

REVIEW

Open Access



The evolutionary roles of nutrition selection and dietary quality in the human brain size and encephalization

Roberto Carlos Burini^{1*}  and William R. Leonard²

Abstract

Background: Humans and other primates have evolved particular morphological and biological traits (e.g., larger brains, slower growth, longer-lived offspring) that distinguish them from most other mammals. The evolution of many distinctive human characteristics, such as our large brain sizes, reduced gut sizes, and high activity budgets, suggest major energetic and dietary shifts.

Main body: Over the course of the last three million years, hominin brain sizes tripled. It is often taken for granted that the benefit of a larger brain is an increase in “intelligence” that makes us stand out among other mammals, including our nearest relatives, the primates. In the case of humans, brain expansion was associated with changes in diet, foraging, and energy metabolism. The first marked expansion occurred with the appearance of the genus *Homo*. Improved diet quality, allomaternal subsidies, cognitive buffering [by earlier weaning and longer juvenile periods], reduced costs for locomotion and by cooperative behavior, and reduced allocation to production, all operated simultaneously, thus enabling the extraordinary brain enlargement in our lineage.

Conclusion: It appears that major expansion of brain size in the human lineage is the product of synergistically interacting dietary/nutritional and social forces. Although dietary change was not being the sole force responsible for the evolution of large brain size, the exploitation of high-quality foods likely fueled the energetic costs of larger brains and necessitated more complex behaviors that would have selected for greater brain size.

Keywords: Human brain evolution, Human encephalization, Evolutionary foraging, High-quality diet

Background

Humans share a common ancestor with the chimpanzee and bonobo that likely existed in East Africa some 6 to 7 million years ago (mya) [1, 2]. The earliest unambiguous fossil hominins, such as *Australopithecus anamensis* and *A. afarensis*, were bipedal, but still retained some aspects of arboreal lifestyles, as demonstrated by a combination of long forelimbs, curving phalanges, and barrel-shaped thorax [3]. With the emergence of the genus *Homo* at 2.0 mya (*H. ergaster/erectus*) [4], there was a marked increase in body size, mainly in females, who almost double in size compared with Australopithecine [5]. The oldest fossil evidence for *Homo sapiens* is from Southern and Eastern Africa, dating to about 160–250 kya [6, 7].

With the emergence of *H. erectus*, the human lineage has experienced remarkable morphological and physiological changes, including (a) marked increases in both brain and body size, (b) the evolution of human-like body proportions, (c) major reductions of posterior tooth size and craniofacial robusticity, and (d) reduction of the gut [8, 9].

The most important of these has been our high levels of encephalization (large brain to body mass). Since the emergence of early hominins, brain volume tripled over the course of human evolution. It is often taken for granted that the benefit of a larger brain is an increase in “intelligence” that makes us stand out among other mammals, including our nearest relatives, the primates [10].

The neocortex volume has grown out of all proportion to the rest of the brain during the course of primate evolution. In small animals, the volume of the neocortex increased from only 16% of the volume of the whole brain,

* Correspondence: burini@fmb.unesp.br

¹Department of Public Health, UNESP Medical School, Botucatu, SP 18.618-970, Brazil
Full list of author information is available at the end of the article



to 74% in Hominoidea. In contrast, the relative volume of the cerebellum remained constant at 13% of whole brain volume, regardless of the absolute size of the brain [11, 12].

When the volume of white matter is plotted against the volume of gray matter, there is a remarkably tight relationship between these two variables in all animals from the pygmy shrew to the elephant. The volume of the white matter approximately increases as the $4/3$ power of the volume of the gray matter. As the size of the neocortex progressively evolved, so also did the volume occupied by myelinated nerve fibers. Therefore, the data supported the view that the neocortex increased in size and complexity and there was necessarily a disproportionate increase in the volume of brain devoted to “wiring” [13].

It is the frontal lobe volume that has increased out of all proportion in humans. As the total brain volume increases, more neural capacity becomes available in the frontal cortex, especially in the frontal lobe. This seems to be associated with markedly improved basic cognitive abilities [10].

Main text

Selection for large brain size

Only with the emergence of the *H. ergaster/erectus* lineage, i.e., an approximate of 4 to 5 mya after the split from the chimpanzee lineage [14, 15], did hominins take the place of the largest brained animal. Hence, this position was obtained only recently, in the last 1.8 mya. The hominin brainy prominence pales in comparison to the approximately 20 to 30 mya that some marine mammals have been maintaining their large brains. Until the beginning of the Pleistocene, dolphins were the largest brained creatures on the planet, exceeding all primates, including the hominins [16].

Because of their high costs, large brains are rare and are achieved only when animals are under strong selection. The trigger for brain expansion in marine mammals was probably environmental, specifically the cooling of the southern ocean [17]. In the case of humans, there have been two environmental periods associated with their two major periods of brain expansion. The first marked increase in hominid brain size occurred with bipedal running and correlates with the appearance of the genus *Homo* (2.0 mya), when absolute brain size increased to an average of 30% from *H. habilis* to the earliest African *H. ergaster* [18].

