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Food for Thought

Dietary change was a driving force in human evolution

By William R. Leonard

We humans are strange primates.

We walk on two legs, carry around enormous brains and have colonized every corner of the globe. Anthropologists and biologists have long sought to understand how our lineage came to differ so profoundly from the primate norm in these ways, and over the years all manner of hypotheses aimed at explaining each of these oddities have been put forth. But a growing body of evidence indicates that these miscellaneous quirks of humanity in fact have a common thread: they are largely the result of natural selection acting to maximize dietary quality and foraging efficiency. Changes in food availability over time, it seems, strongly influenced our hominid ancestors. Thus, in an evolutionary sense, we are very much what we ate.

Accordingly, what we eat is yet another way in which we differ from our primate kin. Contemporary human populations the world over have diets richer in calories and nutrients than those of our cousins, the great apes. So when and how did our ancestors' eating habits diverge from those of other primates? Further, to what extent have modern humans departed from the ancestral dietary pattern?

Scientific interest in the evolution of human nutritional requirements has a long history. But relevant investigations started gaining momentum after 1985, when S. Boyd Eaton and Melvin J. Konner of Emory University published a seminal paper in the *New England Journal of Medicine* entitled "Paleolithic Nutrition." They argued that the prevalence in modern societies of many chronic diseases--obesity, hypertension, coronary heart disease and diabetes, among them--is the consequence of a mismatch between modern dietary patterns and the type of diet that our species evolved to eat as prehistoric hunter-gatherers. Since then, however, understanding of the evolution of human nutritional needs has advanced considerably-- thanks in large part to new comparative analyses of traditionally living human populations and other primates--and a more nuanced picture has emerged. We now know that humans have evolved not to subsist on a single, Paleolithic diet but to be flexible eaters, an insight that has important implications for the current debate over what people today should eat in order to be healthy.

To appreciate the role of diet in human evolution, we must remember that the search for food, its consumption and, ultimately, how it is used for biological processes are all critical aspects of an organism's ecology. The energy dynamic between organisms and their environments--that is, energy expended in relation

to energy acquired--has important adaptive consequences for survival and reproduction. These two components of Darwinian fitness are reflected in the way we divide up an animal's energy budget. Maintenance energy is what keeps an animal alive on a day-to-day basis. Productive energy, on the other hand, is associated with producing and raising offspring for the next generation. For mammals like ourselves, this must cover the increased costs that mothers incur during pregnancy and lactation.

The type of environment a creature inhabits will influence the distribution of energy between these components, with harsher conditions creating higher maintenance demands. Nevertheless, the goal of all organisms is the same: to devote sufficient funds to reproduction to ensure the long-term success of the species. Thus, by looking at the way animals go about obtaining and then allocating food energy, we can better discern how natural selection produces evolutionary change.

Becoming Bipedals

Without exception, living nonhuman primates habitually move around on all fours, or quadrupedally, when they are on the ground. Scientists generally assume therefore that the last common ancestor of humans and chimpanzees (our closest living relative) was also a quadruped. Exactly when the last common ancestor lived is unknown, but clear indications of bipedalism--the trait that distinguished ancient humans from other apes--are evident in the oldest known species of *Australopithecus*, which lived in Africa roughly four million years ago. Ideas about why bipedalism evolved abound in the paleoanthropological literature. C. Owen Lovejoy of Kent State University proposed in 1981 that two-legged locomotion freed the arms to carry children and foraged goods. More recently, Kevin D. Hunt of Indiana University has posited that bipedalism emerged as a feeding posture that enabled access to foods that had previously been out of reach. Peter Wheeler of Liverpool John Moores University submits that moving upright allowed early humans to better regulate their body temperature by exposing less surface area to the blazing African sun.

The list goes on. In reality, a number of factors probably selected for this type of locomotion. My own research, conducted in collaboration with my wife, Marcia L. Robertson, suggests that bipedalism evolved in our ancestors at least in part because it is less energetically expensive than quadrupedalism. Our analyses of the energy costs of movement in living animals of all sizes have shown that, in general, the strongest predictors of cost are the weight of the animal and the speed at which it travels. What is striking about human bipedal movement is that it is notably more economical than quadrupedal locomotion at walking rates.

