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Comparative Biochemistry and Physiology Part A 136 (2003) 17–26

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Review

Survival of the fattest: fat babies were the key to evolution of the large human brain[☆]

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Received 7 July 2002; received in revised form 7 February 2003; accepted 11 February 2003

Abstract

In the past 2 million years, the hominid lineage leading to modern humans evolved significantly larger and more sophisticated brains than other primates. We propose that the modern human brain was a product of having first evolved fat babies. Hence, the fattest (infants) became, mentally, the fittest adults. Human babies have brains and body fat each contributing to 11–14% of body weight, a situation which appears to be unique amongst terrestrial animals. Body fat in human babies provides three forms of insurance for brain development that are not available to other land-based species: (1) a large fuel store in the form of fatty acids in triglycerides; (2) the fatty acid precursors to ketone bodies which are key substrates for brain lipid synthesis; and (3) a store of long chain polyunsaturated fatty acids, particularly docosahexaenoic acid, needed for normal brain development. The triple combination of high fuel demands, inability to import cholesterol or saturated fatty acids, and dependence on docosahexaenoic acid puts the mammalian brain in a uniquely difficult situation compared with other organs and makes its expansion in early humans all the more remarkable. We believe that fresh- and salt-water shorelines provided a uniquely rich, abundant and accessible food supply, and the only viable environment for evolving both body fat and larger brains in human infants.

Keywords: Brain; Infant; Cholesterol; Docosahexaenoic acid; Shellfish; Iodine; Human evolution; Ketone bodies; Hominids; Fat

1. Introduction

Understanding the reason for expansion and increased sophistication of the human brain has been a long-standing concern of those interested in human evolution (Jerison, 1973). The classic concept dwells on a link between evolution of tool making skills, walking on two feet, hunting, more refined social interaction, development of language, and brain expansion. Brain expansion would have helped all these processes just as these other attributes would potentially feedback to improve brain function as humans modernized. Early humans (hominids) clearly learned to make tools and weapons and to hunt large and small game on the savannahs, woodlands and elsewhere. But how did it get started and which came first—the big brain or the language, social refinement and hunting? In explaining the expansion and evolution of the human brain, the basic problem is that the brain makes considerable metabolic and

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Abbreviations: DHA, docosahexaenoic acid ($22:6\omega3$).

[☆] This paper is part of a collection of inter-disciplinary, peer-reviewed articles under the Theme: ''Origin and Diversity of Human Physiological Adaptability'' invited by K.H. Myburgh and the late P.W. Hochachka.

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1095-6433/03/$ - see front matter © 2003 Elsevier Science Inc. All rights reserved.
doi:10.1016/S1095-6433(03)00048-5

Table 1
Absolute and relative brain weights of selected extinct and extant adult hominids and related primates[a]

Species (time period)	Brain weight (g)	Brain/body weight (%)	EQ[b]
Australopithecus afarensis (3.6–2.8 mya)	455	NA	41
Australopithecus africanus (3.0–2.2 mya)	445	1.0	44
Paranthropus robustus (1.8–1.5 mya)	520	1.1	50
Homo habilis (1.9–1.5 mya)	650	1.5	57
Homo erectus (1.8–0.3 mya)	940	1.9	63
Homo heidelbergensis (600–200 kya)	1200	1.8	74
Homo neanderthalensis[c] (200–40 kya)	1420	1.9	75
Homo sapiens[d] (100–25 kya)	1490	2.4	102
Homo sapiens[e]			
Adult male	1400	2.3 (2.9[g])	100
Newborn	400	11.4 (13.8[g])	NA
Pan troglodytes[f]			
Adult male	400	0.9	42
Newborn	150	10	NA

Abbreviations: NA, not available; mya, million years ago; kya, thousand years ago.

[a] Averaged from Aeillo and Dean (1990), Pinker (2000), Ruff et al. (1997), Kappelman (1996), MacKinnon (1978), Falk (1987), Passingham (1985), Blumenberg (1983).

[b] EQ, Encephalization Quotient, pooled from small differences between data given by Ruff et al. (1997), Martin (1981), Kappelman (1996) and standardized relative to extant *H. sapiens* (100).

[c] Neanderthals.

[d] Early modern humans.

[e] Extant modern humans.

[f] Chimpanzees.