In general sense, both episodes of human brain expansion were triggered by environmental factors, specifically foraging, therefore suggesting that diet may have been an important factor in providing the nutritional basis for the selection of larger brains [10].

Bipedalism-derived behavior

The evolution of bipedalism has traditionally been related to changes in the environment, including increasingly dry

conditions and the expansion of open habitats, a more wooded and humid context [19]. These changes in the environment presented new challenges to arboreal apes, some of which started to forage the more scattered resources of the mosaic landscape at ground level [10].

Trunk morphology of the Australopithecines and modern great apes contrasts with that of modern humans in having a conically shaped rib cage, flaring at the waist. The inference is that Australopithecines likely retained large ape-like guts, in contrast to reduced gut sizes of *H. sapiens*. [18].

Gut size is associated with both the bulk and the digestibility of food. Diets characterized by large quantities of food of low digestibility require relatively large guts characterized by voluminous and elaborated fermenting chambers (the stomach and/or large intestine [colon]). Conversely, higher quality, more easily digestible diets require relatively smaller guts and are characterized by simple stomachs, reduced colons, and proportionately long small intestines (emphasizing absorption). An extreme example of folivores is the cow whereas carnivores typify the other pattern [18].

Differences in both diet composition and food processing likely shaped the reductions in jaw and tooth size with the advent of *Homo* [20]. The Australopithecines were characterized by large jaws, faces, and teeth (megadonty), a morphology consistent with the consumption of lower quality, fibrous foods. Recent evidence from dental micro-wear and stable isotope analyses have confirmed the relatively lower-quality diet for the Australopithecines, particularly for the east African robust Australopithecines, who appear to have consumed large amounts of grasses and sedges [21, 22]. Moreover, fruits are more ephemeral and patchy in their distribution and often contained in a protective casing, which may make the foraging niche of frugivores relatively complex [20, 23–25]. Therefore, as folivores have a relatively easy foraging strategy that requires little in the way of learning, primates eating leaves could potentially start foraging fairly early on in life. It has been shown that folivores tend to wean at an earlier age compared with frugivores [26].

Tool use and foraging strategies

Changing environmental conditions in Plio-Pleistocene Africa, involving a decline in plant productivity and an increase in secondary biomass, would favor a shift in diet in hominin species, either to specialization on lower quality plant foods or routine access to meat [27, 28]. Members of the genus *Homo* would be expected to have had a higher-quality diet than those of the Australopithecines. Their diet probably differed by the incorporation of more underground storage organs (soft bulbs, tubers, etc.) or the preferential consumption of animals. Meat consumption by early *Homo* might also be inferred from

polish on tools and by cutmarks on bones. The stone tools appear before *Homo*, at 2.58 mya suggesting “...that hunting and/or aggressive scavenging of large ungulate carcasses may have been part of the behavioral repertoire of hominins” [29].

Tools allowed hunting and/or aggressive scavenging of large ungulate carcasses would have improved the energy intake and the overall quality of the diet. Consequently, there was gut reduction and cranium-dental anatomy changes. It became possible to achieve the food adequacy by eating less frequently and with reduced alimentary bolus. By requiring less time to feed and provided with language, our ancestors have had more time for social familiarity.

The other shift that likely occurred with greater hunting and wider exploitation of animal resources among early members of the genus *Homo* was an increase in ranging behavior, activity budgets and total daily energy expenditure. Contemporary human hunter-gatherers move over much larger areas than modern apes. A typical day ranges for modern foragers average over 13 km/day, significantly greater than those of chimps and gorillas whose ranges are less than 2 km/day [27]. Similarly, adjusting for body mass, home range sizes for human foragers are some five to six times the size of those of the apes [26, 29]. These larger territorial needs for humans appear to be associated with larger daily energy budgets. Recent work by Pontzer and colleagues [30, 31] has shown that humans are indeed the “high energy” apes. Using the doubly labeled water (DLW) technique to quantify total daily energy expenditure (TEE; kcal/day), they have shown that humans have systematically and significantly greater energy budgets than chimpanzees, gorillas, or orangs. It appears likely that the elevation in human total energy demands initially emerged with the evolution of the *Homo*, in association with a foraging regime that was exploiting more animal material and required movement over larger areas than was typical of earlier hominin species [29, 32, 33].

Factors driving brain size evolution

A series of important hypotheses has been advanced to explain the origins of unusual human features and the interrelationships between such variables as brain size and diet, longevity and foraging strategy, social organization, and the evolution of intelligence. The search for plausible explanations for the factors driving brain size evolution raised “Ecological and Social Brain Hypothesis” which highlight ecological and social contexts [10]. Both hypotheses are not exclusive [33]. In both hypotheses, dietary acquisitions are included as major environmental factors for selective brain enlargement. However, it is suggested that human ecological and social intelligence evolved in the context of a distinctive foraging strategy, with strong benefits to

cooperation, selecting for greater social intelligence and subsequently language skills [34]. Specifically, the ecological hypotheses theorize that brain size increased simply as a by-product of increasing body size.