Apes, in contrast, are not economical when moving on the ground. For instance, chimpanzees, which employ a peculiar form of quadrupedalism known as knuckle walking, spend some 35 percent more calories during locomotion than does a typical mammalian quadruped of the same size-- a large dog, for example. Differences in the settings in which humans and apes evolved may help explain the variation in costs of movement. Chimps, gorillas and

orangutans evolved in and continue to occupy dense forests where only a mile or so of trekking over the course of the day is all that is needed to find enough to eat. Much of early hominid evolution, on the other hand, took place in more open woodland and grassland, where sustenance is harder to come by. Indeed, modern human hunter-gatherers living in these environments, who provide us with the best available model of early human subsistence patterns, often travel six to eight miles daily in search of food.

These differences in day range have important locomotor implications. Because apes travel only short distances each day, the potential energetic benefits of moving more efficiently are very small. For far-ranging foragers, however, cost-effective walking saves many calories in maintenance energy needs--calories that can instead go toward reproduction. Selection for energetically efficient locomotion is therefore likely to be more intense among far-ranging animals because they have the most to gain.

For hominids living between five million and 1.8 million years ago, during the Pliocene epoch, climate change spurred this morphological revolution. As the African continent grew drier, forests gave way to grasslands, leaving food resources patchily distributed. In this context, bipedalism can be viewed as one of the first strategies in human nutritional evolution, a pattern of movement that would have substantially reduced the number of calories spent in collecting increasingly dispersed food resources.

Big Brains and Hungry Hominids

No sooner had humans perfected their stride than the next pivotal event in human evolution-- the dramatic enlargement of the brain--began. According to the fossil record, the australopithecines never became much brainier than living apes, showing only a modest increase in brain size, from around 400 cubic centimeters four million years ago to 500 cubic centimeters two million years later. *Homo* brain sizes, in contrast, ballooned from 600 cubic centimeters in *H. habilis* some two million years ago up to 900 cubic centimeters in early *H. erectus* just 300,000 years later. The *H. erectus* brain did not attain modern human proportions (1,350 cubic centimeters on average), but it exceeded that of living nonhuman primates.

From a nutritional perspective, what is extraordinary about our large brain is how much energy it consumes-- roughly 16 times as much as muscle tissue per unit weight. Yet although humans have much bigger brains relative to body weight than do other primates (three times larger than expected), the total resting energy requirements of the human body are no greater than those of any other mammal of the same size. We therefore use a much greater share of our daily energy budget to feed our voracious brains. In fact, at rest brain metabolism accounts for a whopping 20 to 25 percent of an adult human's energy needs-- far more than the 8 to 10 percent observed in nonhuman primates, and more still than the 3 to 5 percent allotted to the brain by other mammals.

By using estimates of hominid body size compiled by Henry M. McHenry of the University of California at Davis, Robertson and I have reconstructed the proportion of resting energy needs that would have been required to support the brains of our ancient ancestors. Our calculations suggest that a typical, 80- to 85-pound australopithecine with a brain size of 450 cubic centimeters would have devoted about 11 percent of its resting energy to the brain. For its part, *H. erectus*, which weighed in at 125 to 130 pounds and had a brain size of some 900 cubic centimeters, would have earmarked about 17 percent of its resting energy-- that is, about 260 out of 1,500 kilocalories a day--for the organ.

How did such an energetically costly brain evolve? One theory, developed by Dean Falk of Florida State University, holds that bipedalism enabled hominids to cool their cranial blood, thereby freeing the heat-sensitive brain of the temperature constraints that had kept its size in check. I suspect that, as with bipedalism, a number of selective factors were probably at work. But brain expansion almost certainly could not have occurred until hominids adopted a diet sufficiently rich in calories and nutrients to meet the associated costs.

Comparative studies of living animals support that assertion. Across all primates, species with bigger brains dine on richer foods, and humans are the extreme example of this correlation, boasting the largest relative brain size and the choicest diet [see "Diet and Primate Evolution," by Katharine Milton; *Scientific American*, August 1993]. According to recent analyses by Loren Cordain of Colorado State University, contemporary hunter-gatherers derive, on average, 40 to 60 percent of their dietary energy from animal foods (meat, milk and other products). Modern chimps, in comparison, obtain only 5 to 7 percent of their calories from these comestibles. Animal foods are far denser in calories and nutrients than most plant foods. For example, 3.5 ounces of meat provides upward of 200 kilocalories. But the same amount of fruit provides only 50 to 100 kilocalories. And a comparable serving of foliage yields just 10 to 20 kilocalories. It stands to reason, then, that for early *Homo*, acquiring more gray matter meant seeking out more of the energy-dense fare.