[g] Using lean body weight, as presumed for all extinct hominids and extant non-human primates.

nutritional demands on the body, the more so as one progresses through animal genera to the larger-brained primates. For the hominid brain to expand in size by at least one-third in less than a million years must have required exceptionally favourable circumstances to meet this increasing metabolic and nutritional demand. What were these circumstances?

2. The modern human brain and its metabolic requirements

By any measure, the modern human brain is large (Table 1). Brains generally increase in size as body weight increases but the human brain is 3.5 times larger than that of our nearest terrestrial relations, the chimpanzees (*Pan troglodytes*), which, as adults, are similar in lean body weight to us. The modern human brain is also approximately three times larger than in the now extinct but smaller very early human ancestors, the Australopithecines. The ‘encephalization quotient’ (Jerison, 1973) is widely used to correct brain size for differences in body size between modern and ancestral humans. Except for the heavier Neanderthals, all the *Homo* lineage leading to *Homo sapiens* are thought to have been of roughly similar adult body weight to us (55–65 kg). However, both our brain weight and our encephalization quotient are approximately twice that in the earliest humans (*Homo habilis*) who existed 1.5–1.9 million years ago (Table 1). The modern human brain is now approximately 6% smaller than it was in the early Modern *Homo sapiens* of 25–100 000 years ago but we are still equally ‘encephalized’ because our body weight is also a little less than theirs was (Ruff et al., 1997).

Table 2
Energy requirements of the human brain from birth to adulthood[a]

Body weight (kg)	Brain weight (g)	Brain's energy consumption (kcal/day)	Body's energy consumption (kcal/day)	Energy to brain (% of whole body)
3.5 (newborn, term)	400	118	161	74
5.5 (4–6 months)	650	192	300	64
11 (1–2 years)	1045	311	590	53
19 (5–6 years)	1235	367	830	44
31 (10–11 years)	1350	400	1160	34
50 (14–15 years)	1360	403	1480	27
70 (adult)	1400	414	1800	23

[a] Modified from Holliday (1971).

For at least 30 years, physiologists have known that the adult brain consumes considerably more energy for its weight than other organs. In adult humans, the brain weighs approximately 1400 g or approximately 2.3% of the body weight but it uses approximately 23% of the body's daily energy requirement (Table 2). As a proportion of the body's energy requirement, this disproportionate energy demand by the brain is even greater in infants. At normal term birth, the brain weighs approximately 400 g or approximately 11% of total body weight but it consumes approximately 74% of the body's energy intake (Table 2). Thus, a valid theory of human brain evolution has to account for the environmental circumstances that would uniquely permit the earliest hominids to start dedicating a high, constant and disproportionate energy and nutrient supply to the brain (Martin, 1981). Martin didn't discuss infants but the brain's energy and nutrient requirement is proportionally higher in infants than in adults.

3. Traditional concepts including the need for a high quality diet

Consumption of meat acquired by hunting is one way to help explain how the energy demands of a larger brain would be met. However, the concept of hunting being used to fulfill the newly increased energy requirement of the larger brain tends to assume that the brain was already large and sophisticated enough to conceive of and build weapons and to develop effective strategies to trap and kill prey. The flaw in this concept is that it assumes sufficient improvement in cognitive abilities such as memory, anticipation and conceptualization, as well as sufficient improvements in physical and social coordination *before* significant brain expansion had occurred, i.e. these new skills would require an already expanded brain. But how did improvements in the brain's wiring occur *before* a larger brain facilitated hunting and better social organization? Furthermore, what explains why the main investment in brain expansion was during fetal and early post-natal development, a stage when a larger brain doesn't confer any survival advantage to humans? Other species do not require a brain equivalent to that in humans to find food, socialize, mate, care for their young, i.e. to survive very capably. Indeed, if diversity and geographical distribution are a good measure of evolutionary success, the monkeys have been more successful than the great apes despite notably smaller brain capacity.

At birth, the young of many species are physically independent of the mother for significant periods but humans are not. How, then, did having large-brained infants confer an advantage on early humans when infants couldn't survive independently during the first several years of life? We suggest that whatever advantages there were to having a large brain, they were probably not necessary for survival—they must have been optional. Indeed, natural selection predicts that we could not need a larger brain, only that we might very gradually, and by chance, benefit from it. What scenario in our evolution could account for the metabolic luxury of developing a much larger brain? And why, amongst terrestrial animals, did it develop uniquely in humans?