The social brain hypothesis

The social brain hypothesis assumes that large brains have been selected for specifically to provide the cognitive basis for maintaining social cohesiveness through time. Indices of social complexity (including group size and the frequency of social play) correlate with relative neocortex volume, in primates and a number of other mammalian orders as well. There is a clear relationship between social group size and neocortex volume across primates [including modern humans], and cooperative acquisition, sharing food and information, and educating young people are all key elements of foraging [10].

In general sense, big neocortices are a primate speciality and, broadly speaking, the neocortex is a mammalian evolutionary invention [35]. Additionally, the fact that the neocortex volume has grown out of all proportion to the rest of the brain during the course of primate evolution constitutes the principal evidence in support of the social brain hypothesis [10].

The ecological hypothesis

Across mammals, brain size scales to body mass in so that as body size increases, so does the brain. As so, early *H. erectus* marked an increase in both brain and body size towards the evolution of human-like body proportions [8, 9]. Hence, ecological hypothesis has an assumption that brain size increased simply as a by-product of increasing body size, since the two do seem to be locked together in a close allometric relationship [10].

This theory has been mainly criticized based on the fact that brains are energetically much more expensive than muscle or skeletal material [18, 35]. Indeed, it can legitimately be argued that rather than brain size being a consequence of body size, larger body size might actually be a consequence of the demand for a larger brain. This follows from the fact that the energy costs of living are not a direct linear function of body mass, but rather increase only as the 0.75 power of body mass (Kleiber’s Law) [36]. This means the bigger the body is, the less energy it needs per kilogram of weight to sustain life, so larger animals can afford less to have relatively larger brains than smaller bodied animals. Thus, body size is acting as a developmental constraint on brain growth, not as a factor selecting for brain growth. The high cost of both growing and running brains means that we still need to provide an explanation as to why a species should want to increase its brain size above the bare minimum necessary to ensure survival and successful reproduction. Unless these two had become energy costless!

Energy constraints for the enlarging brain

The brain is one of the most energetically expensive organs in the vertebrate body; therefore, the large amount of energy required to maintain brain tissue should impose serious constraints on brain size evolution [37]. In fact, humans expend a much larger share of their resting energy budget on brain metabolism than other primates or nonprimate mammals. Human brain sizes are some 2.5–3 times those of other primates, and, in caloric terms, this means that brain metabolism accounts for ~20–25% of resting metabolic rate (RMR) in an adult human body, as compared to about 8–10% in other primate species, and roughly 3–5% for nonprimate mammals. In humans, costs are even greater in infancy, with our brains consuming about 50% of the resting energy as newborns, 66% of RMR at age 4 years, as compared with 20% for adults [38]. The high energetic costs of the human brain highlight the importance of strong selective benefits to having a larger brain and enhanced cognitive abilities in human evolution [39, 40].

The energy cost of evolutionary encephalization could be explained by three proposed hypotheses: the direct metabolic constraints, the expensive tissue trade-off, and the energy trade-off [35].

The direct metabolic constraints hypothesis

The direct metabolic constraints hypothesis suggests that due to the energetic cost of maintaining brain tissue, overall RMR should be positively associated with brain size, as seen in a large sample of placental and marsupial mammals. Hence, larger brains are paid for by a permanent increase in the net energy intake of an organism [41, 42].

The mass-specific metabolic rate of the brain is approximately nine times higher than the average of the mass-specific metabolic rate of the human body as a whole and approximately 16 times that of skeletal muscle [43]. Surprisingly, despite their disproportionately large CNS metabolic rate, humans follow the same relationship for nearly all animals, as the rate of basal energy expenditure increases as the 3/4 power of body weight (Kleiber's Law) [36]. Consequently, RMR does not appear to be significantly elevated in humans and other more encephalized mammals. That is, there is no evidence of an increase in RMR sufficient to account for the additional metabolic expenditure of the enlarged brain.

The expensive tissue trade-off hypothesis

The lack of correlation between RMR and relative brain size in encephalized mammals raises the question of how the increased energetic demands of larger brains are compensated. The "expensive tissue hypothesis" posits that the metabolic accommodation of large brains

is achieved by a reduction in the mass/sizes of other tissues with high energy demands [18].

In addition to the brain, the heart, kidneys, and splanchnic organs [liver and gastrointestinal tract], all make substantial contribution to overall RMR. Together with the brain, they account for 60–70% of RMR despite making up less than 7% of the total body mass. The tissues which make up the remaining 93% of body mass display correspondingly low rates of energy turnover [18].

Specifically, the heart and the kidneys have mass-specific metabolic rates considerably higher than the brain, the energetic demands of which are comparable to those of the splanchnic tissues [18].

The extent to which the liver could be reduced with encephalization is probably constrained by the energy requirements of the brain, which uses glucose exclusively as its fuel. Since the brain effectively contains no energy reserves, it is critically dependent on the continual supply of glucose from the blood, maintained in fasting states, by the liver. Similarly, since most of the mass of the heart consists of the rhythmically contracting cardiac muscle, it is difficult to envisage how any significant reduction in the size of this organ could take place without compromising its ability to maintain an adequate circulation of blood around the body. The maintenance of high tissue perfusion rates will be particularly important to the brain, which requires a continuous supply of high levels of glucose and oxygen [18].

