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Fermentation technology as a driver of human brain expansion

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Abstract

Hypothesis/Thesis Statement: the consumption of externally fermented foods acted as the initial metabolic trigger enabling hominid brain expansion

Because brain tissue is metabolically expensive, it is thought that the evolution of humans' large brains was only possible through a concomitant reduction in the size of another expensive organ system, the gut. However, this gut reduction must have itself been made possible by dietary changes, the nature of which are still unclear. Here, we propose that the initial metabolic trigger of hominid brain expansion may have been the consumption of externally fermented foods. We define "external fermentation" as occurring outside the body, as opposed to the internal fermentation that occurs through the gut microbiome. This practice could have begun accidentally and with limited understanding, but over time, fermentation technologies may have become increasingly intentional, socially-transmitted, and culturally-reinforced. We detail the mechanisms by which external fermentation can mediate the evolution of increased brain size, as well as a reduction in gut size, by increasing the bioavailability of macro- and micronutrients while reducing digestive energy expenditure. Importantly, we calculate that the reduction in human gut size relative to modern apes is mainly due to a reduction in the colon, the site of internal fermentation. We also discuss the explanatory power of our hypothesis relative to others, including realistic plausibility in hominids with brains roughly the size of modern chimpanzees. Finally, we survey external fermentation practices across human cultures to demonstrate its viability across a huge range of

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environments, temperatures, and food sources. We close with suggestions for empirical tests.

I. Introduction: The Problem of Hominin Brain Expansion

Human brains are notable for their large size. Over the course of 2 million years of evolution, the human brain has tripled in volume. Australopiths possessed brain volumes that were roughly the size of our closest living ape relatives, chimpanzees and bonobos (*Pan troglodytes* and *Pan paniscus*) (Holloway 1970; Tobias 1963; Dart and Salmons 1925). With the appearance of *Homo*, brain expansion in the human lineage began to accelerate, and continued through to the emergence of *H. sapiens* and *H. neanderthalensis*. Although we have much information on the timeline and extent to which the human brain has expanded in our evolution, the mechanisms which drove this expansion are more difficult to determine. Several theories have been proposed, briefly summarized below.

Metabolic constraints on brain evolution

The Expensive Tissue Hypothesis (Aiello and Wheeler 1995) argues that the expansion of brain size in the hominin lineage required the reallocation of resources from the digestive system. In this view, the limiting factor for brain expansion is the availability of caloric resources, because brain tissue is metabolically expensive compared to most other tissue. Mutations leading to increased brain size, though they might support more adaptive behavior by the organism, could not actually be adaptive if they carried with them an increased risk of starvation. A reduction in the amount of gut tissue, which has metabolic needs similar to brain tissue, would free up the calories that would otherwise be used to support and maintain digestion and permit its reallocation to supporting the brain. Supporting this model is the fact that in addition to having relatively large brains, the size of the human gastrointestinal tract is 60% of that expected for a primate of our size (Aiello and Wheeler, 1995). However, because gut tissue is itself responsible for extracting nutrients from food, mutations leading to reduced gut size could not be adaptive without a prior shift to a more energy-dense, easy-to-digest food source. The Expensive Tissue Hypothesis has generated extensive empirical research, including studies that support this model (Kaufmann et al., 2003; Kotrschal et al., 2011; Tsuboi et al., 2015; Jin et al., 2015; Liao et al., 2016) as well as several that did not find a direct, causal tradeoff between metabolic investment in different tissue types, or instead support a more complex relationship with other metabolic investments (Isler and van Schaik, 2005, 2006; Liu et al., 2014; Kotrschal et al., 2015). In particular, in a study of over 100 mammalian species, a consistent inverse relationship between gut size and brain size was not observed (Navarette et al., 2011). In a revised and elaborated model, Isler and van Schaik (2014) emphasize a complex system of tradeoffs between fitness benefits and multiple energetic costs including development, reproduction, digestion, and locomotion, where the cognitive benefits of a larger brain can only produce an increase in net fitness if the corresponding energetic costs are accounted for; notably, dietary changes are one proposed mechanism that could contribute to this.