In recent years, the important role of a 'high quality' diet in human brain evolution has been increasingly recognised (Cordain et al., 2001; Leonard, 2002). A high quality diet contains more fat and meat and less plant material; in short, a high quality diet has a higher concentration of nutrients and energy. Apart from nuts, an equivalent weight of plants, whether shoots, leaves or fruit, has much less energy content and is usually more slowly digested than meat or fish. Indeed, it has been clear for a long time that jaw and tooth structure in modern humans is not designed for heavy or sustained grinding, nor is the modern human gut, especially the colon, designed for digestion and fermentation of large amounts of plant material. Anatomical and fossil evidence shows that as humans modernized, they ate diets that required less grinding and chewing than the diets of other primates. The assumption has been that this occurred because early humans learned how to hunt live game or outsmart other scavengers for animal carcasses.

How did we learn to hunt animals or outsmart other scavengers to a sufficient extent to promote our survival and brain evolution without already having a bigger brain? How did early humans but not other primates achieve this if they both evolved in the same ecological niche of woodlands or savannah and both ate a plant-based diet of low to moderate energy density? Expanding a major organ like the brain would have required incremental, sustained and co-ordinated changes in gene expression. Random mutations would have almost zero likelihood of achieving such an outcome. The main environmental variable that could act in concert with and might promote a change in gene expression is diet.

Plants, available carrion and occasionally successful hunting are unlikely to have induced a sustained, unidirectional change in expression of genes controlling refined brain architecture in hominids because there would still have been too much variability in nutrient and energy intake on such a diet. Fruits and nuts are seasonal. Hunting successes would initially be sporadic, as they mostly still are today, and carrion is often not available or in an edible state. These limitations challenge the suitability of a savannah or woodland niche to meet the molecular and genetic requirements for human brain expansion.

Expression of genes promoting expansion and further sophistication of the brain would have been linked to genes helping expand the brain's blood supply in order to meet the increased need for oxygen and nutrients. Simultaneously (or perhaps even before brain expansion started), genes controlling fetal fat deposition also needed to be expressed because the body's fat deposits are needed as insurance for the developing brain. Sustained expression of this cluster of genes, whether acting in concert or not, would have required long-term stability in the maternal nutrient and energy supply during pregnancy and lactation. In order to meet these metabolic requirements and have improvements in diet quality affect brain evolution, the same high food quality had to be available to most people in the clan for hundreds if not thousands of generations. It seems implausible that genes for fat deposition would continue to promote fat deposition in the mother and fetus when the mother's clan was forced to continually move due to seasonal changes in preferred foods, or due to drought or persistent competition, i.e. when the food supply was variable on a daily or seasonal basis. On the contrary, the developing brain is vulnerable to maternal nutritional deprivation before, during or after pregnancy (see Section 5—Survival of the fattest).

4. The shore-based diet

Contrary to the prevailing idea of hominids eking out subsistence under adverse conditions, we believe human brain evolution depended on finding an abundant, reliable and nutritious food supply. With the right genetic predisposition, a sustained improvement in diet would have allowed evolution of a marginally bigger brain but with two important caveats: (i) it would have had no specific functional advantages; and (ii) such improvements could not have been needed for survival. Over a long period and if they were lucky, natural selection of those with somewhat bigger brains would conceivably lead to a modest improvement in hominid intelligence. A larger, more sophisticated brain would undoubtedly have helped improve hunting skills but wasn't necessary for survival because there was always a high quality diet nearby to keep the genes for brain expansion expressed if the hunt didn't go well.

Without hunting, how would hominids have found a better quality diet than that of other non-human primates? We have postulated for several years now that early hominids fortuitously discovered and then exploited the abundant food selection available on lakeshores, estuaries, river deltas, marshes and seashores of East and South Africa (Crawford and Marsh, 1989; Cunnane et al., 1993;

Broadhurst et al., 1998; Crawford et al., 1999; Broadhurst et al., 2002). Whether on the shores of fresh or salt water, mollusks, crustaceans, birds' eggs, spawning fish, frogs, turtles and a variety of plants would have provided an extensive selection of nutrient- and energy-rich, highly accessible foods. Unlike roots and tubers, none of these shore-based foods would have required a well-developed intestine (colon) or cooking (fire) to release their full energy and nutrient value. Most of these types of food would have been less challenging to collect than hunting small let alone large game. A diet based on shore-based foods would not have precluded foraging for carrion, roots, fruit or insects, or more advanced hunting of mammals. However, we believe that shore-based evolution had the substantial and unique advantage of making hunting *optional*. In modern times we have stripped lake- and seashores of their food resources but, prior to the last century, we had neither the population density nor the mechanization to destroy this uniquely rich and valuable food supply.