Along with the brain, the kidneys have an extremely high metabolic rate associated with high levels of active ion transport. It is likely that any reduction in either its energetic expenditure or its size will reduce the maximum urine concentration it is capable of excreting. The production of a more dilute urine would have been a particular problem for hominids if they were exploiting relatively open equatorial habitats where drinking opportunities were scarce and thermoregulatory requirements were already placing considerable demands on their water budgets [18].

A reduction in the mass of skeletal muscle would likely not entirely balance the extra costs of large brains, because the mass-specific RMR of muscle tissue is considerably lower than those of the more "expensive organs" noted above. To compensate for the increased energy expenditure of the enlarged human brain, approximately 19 kg of muscle, about 70% of the total, would have to be replaced by an equal amount of tissue with no metabolic cost at all [18]. Nonetheless, comparative analyses have shown that human and other primates are relatively "under-muscled" compared to other mammalian species [44].

In the case of humans, reduced muscularity appears to be, in part, a consequence of increased stores of body fat. Indeed, humans show important adaptations in fat

metabolism to accommodate the high energy demands of the brain early in life when key aspects of human growth and development of body composition are shaped by the very high metabolic demands of brain metabolism. 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. It is therefore possible that encephalization and fat storage are complementary strategies to buffer against starvation [45].

Lastly, the human brain and gastrointestinal tract have a similarly high rate of organ-specific basal metabolic energy expenditure (250 kcal/day/kg). The gut is the only one of the expensive metabolic tissues that could vary in size sufficiently to offset the metabolic cost of the encephalized brain (the brain-gut trade-off hypothesis). In fact, there is a close [inverse] relationship between relative gut size and relative brain size. Thus, the brain-gut trade-off hypothesis suggests that the massive expansion of the neocortex in humans came at the expense of the gastrointestinal tract [18].

Recent work by Navaretti et al. [46] re-examined the possible association between the size of various visceral organs (heart, lungs, stomach, intestines, kidneys, spleen, and liver) and brain size in a sample of 100 mammalian species, including 23 primate species. This study used free-fat mass as the best proxy for body size because body mass is highly affected by variation in the size of adipose depots. Contrary to the predictions of the expensive tissue hypothesis, these authors found no inverse correlation between the relative size of the brain and the digestive tract. These results therefore indicate that the expensive tissue hypothesis does not provide general explanation for interspecific variation of relative brain size in mammals. This finding reduces the plausibility of the argument that human encephalization was made possible by a reduction of the digestive tract [46].

The energy trade-off hypothesis

The lack of support for the expensive tissue hypothesis (investment into other costly tissues) raises questions about the determinants of the evolution of the greatly enlarged human brain and an increased energy allocation to the brain by savings on other expensive functions would be a pathway to brain enlargement. The “energy trade-off hypothesis” suggests that the cost of an increased brain size can be met through a series of life history trade-offs involving changes in locomotion, growth, and reproduction [46].

Another likely trade-off could be found between brain size and the costs of growth and reproduction. The increased reproductive costs associated with larger body size in *H. erectus* females suggest a range of reproductive and social solutions that could have met those costs. In

fact, having large, slow-growing babies is energetically costly for mothers during gestation and lactation.

The constraints of our bipedal gait require a narrower pelvic inlet so that the infant’s skull can pass through the pelvic canal. Consequently, human babies are altricially born, with skulls not fully formed and, although humans have the largest relative brain sizes of all animals, they are born with brains that are approximately 12% of their body size, similar to other apes. However, in humans, dramatic brain growth (similar to prenatal brain growth) occurs postnatally in the first year of life, providing a uniquely longer and more rapid phase of growth compared with all other mammals. Following this, our brain consumes 50% of the total energy intake as newborns, and 66% of RMR by age 4 years, as compared with 20% for adults. To accommodate for these high energetic demands of brain early in life, human infants are born with large quantities of body fat and show marked reductions in body weight growth around 4 years—the time during which brain energy demands are greatest [38].

Moreover, it is believed that a dietary impact on human brain size should occur during this brain fast-growth period, i.e., through maternal milk [10]. Indeed, recent comparative analyses have shown that across primates.

It is expected that species with larger brains need a longer period of postnatal brain growth, and this is generally completed at weaning. Earlier weaning is likely to have occurred in *H. erectus*, in response to a major increase in reproductive costs associated with increasing female body size. Shortening the inter-birth interval, by weaning children earlier, increases the female reproductive rate and allows some of the costs of caring for dependent weanlings to be shared among others [47]. Hence, encephalization has implications for maternal energetic costs in childrearing and thus for parenting strategy. Similarly, early weaning may have been important for the continued pattern of brain growth in childhood. In fact, providing such care could increase the fitness of grandparents, leading to selection for longer lifespans, and an extension of life history phases generally [48]. Furthermore, humans wean children early relative to their dental development, but provision them with suitable foods throughout their childhood. They are therefore able to offer more energy and nutrients than would be available just from maternal milk [49].