Fossils, too, indicate that improvements to dietary quality accompanied evolutionary brain growth. All australopithecines had skeletal and dental features built for processing tough, low-quality plant foods. The later, robust australopithecines-- a dead-end branch of the human family tree that lived alongside members of our own genus-- had especially pronounced adaptations for grinding up fibrous plant foods, including massive, dish-shaped faces; heavily built mandibles; ridges, or sagittal crests, atop the skull for the attachment of powerful chewing muscles; and huge, thickly enameled molar teeth. (This is not to say that australopithecines never ate meat. They almost certainly did on occasion, just as chimps do today.) In contrast, early members of the genus *Homo*, which descended from the gracile australopithecines, had much smaller faces, more delicate jaws, smaller molars and no sagittal crests-- despite being far larger in terms of overall body size than their predecessors. Together these features suggest that early *Homo* was consuming less plant material and more animal foods.

As to what prompted *Homo*'s initial shift toward the higher-quality diet necessary for brain growth, environmental change appears to have once more set the stage for evolutionary change. The continued desiccation of the African landscape limited the amount and variety of edible plant foods available to hominids. Those on the line leading to the robust australopithecines coped with this problem morphologically, evolving anatomical specializations that enabled them to subsist on more widely available, difficult-to-chew foods. *Homo* took a different path. As it turns out, the spread of grasslands also led to an increase in the relative abundance of grazing mammals such as antelope and gazelle, creating opportunities for hominids capable of exploiting them. *H. erectus* did just that, developing the first hunting-and-gathering economy in which game animals became a significant part of the diet and resources were shared among members of the foraging groups. Signs of this behavioral revolution are visible in the archaeological record, which shows an increase in animal bones at hominid sites during this period, along with evidence that the beasts were butchered using stone tools.

These changes in diet and foraging behavior did not turn our ancestors into strict carnivores; however, the addition of modest amounts of animal foods to the menu, combined with the sharing of resources that is typical of hunter-gatherer groups, would have significantly increased the quality and stability of hominid diets. Improved dietary quality alone cannot explain *why* hominid brains grew, but it appears to have played a critical role in enabling that change. After the initial spurt in brain growth, diet and brain expansion probably interacted synergistically: bigger brains produced more complex social behavior, which led to further shifts in foraging tactics and improved diet, which in turn fostered additional brain evolution.

A Movable Feast

The evolution of *H. erectus* in Africa 1.8 million years ago also marked a third turning point in human evolution: the initial movement of hominids out of Africa. Until recently, the locations and ages of known fossil sites suggested that early *Homo* stayed put for a few hundred thousand years before venturing out of the motherland and slowly fanning out into the rest of the Old World. Earlier work hinted that improvements in tool technology around 1.4 million years ago--namely, the advent of the Acheulean hand ax--allowed hominids to leave Africa. But new discoveries indicate that *H. erectus* hit the ground running, so to speak. Rutgers University geochronologist Carl Swisher III and his colleagues have shown that the earliest *H. erectus* sites outside of Africa, which are in Indonesia and the Republic of Georgia, date to between 1.8 million and 1.7 million years ago. It seems that the first appearance of *H. erectus* and its initial spread from Africa were almost simultaneous.

The impetus behind this newfound wanderlust again appears to be food. What an animal eats dictates to a large extent how much territory it needs to survive. Carnivorous animals generally require far bigger home ranges than do herbivores of comparable size because they have fewer total calories available to them per unit area.

Large-bodied and increasingly dependent on animal foods, *H. erectus* most likely needed much more turf than the smaller, more vegetarian australopithecines did. Using data on contemporary primates and human hunter-gatherers as a guide, Robertson, Susan C. Antón of Rutgers University and I have estimated that the larger body size of *H. erectus*, combined with a moderate increase in meat consumption, would have necessitated an eightfold to 10-fold increase in home range size compared with that of the late australopithecines-- enough, in fact, to account for the abrupt expansion of the species out of Africa. Exactly how far beyond the continent that shift would have taken *H. erectus* remains unclear, but migrating animal herds may have helped lead it to these distant lands.

As humans moved into more northern latitudes, they encountered new dietary challenges. The Neandertals, who lived during the last ice ages of Europe, were among the first humans to inhabit arctic environments, and they almost certainly would have needed ample calories to endure under those circumstances. Hints at what their energy requirements might have been come from data on traditional human populations that live in northern settings today. The Siberian reindeer-herding populations known as the Evenki, which I have studied with Peter Katzarzyk of Queen's University in Ontario and Victoria A. Galloway of the University of Toronto, and the Inuit (Eskimo) populations of the Canadian Arctic have resting metabolic rates that are about 15 percent higher than those of people of similar size living in temperate environments. The energetically expensive activities associated with living in a northern climate ratchet their caloric cost of living up further still. Indeed, whereas a 160-pound American male with a typical urban way of life requires about 2,600 kilocalories a day, a diminutive, 125-pound Evenki man needs more than 3,000 kilocalories a day to sustain himself. Using these modern northern populations as benchmarks, Mark Sorensen of Northwestern University and I have estimated that Neandertals most likely would have required as many as 4,000 kilocalories a day to survive. That they were able to meet these demands for as long as they did speaks to their skills as foragers.