A shore-based diet provides the highest nutrient quality available anywhere. Its high food quality meets the first and mostly widely accepted requirement for hominid brain expansion, i.e. that the early human diet had to have a high enough energy content that the genetic potential for the primate brain to expand could begin without any obligation that the expansion pay dividends in terms of improved survival. The abundance, accessibility and easy availability of high quality shore-based foods meets the other prerequisite for brain expansion, which is that the brain not be sophisticated enough for successful hunting of live game to feed family groups *before* it had expanded. A third fundamental point raised by Elaine Morgan (Morgan, 1994) is that this particular food supply could be gathered by children, adolescents, pregnant or lactating women, and the elderly; in short, by anyone irrespective of gender, social position, physical stature or degree of specialized hunting skills. This point is important because virtually all ages could then feed themselves, thereby allowing those that were so motivated to try their skills at tool making, hunting, trapping, fishing or scavenging carcasses.

5. Survival of the fattest

When they are 45–50 days old, embryos of both humans and non-human primates have heads accounting for a similar and large proportion (approx. 40%) of their body weight (Schultz, 1969). This and the similar genetic make up of humans and non-human primates suggest that primates, whether human or non-human, have the same early embryonic potential to have a large brain. Infants of non-human primates such as chimpanzees have a brain to body weight ratio that is closer to that of human infants than between the respective adults (Table 2). Thus, what we think of as brain expansion as hominids modernized may in fact be more accurately thought of as a process by which hominids avoided the relative brain shrinkage that occurred in other mammals, especially the large savannah species (Crawford and Marsh, 1989).

Despite the similarity in brain size at birth, a major difference between humans and chimpanzees (or other non-human primates) is the virtual absence of body fat in the chimpanzee infant. That's where 'survival of the fattest' comes from. It derives from 'survival of the fittest', which is widely attributed to Darwin but was actually coined by Herbert Spencer. Our hypothesis is that to permit the brain to start to increase in size, the *fittest* early humans were those with the *fattest* infants. Fatness during late fetal development and on through the first 5 years of life is a key determinant of optimal brain development in humans. Prematurity prevents appropriate fatness at birth and leads to developmental delay through childhood to adulthood (Hack et al., 1994; Crawford et al., 1997; Hack et al., 2002). At normal term birth, babies have approximately 500 g of fat, most of it directly under the skin (Harrington et al., 2002). Indeed, chubbiness is one of their more endearing features. Between feeds, fat also is an essential fuel reserve to supply the voracious energy demands of the already large and still rapidly developing infant brain.

Babies born prematurely (3 or more weeks earlier than normal term birth which is at 40 week's gestation) or born at very low birth weight have much less body fat than babies born at term (Fig. 1). Even 10 weeks early, which is by no means unusual today, there is, like in the chimpanzee, only approximately 10% of the fat on the human body that there would be at normal term birth. In addition to a marked lack of body fat, premature infants also have a much higher risk of slower neurological development and somewhat smaller brain size than do term infants (Hack et

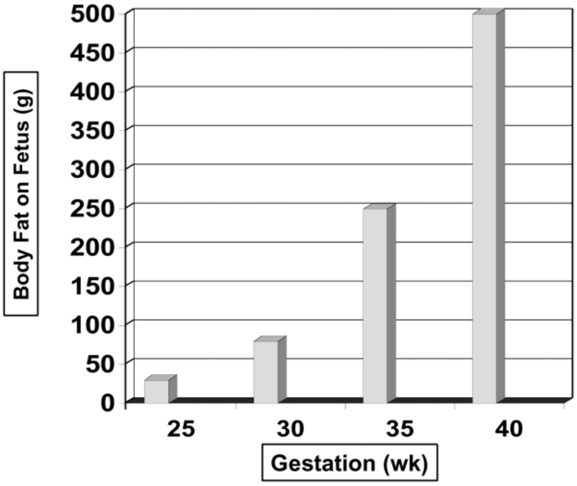

Fig. 1. Fat deposition during normal human fetal development.

al., 1994; Crawford et al., 1997). Thus, to this day, the infant human brain remains extremely vulnerable to its nutrient and energy supply both in an acute sense (oxygen deprivation) and in a chronic sense (normal development). The long-term vulnerability is much less acute in the chimpanzee because its brain is not continuing to expand nearly as much or for as long as in the human infant.

