnant and lactating females for normal brain development [51]. Hence, at the upper physiologic limits of protein ingestion, lean muscle, as well as liver (table 2) contains both sufficient AA and DHA to allow for encephalization to occur.

However, similar to the situation for subcutaneous and depot fat, it is unlikely that high amounts ($\geq$ 1.0 kg per day) of muscle tissue or liver would have been regularly available to early hominids because of their ineffective ability to hunt and kill large animals. Again, the passive scavenging of defleshed carcasses that our ancestors most likely practiced would have supplied long bone and skull contents, but little or no muscle tissue [40–42, 44–47]. Further, even assuming that high amounts of lean muscle tissue were regularly available, there is evidence to

suggest that the physiological protein ceiling is reduced for females during pregnancy [52]. Because of muscle tissue's relatively low (DHA/protein) ratio, the absolute amount of DHA that can be consumed by pregnant and lactating females is under physiologic constraints, particularly during the critical fetal and postnatal periods when extensive brain growth occurs. In summary, both liver and muscle tissues represent a moderate source of DHA, a good source of AA and a low to moderate energy source.

Ruminant Brain and Freshwater Fish

Table 2 shows that the richest dietary source for early hominids of both AA and DHA, either on an energy or protein basis is ruminant brain. Ruminant brain contains 56% more DHA and 97% more AA on an energetic basis (mg/kcal) than the mean values for these fatty acids from four species of East African freshwater fish. Additionally, because of its greater fat content and lower protein content, ruminant brain maintains a more favorable DHA/protein ratio (87.9) than freshwater fish (29.2). However, because of their high concentrations of DHA and AA, both ruminant brain and fish would be able to provide far in excess of the recommended daily intake of DHA (100 mg) necessary for normal brain development in modern humans without encroaching upon the physiologic protein ceiling. Regular consumption of either one of these foods would have supplied early hominids with sufficient AA and DHA to allow for the natural selection of a larger brain, as long as a high-energy food source would have been simultaneously available. Neither brain (126 kcal/100 g) nor freshwater fish (119 kcal/100 g) are highly energy dense foods, though brain does contain about twice as much fat (9.3 g/100 g) as does freshwater fish (4.5 g/100 g).

As has been previously argued, scavenged ruminant marrow would have been the most likely food candidate capable of increasing the DQ and providing a concentrated energy source needed for encephalization in early hominids. Field studies of large herbivore carcass consumption sequences by carnivores have indicated that the two most frequently abandoned items were marrowbones and skulls [45]. Hence, these two food items quite often occur together and in close proximity to one another [45, 47]. Scavenging hominids that encountered marrowbones would have also frequently encountered skulls. There is extensive documentation in the fossil record that hominids regularly processed both marrowbones and skulls to extract both brains and marrow [41, 42, 44–46]. If marrow represents the most likely concentrated energy source that allowed for hominid encephalization, then the association and concurrent presence of skulls with marrowbones indicates that consumption of brain would have been the most reliable and concentrated source of DHA and AA in early hominids.

Although certain authors [12–15] have argued that fish and aquatic invertebrates may have provided both the energy and fatty acid sources necessary for

hominid encephalization, there are a number of lines of evidence to suggest otherwise. Table 2 shows the average energy density of four species of East African fish to be 119 kcal/g, which is slightly lower than the mean energy density for a mixed sample of edible, wild plants consumed by hunter-gatherers. Thus, increased fish consumption would not have significantly increased the DQ of the plant-based diets of non-encephalized hominids.

There is little doubt that if fish and aquatic invertebrates had been increasingly consumed by early hominids, the dietary intake of both AA and DHA would have been increased, even though the mean energy density may have not. However, there is little fossil evidence to support the notion that either early hominids or later hominids extensively exploited the aquatic environment until upper Paleolithic times [53–55]. Admittedly, the capture and consumption of small fish and aquatic invertebrates by hand would leave few traces in the fossil record, but there are other arguments suggesting that exploitation of aquatic animals may have been an infrequent endeavor by early members of the *Homo* genus.