Modern Quandaries

Just as pressures to improve dietary quality influenced early human evolution, so, too, have these factors played a crucial role in the more recent increases in population size. Innovations such as cooking, agriculture and even aspects of modern food technology can all be considered tactics for boosting the quality of the human diet. Cooking, for one, augmented the energy available in wild plant foods. With the advent of agriculture, humans began to manipulate marginal plant species to increase their productivity, digestibility and nutritional content-- essentially making plants more like animal foods. This kind of tinkering continues today, with genetic modification of crop species to make "better" fruits, vegetables and grains. Similarly, the development of liquid nutritional supplements and meal replacement bars is a continuation of the trend that our ancient ancestors started: gaining as much nutritional return from our food in as little volume and with as little physical effort as possible.

Overall, that strategy has evidently worked: humans are here today and in record numbers to boot. But perhaps the strongest testament to the importance of energy- and nutrient-rich foods in human evolution lies in the observation that so many health concerns facing societies around the globe stem from deviations from the energy dynamic that our ancestors established. For children in rural populations of the developing world, low-quality diets lead to poor physical growth and high rates of mortality during early life. In these cases, the foods fed to youngsters during and after weaning are often not sufficiently dense in energy and nutrients to meet the high nutritional needs associated with this period of rapid growth and development. Although these children are typically similar in length and weight to their U.S. counterparts at birth, they are much shorter and lighter by the age of three, often resembling the smallest 2 to 3 percent of American children of the same age and sex.

In the industrial world, we are facing the opposite problem: rates of childhood and adult obesity are rising because the energy-rich foods we crave--notably those packed with fat and sugar--have become widely available and relatively inexpensive. According to recent estimates, more than half of adult Americans are overweight or obese. Obesity has also appeared in parts of the developing world where it was virtually unknown less than a generation ago. This seeming paradox has emerged as people who grew up malnourished move from rural areas to urban settings where food is more readily available. In some sense, obesity and other common diseases of the modern world are continuations of a tenor that started millions of years ago. We are victims of our own evolutionary success, having developed a calorie-packed diet while minimizing the amount of maintenance energy expended on physical activity.

The magnitude of this imbalance becomes clear when we look at traditionally living human populations. Studies of the Evenki reindeer herders that I have conducted in collaboration with Michael Crawford of the University of Kansas and Ludmila Osipova of the Russian Academy of Sciences in Novosibirsk indicate that the Evenki derive almost half their daily calories from meat, more than 2.5 times the amount consumed by the average American. Yet when we compare Evenki men with their U.S. peers, they are 20 percent leaner and have cholesterol levels that are 30 percent lower.

These differences partly reflect the compositions of the diets. Although the Evenki diet is high in meat, it is relatively low in fat (about 20 percent of their dietary energy comes from fat, compared with 35 percent in the average U.S. diet), because free-ranging animals such as reindeer have less body fat than cattle and other feedlot animals do. The composition of the fat is also different in free-ranging animals, tending to be lower in saturated fats and higher in the polyunsaturated fatty acids that protect against heart disease. More important, however, the Evenki way of life necessitates a much higher level of energy expenditure.

Thus, it is not just changes in diet that have created many of our pervasive health problems but the interaction of shifting diets and changing lifestyles. Too often modern health problems are portrayed as the result of eating "bad" foods

that are departures from *the* natural human diet--an oversimplification embodied by the current debate over the relative merits of a high-protein, high-fat Atkins-type diet or a low-fat one that emphasizes complex carbohydrates. This is a fundamentally flawed approach to assessing human nutritional needs. Our species was not designed to subsist on a single, optimal diet. What is remarkable about human beings is the extraordinary variety of what we eat. We have been able to thrive in almost every ecosystem on the earth, consuming diets ranging from almost all animal foods among populations of the Arctic to primarily tubers and cereal grains among populations in the high Andes. Indeed, the hallmarks of human evolution have been the diversity of strategies that we have developed to create diets that meet our distinctive metabolic requirements and the ever increasing efficiency with which we extract energy and nutrients from the environment. The challenge our modern societies now face is balancing the calories we consume with the calories we burn.

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More to Explore:

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