Body fat at birth provides insurance for the brain in between feeds. This insurance comes in two forms—fuel and nutrients. Because they have little or no body fat, non-human primates and premature infants have much less of this insurance. In fact, among terrestrial mammals, the capacity to deposit fat on the fetus during pregnancy is apparently almost a uniquely human feature (Widdowson, 1974). Guinea pigs are born with some fat but are also much more mature at birth than humans. Fat deposition on the human fetus accounts for 90% of its weight gain just before birth (Battaglia and Meschia, 1973). This is a phenomenal metabolic commitment that, we believe, is directly linked to providing insurance for the human brain's high energy requirement after birth.

6. Body fat and ketogenesis

The link between infant fat stores and human brain expansion during evolution involves more than providing fatty acids for oxidation to meet energy needs. It also involves three breakdown products of fat oxidation collectively called ketone bodies (ketones; β-hydroxybutyrate, acetoacetate and acetone). There are two reasons why ketones became important to human brain evolution.

First, the brain can oxidize ketones but it does not oxidize the fatty acids they come from. In adults, glucose is the main fuel for the brain. If food is restricted, body glucose stores (glycogen) last less than 24 h. Without ketones, brain function would be rapidly compromised or muscle protein would need to be degraded to release amino acids that can be converted to glucose. Hence, ketones are an essential alternative fuel to glucose for the brain. Healthy human infants have a large store of fat that is available to make ketones. In infants, slightly elevated blood ketones are present all the time (mild ketonemia) regardless of feeding status. This is not the case with fed adults. In human fetuses at mid-gestation, ketones are not just an alternative fuel but appear to be an *essential* fuel because they supply as much as 30% of the energy requirement of the brain at that age (Adam et al., 1975).

Second, ketones are a key source of carbon for the brain to synthesize the cholesterol and fatty acids that it needs in the membranes of the billions of developing nerve connections. The mammalian brain has protected itself from variations in the types and amount of fats we eat by developing the ability to: (i) make almost all the saturated fatty acids and cholesterol it needs; and (ii) exclude most fatty acids (except certain polyunsaturates) and all cholesterol that are present in the circulation and that are available to all other organs (Cunnane, 2001). Since the brain requires cholesterol and saturated fatty acids in its membranes but does not take them up from the blood, it needs an abundant, water-soluble source of the carbon that accesses the brain and can be used to make these lipids. Ketones are the preferred carbon source for brain lipid synthesis and they come from fatty acids recently consumed or stored in body fat. This means that, in infants, brain cholesterol and fatty acid synthesis are indirectly tied to mobilization and catabolism of fatty acids stored in body fat.

Hence, in all mammals studied, ketones have two important roles in the brain—they provide a reliable source of brain energy in between feeds, and they provide a major proportion of the lipid building blocks for developing brain cells. The uniqueness of the human situation is that babies are endowed with proportionally by far the largest ketone reserve (body fat) of any mammalian infants (Widdowson, 1974), a reserve which is suitably matched to the high energy and structural demands of the developing infant brain.

7. The dual functions of fat

Body fat is more than a cosmetic annoyance and a fuel reserve for an expensive organ like the developing brain. All cells in the body have membranes surrounding them, and separating the various compartments within the cell. Membranes consist of variable mixtures of fatty acids, cholesterol, carbohydrates and proteins. The organization of these membrane constituents is highly regulated and controls the life-supporting activities of cells and organs—digestion, excretion, respiration, heart beat, photoreception, cognition, etc. Membranes of cells that have lots of electrical activity (photoreceptor, brain, heart) have higher proportions of the specialized polyunsaturated fatty acid, docosahexaenoic acid (DHA). All mammals have brains with approximately the same *proportion* of protein, cholesterol, and fatty acids such as DHA, so what makes the human brain more sophisticated is not its composition but its size and the increased density of its wiring, i.e. the greater number of connections between neurons.