Among primates, the prevalence of non-maternal care varies greatly from none at all to occasional grooming and playing to feeding and holding infants. Data for hunter-gatherer societies show that children are held or carried by someone other than the mother for 20–50% of the time. Childcare, provisioning or even education by grandparents, may affect the survival of their grandchildren or reproductive rate of their children, with implications for the evolution of slower or later

maturation. Humans have a unique period, childhood, in their life cycle, in which body growth is very slow but brain growth continues. The childhood phase is particularly important for learning, because children have few responsibilities to take up their time, because of cognitive abilities that help efficient learning of particular skills (i.e., language), and because environmental complexity during childhood can have a positive and direct effect on brain structure [49].

Thus, species with larger brains need a longer period of postnatal brain growth and, since this is generally completed at weaning, a later age at weaning, which has implications for development, the dependency of offspring, birth spacing, and hence population growth.

Brain growth to adult size is almost complete by the age of seven, when childhood ends. After this period, body size starts to increase steadily. However, there is another uniquely human life history phase, adolescence, characterized by a spurt in skeletal growth, culminating in sexual and behavioral maturity [50, 51].

Overall, this model of human life history evolution posits that large brain size, a longer juvenile period, and a longer lifespan all co-evolved in the context of a complex foraging niche. Human foraging is relatively complex and skill intensive that it requires a longer juvenile period for learning this skill set. As such, it is only later in adulthood that an individual becomes a fully productive forager, generating a surplus of energy to support the long developmental period for the sub-adults [52, 53].

Thus, we humans combine a long juvenile period and lifespan, with caring and providing food for inefficient weanlings, thereby increasing not only the period of growth and time available for learning but also the reproductive rate [10].

A number of contexts in human evolution could have favored cooperative behavior relatively early, for instance, group defense and hunting large mammals at close quarters. The exploitation of large “packet” food resources that can be divided provides incentives for food sharing [54]. Additionally, provisioning and food sharing probably arose with the adoption of cooperative breeding and substantial meat acquisition among the earlier representatives of the genus *Homo* [54].

Relationship between human relative brain size and diet

The energetic constraint of large brain size evolution was not overcome solely by greater food intake, but also by higher-quality diets. Leonard and colleagues (2007) [55] have shown a positive correlation between brain size and dietary quality for 33 different primate species, including humans, after adjusting for differences in body size. Thus, across all primates, greater energy allocation to brain metabolism is associated with consumption of a higher quality, more energy-rich diet. Humans fall at the

positive extremes for both parameters, having the largest relative brain size and the highest quality diet [45].

A high-quality diet could have benefited encephalization by directly increasing the total energy available to fuel an increased RMR and, also by permitting a relatively smaller gut, thereby reducing the considerable metabolic cost of this tissue. Hence, the relationship between relative brain size and diet is primarily a relationship between relative brain size and relative gut size [18].

Humans had, in effect, conserved energy by greatly reducing the size of the intestine and then shifted this basal energy expenditure to support a much larger brain [the brain-gut trade-off hypothesis], but the two were independent. Therefore, a reduction in gut size would only be compatible with high-quality, easy-to-digest food [18].

Dietary quality has been shown to be correlated with brain size, in that folivorous (leaf-eating) primates have smaller brains, while primates who eat fruit and animal foods (insects, meat) generally have larger brains [56]. Similarly, members of the genus *Homo* would have had an even higher-quality diet than the Australopithecines by the incorporation of more underground storage organs (soft bulbs, tubers, etc) or the preferential consumption of animals. The 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 [45].

The role of the meat

Changing environmental conditions in Plio-Pleistocene Africa, involving a decline in plant productivity and an increase in secondary biomass [26], would have favored a shift in diet in hominin species, either to specialization on lower quality plant foods or routine access to meat. Meat is a very useful source of protein, many minerals and vitamins, and also essential fatty acids that humans require [57]. Although there is considerable variation in the diets of modern human foraging groups, studies have shown that modern human foragers typically derive over half of their dietary energy intake from animal foods [58].

Recent analyses of stabilize isotopes and dental micro-wear of early East African hominins appear to support this model, suggesting two distinct dietary pathway in latest Australopithecines and early members of the genus *Homo*. The robust Australopithecines (*A. boisei*) appear to have subsisted on larger amount of low-quality plant foods (e.g., C4 plants, such as savanna grasses and sedges), whereas early *Homo* appears to have had a broader, more varied diet [59].

The role of fat

The evolutionary “higher quality” diet means that we need to eat less volume of food to get the energy and

nutrients we require. 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 [60].

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. Relative to other large-bodied apes, modern humans derive a much larger share of their dietary energy from fat. Dietary fat is our second most important energy-producing macronutrient. 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 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 [58].

Besides, yielding energy dietary fat also contains functional fatty acids and vitamins essential for growth, development, and maintenance of good health [45]. Therefore, while dietary change might not be 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 [46].

Requirements of LCPUFAs

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 [60].

Half of human brain composition is fat, and 20% of its dry weight is long-chain polyunsaturated fatty acids (LCPUFAs). Consequently, improvements in consumption of dietary fat were a necessary condition for promoting encephalization [61, 62].