Hominids, like all other organisms must obtain more energy from the food they capture and consume than the energy required to obtain the food. The concept of maximizing the (energy capture/energy cost) is referred to as 'optimal foraging theory', and has generally been shown to be true for foraging humans [56]. Studies examining the energy return rate from fishing show it to be low, even for modern day hunter-gatherers employing nets, weirs, and other sophisticated fishing tackle [57]. Consequently, it is likely that the energy return rate for early hominids, using nothing more than bare hands to capture freshwater fish would have been lower still. Because scavenged marrow represents a more highly concentrated energy source (488 kcal/100 g) than freshwater fish (119 kcal/100 g), the energy return versus the energy expenditure for scavenged marrowbones would have far exceeded that available from the manual capture of freshwater fish. Further, because the (energy/protein) ratio in African fish (6.3) is about one tenth that in African ruminant marrow (69.7), fish consumption would have been constrained by the physiologic protein ceiling whereas, marrow consumption would not have been. Thus, when the option was available, scavenged ruminant marrow and the brain that was concurrently present in skull of the defleshed skeleton would have almost always been chosen over active capture of either fish or aquatic invertebrates. Taken together the data indicate that scavenged marrow from ruminant longbones would have represented the concentrated energy source required for hominid encephalization, and the brains of scavenged skulls would have represented the predominant source of DHA and AA.

Plant Food Considerations

Although the authors of two recent papers [24, 58] have suggested that increased consumption of tubers, roots and underground plant storage organs

represented the 'energy dense' food source that allowed for the evolution of complex behavior associated with encephalization, the data in table 2 provides little support for this contention. Plant foods rarely contain long chain PUFA, and when apparent, they are present either in trace quantities, or may be technical artifacts of the measurement [23, 36]. Wild tubers and roots are not only usually devoid of the long chain PUFA necessary as substrate for neuronal cell synthesis, but generally maintain a low caloric density regardless of their geographical origin [37, 38]. Examination of table 2 reveals that wild tubers maintain the lowest caloric density of all the candidate foods implicated in hominid encephalization. More succulent roots and tubers, such as domesticated radishes, onions, carrots are edible in their raw state, whereas tuber and roots containing high amounts of starch, such as domesticated potatoes, yams and cassava are inedible or poorly digested unless cooked. Cooking serves to gelatinize the starch granules and make it available for digestion [59] as well as to denature potentially toxic antinutrients [60]. There is little or no evidence to indicate that the controlled use of fire and hence cooking had been mastered by the early hominids undergoing encephalization 2 million or more years ago. Indeed, the first conclusive use of controlled fire appears in the fossil record between 200,000 and 300,000 years ago [61]. Consequently, only the less starchy tubers, roots and underground storage organs, which have even lower caloric densities than their starchy counterparts [37, 38], would have been completely edible to early, non-fire using hominids. The low caloric density of raw, edible underground storage organs in plants combined with their low fat content and absence of long chain PUFA disqualify them as a potential food source that would have permitted the natural selection of a large, metabolically active brain in our hominid ancestors.

The only plant foods with sufficient caloric density to increase the DQ and allow for the relaxation of selective pressures formerly requiring a large gut in pre-encephalized hominids would have been oily seeds or nuts. However, as shown in table 2, these plant foods contain no discernable amounts of either AA or DHA. Hence the consumption of energetically dense plant foods without an animal source of preformed DHA and AA would not allow the encephalization process to proceed.

Conclusions

Our analysis demonstrated that muscle tissue would have been a relatively good source of AA, but not of DHA or energy. Scavenged marrow would have likely been the most frequently obtainable concentrated energy (fat) source for early hominids, except that it would have been devoid of DHA and AA. Subcutaneous fat contained trace amounts of DHA and moderate amounts of AA, how-

ever, this fat was unlikely to have been frequently encountered and therefore would have provided little energy or FA needed for encephalization. The scavenged brain tissue of ruminants would have provided a moderate energy source for encephalization and a rich source of both DHA and AA. Fish would have provided a rich source of DHA and AA, but not energy, and the fossil evidence provides scant evidence for their consumption. Plant foods generally are of a low energetic density and contain little or no DHA and AA. Because early hominids were probably not successful in hunting large ruminants, the scavenged skulls (containing brain) likely provided the greatest DHA and AA sources, and long bones (containing marrow) likely provided the concentrated energy source necessary for the evolution of a large, metabolically active brain in ancestral humans.

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