This key point —that brain size increases are evolutionarily limited by metabolic constraints -- has led to a search for possible changes in diet during the period when encephalization quotients began to depart from earlier anthropoids. Some proposed changes include increased meat consumption via hunting or scavenging, a specialization for the consumption of starchy underground tubers, or the development of cooking technology using fire.

Proposed dietary specializations of early human ancestors

Increased meat-eating has been argued to have been central to human evolution (Speth 1989; Katharine Milton 1999). Aiello and Wheeler (Aiello and Wheeler 1995) have further proposed that meat-eating is a plausible source of the extra calories needed to allow for brain expansion, and analysis of gut morphology in humans suggests it may be adapted to an intermediate diet with aspects of both frugivory and carnivory (Mann 2000). The archaeological record also supports the importance of meat eating in human ancestors, with fossil evidence of butchery in early *Homo* (Semaw 2000; de Heinzelin et al. 1999). It is certainly inarguable that modern human diets frequently involve more meat consumption than our anthropoid relatives, and data from modern hunter-gatherers support this view; however, some authors (e.g., (Cordain et al. 2002) argue that evidence for human hunting appears later in human evolution - in the Middle to Late Paleolithic. Another possibility is that meat was acquired by other means.

(Binford 1985) proposed scavenging after carnivores have finished with a carcass, rather than hunting, was the most likely source of meat for human ancestors. Archaeological evidence has favored scavenging over hunting (Capaldo 1997; Blumenschine 1986) but evidence from modern hunter-gatherers suggests scavenging is less important than previously claimed (O'Connell, Hawkes, and Jones 1988). More recent analyses of the archaeological record indicate that passive scavenging by hominins offered low meat yields (Domínguez-Rodrigo 2002; Domínguez-Rodrigo and Pickering 2003). Bunn and colleagues have proposed that "power scavenging" better explains the patterns of butchery found in the hominin archaeological record (Henry T. Bunn and Ezzo 1993; H. T. Bunn 1996). In this model, human ancestors (*Homo*) are proposed to have confronted carnivores to drive them from fresh kills in order to obtain more valuable portions of meat than are available to passive scavengers.

Another candidate modification to early hominin diets is the consumption of underground storage organs, or tubers (Hatley and Kappelman 1980). The importance of foraging in human evolution, particularly linked to the Grandmother Hypothesis, has also been highlighted in the tuber-based model of increased calories (O'connell, Hawkes, and Blurton Jones 1999). The importance of tubers as a source of calories for hominins has been debated, however. One frequently cited source of nutritional data (Vincent 1985) calculated the caloric value of the //ekwa tuber using samples of tubers to determine calories per gram and then multiplying by the total mass of the unearthed tuber. But in the field, Hadza hunter-gatherers discard large fibrous portions of foraged wild tubers during consumption (Schoeninger et al. 2001). These authors found that in addition to being labor-intensive to unearth, wild foraged tubers have as little as ¼ of the caloric density reported by Vincent (1985), even after cooking.

Another possibility is that the modifications to food through cooking provided the necessary additional calories and nutrients to support a reduction of gut and increase in encephalization (Wrangham et al. 1999). The hypothesis has been extended to encompass others. For example, cooked tubers have been proposed as an important component of the “cooked foods” diet (O’connell, Hawkes, and Blurton Jones 1999; Wrangham et al. 1999; Hatley and Kappelman 1980) and it has been suggested that scavenged carcasses were cooked to mitigate microbiological contamination (Smith et al. 2015). The trend of reduction of molar size in hominin evolution, suggested to be an adaptation from moving from tougher to softer foods (McHenry and Coffing 2000), fits well with this hypothesis (Zink, Lieberman, and Lucas 2014). The benefits of cooking - increase in bioavailability of calories, easier mechanical digestion (especially chewing), and the lowering of energy requirements for digestion - are undoubtable. However, there is a lack of archaeological evidence for the usage of fire by australopiths and early hominins; the earliest date for the evidence of fire by hominins is frequently cited at 0.5 mya by *H. erectus* during the Middle Pleistocene (James et al. 1989). Evidence for fire mastery in the Lower Pleistocene (Goren-Inbar et al. 2004) still puts this behavior well after the initial emergence of *H. erectus*, which is well after selection for brain expansion put hominins on a different course than the *Pan* lineage. It is almost certainly the case that the actual origins of human-controlled fire predate its oldest surviving archaeological evidence. However, more importantly, mastery of fire technology requires individuals to have the cognitive capacity to plan, create, maintain, and use fire effectively; this seems a tall order for an organism with a brain-to-body ratio not much exceeding that of modern nonhuman apes. This suggests that we should continue to search for other mechanisms that could have kicked off our ancestors' initial encephalization.