Mammalian brain growth is dependent upon sufficient amounts of two LCPUFAs: docosahexaenoic acid (DHA) and arachidonic acid (AA), and it appears that mammals have a limited capacity to synthesize these fatty acids from dietary precursors. Hence, species with higher levels of encephalization would have greater requirements for DHA and AA [62]. Consequently, dietary sources of DHA and AA were likely limiting nutrients that constrained the evolution of larger brain size in many mammalian lineages [63].

Conclusion

The evolution of large human brain size was driven by a complex web of interacting forces, social, developmental, and nutrition. While it is clear that the high levels of encephalization of humans and other primate species

are reflective of higher levels of sociality and cooperation, and behavioral complexity, it also appears that the metabolic fuel for evolving large brains was based on important shifts in diet, foraging, and energy metabolism.

Humans, as a group, have a higher-quality diet than expected for our size, supporting the high energy costs of our large brains. Additionally, while the RMRs of humans do not appear to be significantly elevated over what is predicted for a primate of our size, our TEE and activity levels are considerably higher than those of other apes. These relatively higher levels of energy expenditure appear to have been the product of selection for foraging regimes that necessitated movement over larger areas, and higher activity budgets to procure energy-rich diets.

Large brain size may have facilitated also more complicated extractive foraging strategies and acted as a secondary selection pressure for encephalization [52]. Additionally, primates have evolved key differences that can be related to diet and lifestyles directly, such as slower growth rate, a reduction in litter size, and producing larger offspring that live longer compared with other mammals [10].

If the exploitation of the high-quality foods, such as animal products, nuts, or underground tubers, required more complex behaviors, then this also could have acted as one of the selection pressures for the observed increase in brain size. It has therefore been suggested that early hominins evolved larger brains as a dietary shift towards more meat, and other higher quality resources that allowed for a smaller digestive tract and reduction in craniofacial architecture [18].

Overall, body and brain size are intimately tied to diet and life history patterns across mammalian species. As such, the evolution of distinctive human life history characteristics are reflective of processes that operate among mammals, in general. Overall, one can propose that during human evolution improved diet quality, allo-maternal subsidies, cognitive buffering, reduced locomotion costs, and reduced allocation to production all operated simultaneously, thus enabling the extraordinary brain enlargement in our lineage [46].

Abbreviations

A: *Australopithecus*; AA: Arachidonic acid; CNS: Central nervous system; DHA: Docosahexaenoic acid; DLW: Doubly labeled water; H: *Homo*; i.e.: For example; kya: Thousand years ago; LCPUFAs: Long-chain polyunsaturated fatty acids; mya: Million years ago; RMR: Resting metabolic rate; TEE: Total daily energy expenditure

Acknowledgements

The authors acknowledge the CNPq-Brazilian National Research Council [RCB's fellowship].

Funding

The authors provided personal resources for funding this paper.

Availability of data and materials

Not applicable.

Authors' contributions

The authors contributed equally to the concept, conclusions, and writing. Both authors read and approved the final manuscript.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Author details

¹Department of Public Health, UNESP Medical School, Botucatu, SP 18.618-970, Brazil. ²Department of Anthropology, Northwestern University, Evanston, IL 60208, USA.