On a per weight basis, body fat contains more DHA at birth than at any other time in the life cycle. Infants with normal amounts of body fat at birth have a supply of DHA in their fat that would meet the brain's requirement for approximately the first 3 months of life irrespective of what was in the milk or mother's diet (Cunnane et al., 2000). Body fat therefore contains two types of insurance—fatty acids to make ketones for brain fuel and lipid synthesis, and specialized fatty acids such as DHA for brain membranes. Other mammals have essentially no body fat at birth so they lack the fuel and DHA insurance bestowed on human infants born at term. Hence, in principle, they lack the metabolic prerequisites for brain expansion. Terrestrial plants contain no DHA and, except for the brain, animal tissues have very little. However, shellfish and fish are rich in DHA and its precursor, eicosapentaenoic acid. Consuming a shore-based diet would have provided the best available source of both DHA and other nutrients needed by the developing brain. Additional DHA would be available to the brain from both baby fat stores and in mothers' milk.

8. Evolution of fetal body fat

Mechanisms permitting the evolution of fat deposits require appropriate enzymes to capture glucose or fatty acids in the circulating blood and build them into fat molecules (triglycerides, each made up of three fatty acids) that can be deposited in fat cells primarily under the skin or in the abdomen. The mechanism controlling fat deposition starting in the third trimester human fetus is unknown but it probably involves insulin. Extra dietary energy in the form of fat or carbohydrate is needed regardless of when or where fat is deposited. All mammals can store extra carbohydrate energy as glycogen and, to a limited extent, as amino acids in protein. In the absence of food intake, glycogen stores last only approximately 1 day. Protein stores last longer but, to be released, require degradation of muscle protein, a process only intended for short-term relief or extreme situations. In contrast, the 500 g of fat at normal term birth constitute an energy reserve that could last for 3 weeks if necessary. It therefore seems implausible to evolve a bigger, more energy-demanding brain without first, or at least simultaneously, developing body fat stores during fetal development.

How did early humans acquire the unique ability to deposit fat on the fetus during pregnancy? No one knows for sure but this key attribute can only have arisen because some hominid clades were exposed to a diet containing both high energy and nutrient density for a sufficiently long time that pre-existing genes were expressed which were capable of promoting human subcutaneous fetal fat cell development and metabolism in hominid fetuses. The abundant, shore-based diet was the first real opportunity in hominid evolution to deposit extra dietary energy as fat, and it occurred at all ages, including during pregnancy and in the third trimester fetus. Non-human primates deposit body fat if they are relatively inactive, i.e. if they are captive, have an abundant high-energy diet, and have little need to exercise or escape predators. This is a rare combination in the wild. Even in captivity, they deposit fat mainly around abdominal organs as well as under the skin of the trunk and limbs. Abdominal fat deposition in adult humans and captive mammals is distinctly unlike that in human term infants who have $>90\%$ of their fat under the skin and almost none surrounding the visceral organs (Harrington et al., 2002).

The easy accessibility and abundance of shore-based food would have been as important as the high energy value of these foods to pre-human hominids because it would have meant less energy would have been expended in foraging over large distances. This would facilitate accumulation of fat, especially during pregnancy and lactation. Initially, the increasing fatness in babies of early hominids would simply have been a fortuitous consequence of the higher quality and more reliable shore-based food supply. It would also have had no immediate positive consequences for the brain, i.e. we believe it would have been entirely optional for survival per se. Humans have considerably more difficult and longer parturition than other primates which would have made survival of newborns *less* certain because fatter babies with larger heads would have been harder to deliver through the same narrow birth canal. Looking ahead, however, the disadvantage of more body fat at birth and bigger heads would become essential to subsequent human brain expansion, improved wiring and eventual evolution.

9. The fossil evidence

Fossil evidence that hominids utilized shore-based food resources dates at least from Richard Leakey's observations at Lake Turkana, Kenya, over 30 years ago (Leakey and Lewin, 1978). The past decade has seen a steady increase in reports linking early and later hominid evolution to lake- and seashores (Crawford and Marsh, 1989; Verhaegen, 1991; Cunnane et al., 1993; Ellis, 1993; Stewart, 1994; Morgan, 1994; Parkington, 1999; Broadhurst et al., 1998; Crawford et al., 1999; Walter et al., 2000; Tobias, 2002; Broadhurst et al., 2002). Hominid exploitation of the rich and mostly sessile shore-based foods would, as skills improved, have been gradually supplemented by fishing, hunting and experimenting with cooking less nutritious roots, tubers, etc. Like hunting live game, any attempt to fish had to be optional because the necessary tools and hand–eye co-ordination to become efficient hunters would initially have been lacking. Fish would have been an excellent addition to the diet and often plentiful but, unless spawning or trapped in shallow water, would still have been optional for many generations to come because they could escape capture. Shore-based foods such as shellfish would have been a primary staple. Crustaceans, turtles, frogs, fledglings, molting waterfowl, eggs and marsh plants would also have been available but little trace of these would remain in the fossil record.