Received: 5 April 2018 Accepted: 18 July 2018

Published online: 15 August 2018

References

- Haile-Selassie Y. Late Miocene hominids from the Middle Awash Ethiopia. *Nature*. 2001;412:178–81.
- Brunet M, Guy F, Pilbeam D, Mackaye HT, Likius A, Ahounta D, et al. A new hominid from the Upper Miocene of Chad Central Africa. *Nature*. 2002;418:145–51.
- Wood B. Hominid revelations from Chad. *Nature*. 2002;418:133–5.
- Wood B, Collard MC. The human genus. *Science*. 1999;284:65–71.
- Aiello LC, Key C. The energetic consequences of being a *Homo erectus* female. *Am J Hum Biol*. 2002;14:551–65.
- White TD, Asfaw B, DeGusta D, Gilbert H, Richards GD, Suwa G, et al. Pleistocene *Homo sapiens* from Middle Awash Ethiopia. *Nature*. 2003;423:742–7.
- Antón SC. A natural history of *Homo erectus*. *Yrbk Phys Anthropol*. 2003;46:126–70.
- Ruff CB, Trinkaus E, Holliday TW. Body mass and encephalization in Pleistocene *Homo*. *Nature*. 1997;387:173–6.
- McHenry HM, Coffing K. Australopithecus to *Homo*: transformations in body and mind. *Annu Rev Anthropol*. 2000;29:125–46.
- Anwar N, MacDonald K, Roebroeks W, Verpoorte A. The evolution of the human niche: Integrating models with the fossil record. In: Roebroeks W, editor. *Guts and Brains - An Integrative Approach to the Hominin Record*. The Netherlands: Leiden University Press; 2007. p. 235–69.
- Northcutt RG, Kaas JH. The emergence and evolution of mammalian neocortex. *Trends Neurosci*. 1995;18:373–9.
- Clark DA, Mitra PP, Wang SS. Scalable architecture in mammalian brains. *Nature*. 2001;411:189–93.
- Zhang K, Sejnowski TJ. A universal scaling law between gray matter and white matter of cerebral cortex. *Proc Natl Acad Sci U S A*. 2000;97:5621–6.
- Cela-Conde CJ, Ayala FJ. Genera of the human lineage. *PNAS*. 2003;100:7684–9.
- Stauffer RL, Walker A, Ryder OA, Lyons-Weiler M, Blair HS. Human and ape molecular clocks and constraints on paleontological hypotheses. *J Hered*. 2001;92:469–74.
- Marino L. A Comparison of Encephalization between Odeontocete Cetaceans and Anthropoid Primates. *Brain Behav Evol*. 1998;51:230–8.
- Fordyce RE. Whale evolution and Oligocene southern-ocean environments. *Palaeogeogr Palaeoclimatol Palaeoecol*. 1980;31:319–36.
- Aiello LC, Wheeler P. The expensive-tissue hypothesis—the brain and the digestive system in human and primate evolution. *Curr Anthropol*. 1995;36:199–221.
- Reed KE. Early hominid evolution and ecological change through the African Plio-Pleistocene. *J Hum Evol*. 1997;32:289–322.
- Clutton-Brock J, Harvey PH. Primates brains and ecology. *J Zool*. 1980;190:309–23.
- Cerling TE, Mbua E, Kirera FM, Manthi FK, Grine FE, Leakey MG, Sponheimer M, Uno KT. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proc Nat Acad Sci Jun*. 2011;108(23):9337–41. <https://doi.org/10.1073/pnas.1104627108>.
- Ungar PS, Sponheimer M. The Diets of Early Hominins. *Science*. Oct 2011;14:190–3.
- Harvey PH, Krebs JB. Comparing brains. *Science*. 1990;249:150–6.
- Parker ST, Gibson KR. Object manipulation tool use and sensorimotor intelligence as feeding adaptations in great apes and cebus monkeys. *J Hum Evol*. 1977;6:623–41.
- Godfrey LR, Samonds KE, Jungers WL, Sutherland MR. Teeth brains and primate life histories. *Am J Phys Anthropol*. 2001;114:192–214.
- Boinski S, Garber P, editors. *On the Move and Why Animals Travel in Groups*. Chicago: The University of Chicago Press; 2000. p. 628–48.
- Leonard WR, Robertson ML. Comparative primate energetics and hominid evolution. *Am J Phys Anthropol*. 1997;102:265–81.
- Domínguez-Rodrigo M, Rayne Pickering R, Semaw S, Rogers MJ. Cutmarked bones from Pliocene archaeological sites at Gona Afar Ethiopia: implications for the function of the world's oldest stone tools. *J Hum Evol*. 2005;48:109–22.
- Antón SC, Leonard WR, Robertson ML. An ecomorphological model of the initial hominid dispersal from Africa. *J Hum Evol*. 2002;43:773–85.
- Pontzer H, Raichlen DA, Gordon AD, Schroepfer-Walker KK, Hare B, O'Neill MC, et al. Primate energy expenditure and life history. *Proc Natl Acad Sci U S A*. 2014;111:1433–7.
- Pontzer H, Brown MH, Raichlen DA, Dunsworth H, et al. Metabolic acceleration and the evolution of human brain size and life history. *Nature*. 2016;533:390–2. <https://doi.org/10.1038/nature17654>.
- Antón SC, Potts R, Aiello LC. Evolution of early Homo: An integrated biological perspective. *Science*. 2014;345:6192.
- Deaner RO, Nunn CL, van Schaik CP. Comparative tests of primate cognition: different scaling methods produce different results. *Brain Behav Evol*. 2000;55:44–52.
- Kaplan HS, Robson AJ. The emergence of humans: The coevolution of intelligence and longevity with intergenerational transfers. *Proc Natl Acad Sci U S A*. 2002;99:10221–6.
- Tsuboi M, Husby A, Kotschal A, Buechel SD, Zidar J, Levlie H, et al. Comparative support for the expensive tissue hypothesis: Big brains are correlated with smaller gut and greater parental investment in Lake Tanganyika cichlids. *Evolution*. 2015;69:190–200.
- Kleiber M. Body size and metabolic rate. *Physiol Rev*. 1947;27(4):511–41.
- Mink JW, Blumenschine RJ, Adams DB. Ratio of central nervous-system to body metabolism in vertebrates: its constancy and functional basis. *Am J Phys*. 1981;241(3):R203–12.
- Kuzawa C, Chugani HT, Grossman LI, Lipovich L, Muzik O, Hof P, Wildman D, Sherwood C, Leonard W, Lange N. Metabolic costs and evolutionary implications of human brain development. *Proceedings of the National Academy of Sciences of the United States of America*; 2014. p. 111. <https://doi.org/10.1073/pnas.1323099111>.
- Kotschal AB, Rogell A, Bundsen B, Svensson S, Zajitschek I, Brannstrom S, et al. Artificial selection on relative brain size in the guppy reveals costs and benefits of evolving a larger brain. *Curr Biol*. 2013;23:168–71.
- Kotschal AB, Rogell A, Bundsen B, Svensson S, Zajitschek I, Brannstrom S, et al. The benefit of evolving a larger brain: big-brained guppies perform better in a cognitive task. *Anim Behav*. 2013;86:e4–6.
- Martin R. Relative brain size and basal metabolic-rate in terrestrial vertebrates. *Nature*. 1981;293:57–60.
- Isler K. Energetic trade-offs between brain size and offspring production: marsupials confirm a general mammalian pattern. *BioEssays*. 2011;33:173–9.
- Isler K, van Schaik CP. Metabolic costs of brain size evolution. *BiolLett*. 2006;2:557–60.
- Snodgrass JJ, Leonard WR, Robertson ML (2009) The Energetics of Encephalization in Early Hominids. In: Hublin JJ, Richards M.P. (eds) *The Evolution of Hominin Diets. Vertebrate Paleobiology and Paleoanthropology*. Springer, Dordrecht.
- Leonard WR, Snodgrass JJ, Robertson ML. Evolutionary perspectives on fat ingestion and metabolism in humans. In: Montmayeur JP, le Coutre J, editors. *Fat Detection: Taste, Texture, and Post Ingestive Effects*. Boca Raton, FL: CRC Press; 2011. p. 3–18. <https://www.ncbi.nlm.nih.gov/pubmed/21452472>.
- Navarrete A, van Schaik CP, Isler K. Energetics and the evolution of human brain size. *Nature*. 2011;480:91–4.

47. Aiello LC, Key C. Energetic consequences of being a *Homo erectus* female. *Am J Hum Biol.* 2002;14(5):551–65.
48. O'Connell JF, Hawkes K, Jones NGB. Grandmothering and the evolution of *Homo erectus*. *J Hum Evol.* 1999;36(5):461–85.
49. Kennedy GE. From the ape's dilemma to the weanling's dilemma: early weaning and its evolutionary context. *J Hum Evol.* 2005;48:123–46.
50. Cabana T, Jolicœur P, Michaud J. Prenatal and Postnatal Growth and Allometry of Stature Head Circumference and Brain Weight in Quebec children. *Am J Hum Biol.* 1993;5:93–9.
51. Bogin B, Smith BH. Evolution of the human life cycle. *Am J Hum Biol.* 1996; 8:703–16.
52. Kaplan H, Hill K, Lancaster J, Hurtado AM. A theory of human life history evolution: diet intelligence and longevity. *Evol Anthropol.* 2000;9:156–85.
53. Winterhalder B, Smith EA. Analyzing adaptive strategies: human behavioural ecology at twenty-five. *Evol Anthropol.* 2000;9:51–72.
54. Burkart JM, Hrdy SB, van Schaik CP. Cooperative breeding and human cognitive evolution. *Evol Anthropol.* 2009;18:175–86.
55. Leonard WR, Snodgrass JJ, Robertson ML. Effects of brain evolution on human nutrition and metabolism. *Annu Rev Nutr.* 2007;27:311–27.
56. Foley RA, Lee PC. Ecology and energetics of encephalization in hominid evolution. *Phil Trans Royal Soc London Ser B.* 1991;334:223–32.
57. Milton K. A hypothesis to explain the role of meat-eating in human evolution. *Evol Anthropol.* 1999;8:11–21.
58. Cordain L, Brand-Miller J, Eaton SB, Mann N, Holt SHA, Speth JD. Plant to animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. *Am J Clin Nutr.* 2000;71:682–92.
59. Ungar PS. The Real Paleo Diet. Microscopic wear patterns on fossil teeth reveal what our ancestors ate-and provide insights into how climate change shaped human evolution. *Scientific American*, July 2018, Vol. 319, Issue 1.
60. Cordain L, Watkins BA, Mann NJ. Fatty acid composition and energy density of foods available to African hominids. *World Rev Nutr Diet.* 2001;90:144–61.
61. Burini RC, Nunes CNM, Kano HT, Nakagaki MS. Epygenetics of Plasma Cholesterol Variation: From an Evolutionary Genome and Environmental-Induced Frugality to Contemporary Diseases-Basis for Primary Care with Lifestyle Modifications. In: ed. *Advances in Dyslipidemia*. Avidscience.com. Chap. 5. 2016. <http://www.avidscience.com/wp-content/uploads/2016/08/DP-15-05.pdf>
62. Burini RC, Nunes CNM, Burini FHP. Evolution and therapy of brain by foods containing unsaturated fatty acids. In: Naofumi Shiomi eitor. *Superfood and Functional Food-Development of Superfood and its Role in Medicine*. InTech open Science. 2017. Print ISBN 978-953-51-2941-7. <https://cdn.intechopen.com/pdfs-wm/53864.pdf>
63. Crawford MA, Bloom M, Broadhurst CL, Schmidt WF, Cunnane SC, Galli C, et al. Evidence for unique function of docosahexaenoic acid during the evolution of the modern human brain. *Lipids.* 1999;34:S39–47.

Ready to submit your research? Choose BMC and benefit from:

- fast, convenient online submission
- thorough peer review by experienced researchers in your field
- rapid publication on acceptance
- support for research data, including large and complex data types
- gold Open Access which fosters wider collaboration and increased citations
- maximum visibility for your research: over 100M website views per year

At BMC, research is always in progress.

Learn more biomedcentral.com/submissions