Shore-based human evolution does not eliminate hunting, whether for insects, carrion, or big game, nor does it reject edible fruit, nuts, roots, or termites as valuable components of the diet right up to the present. However, diets that exclude shore-based foods were insufficiently reliable, accessible or nutritious to have permitted brain expansion similar to that seen in humans or it should have happened to a similar extent in at least one other non-human primate species. Woodlands are now widely viewed as the principal habitat of hominids in East and South Africa. Within such a setting, we feel hominids would have exploited a shore-based existence on river and estuary banks, marshes, lakeshores or seashores. Lakes Turkana and Victoria existed in larger form a million years ago and are prime examples of shore-based niches for hominid brain evolution. Forests that flood with the tide exist in several areas of the world today and, if inhabited by proto-hominids, would have been ideal ecosystems for shore-based human evolution.

10. Other brain-selective nutrients

Fetal and neonatal fat deposits were necessary but were probably insufficient on their own to propel human brain expansion. In addition to DHA, other nutrients that are also more abundant in shore-based than inland or woodland foods, were also probably required for this process to be successful. Amongst these, iodine would have been a key '*brain-selective*' nutrient because of its role in metabolism and energy expenditure. Iodine deficiency is the most common nutrient deficiency and affects 1.6 billion people worldwide, almost exclusively those living inland (Verma and Raghuvanshi, 2001). Iodine deficiency causes mental retardation and infertility, which are two major deterrents to human social integration and population growth. The cause and treatment of iodine deficiency disorders were, in principle, solved at the start of the twentieth century. Nevertheless, as diets have become more vegetarian and salt intake has been reduced, concerns about human iodine deficiency in Europe are again being raised at the start of the twenty-first century (Wynn and Wynn, 1998).

Table 3
Key advantages to the shore-based food supply for the evolution of baby fat and large brains uniquely in humans[a].

1.	Reliable, abundant, accessible food supply.
2.	Relatively little primate competition.
3.	Relatively little predation from carnivores.
4.	Less energy expenditure in food gathering.
5.	Points 1-3 reduce time spent in food gathering, leading to more free time and greater opportunity for social interaction, development of tools and language.
6.	Points 1-3 also mean that there was a better opportunity for expression of genes controlling fat deposition on the third trimester human fetus[a].
7.	All ages participate in food gathering.
8.	Uniquely rich in brain-selective nutrients, especially long chain polyunsaturates, iodine, zinc, copper, iron and selenium.

[a] Compared with other terrestrial mammals.

Widespread iodine deficiency has been suggested to have contributed to intellectual stagnation, skeletal anomalies, and the eventual demise of the Neanderthals (Dobson, 1998). Several edible plants are goiterogenic, making it more difficult to assimilate sufficient iodine from a plant-based diet. It is therefore possible that mild iodine deficiency developed as early humans started to populate more inland areas and may have contributed to the moderate but unexplained decline in human brain size over the past 25–90 000 years.

11. Conclusion

The focus here has been on the probable necessity and considerable advantages of an accessible and abundant shore-based diet in the evolution of fetal fat deposits in humans (Table 3). We view this as an essential prerequisite to evolution of the hominid brain to its current large and uniquely complex stature in modern humans. Our aim has been to account for the unique evolution of the metabolic and nutritional prerequisites of present-day human brain function. These prerequisites exist to varying degrees in all present-day mammals in which brain composition and metabolism have been studied so there is no reason to assume that they have changed substantially over the last 2 million years of human evolution. Therefore we need to project backwards and arrive at a form of subsistence that can account for the unique ability of humans to have fat babies and big, metabolically expensive yet still vulnerable brains. The hominid fossil record, incomplete as it is, supports the concept that a shore-based diet gave us a crucial advantage, allowing the fattest to become the mentally fittest.

Acknowledgments

The concept described here has benefited from discussions with many people, particularly Leigh Broadhurst, Tom Brenna, Jerry Dobson, John Langdon, David Horrobin, Elaine Morgan, Henry Schwarcz, Philip Tobias, and Marc Verhaegen. NSERC provided financial support for research by SCC.

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