A New Hypothesis: External Fermentation

If we are to explain the dietary changes that supported brain expansion and gut reduction in the hominin lineage, we will need to identify strategies that were accessible by individuals with brains that were roughly the size of a chimpanzee's. Here, we outline a novel hypothesis, the *External Fermentation Hypothesis* (**Figure 1**). Central to this hypothesis is the realization that the gut *is itself a machine for internal fermentation*: digestion is accomplished via the the endogenous microbiome. Culturally-transmitted food handling practices which promoted the externalization of this functionality to the extra-somatic environment could have offloaded energetic requirements from the body and freed up the surplus energy budget for brain expansion.

In this paper, we begin with a mechanistic discussion on how external fermentation provides adaptive benefits: it increases macronutrient absorption; it increases the bioavailability of micronutrients, some of which are essential for brain development and function; it supports internal fermentation by the endogenous microbiome; and it provides additional immune benefits. Following this, we present evidence that external fermentation specifically addressed the expensive tissue problem: the reduction in human gut size is attributable mainly to reduction in the colon, which is the primary site of internal fermentation; furthermore, humans receive a surprisingly low amount of their calories from short-chain fatty acids (SCFAs), which are the products of colon fermentation on carbohydrates. Next, we consider the plausibility and explanatory power of the External Fermentation Hypothesis compared to other hypotheses.

II. Fermentation plays an important role in digestion

Fermentation is the breakdown of organic compounds by enzymes into alcohol, acids, or both. When discussed in the context of human metabolism and nutrition, the enzymatic activity typically originates from bacteria, yeasts or both, and transforms starches, sugars, and proteins into alcohol and/or acids. Rather than relying on the microorganisms living inside an animal's gut to ferment macronutrients, external fermentation is carried out by organisms living wild in the environment or on the surface of the organic material itself. Like internal, or intestinal, fermentation, external fermentation increases the bioavailability of ingested nutrients.

Digestion is the process of mechanically and enzymatically breaking down organic food matter into macronutrients small enough for absorption through the intestinal barrier and into the bloodstream. Any foodstuffs not broken down by enzymes, bile or other digestive chemicals pass through the upper gastrointestinal tract unabsorbed, offering the body no nutritional value. The digestion of fibrous, starchy vegetable matter requires a specialized digestive system with modifications that support fermentation. In ruminant animals, this is achieved through additional stomachs - these species are known as foregut fermenters. The hindgut fermenters, which include humans and other primates, as well as non-ruminant mammals - have evolved a large colon, large cecum, or both. A large colon and/or cecum means a large amount of surface area for absorption, but it also means a large amount of internal fermentation.

While both the large and small intestine contain active, symbiotic bacteria, the small intestine contains approximately one million bacteria per mL while the colon contains up to one trillion bacteria per mL (Gibson and Rastall 2004; Sender, Fuchs, and Milo 2016; Whitman, Coleman, and Wiebe 1998). Combined with a longer transit time than the small intestine (approximately 1-4 hours versus 18-39 hours), this means the action within the colon is focused on bacteria-driven fermentation. Although previously it was thought that in humans, the large intestine did little more than resorb water, there is a new focus on the significance of colon for human health, including immune responsivity (O’Hara and Shanahan 2006), nutrient absorption, and energy regulation (Krajmalnik-Brown et al. 2012).

Fermentation promotes macronutrient absorption

Fermentation within the gut increases the body’s capacity to absorb macronutrients beyond the normal function of the upper gastrointestinal tract. Fermented soluble fiber provides an average of 2 cal/g, an additional 50% to the 4 cal/g available from digestible starch and sugars. This energy is only available via the salvaging of otherwise undigested fiber through internal fermentation by gut microbes (World Health Organization 1997; Popovich et al. 1997); CFIA 2017; WHO/UN 1998). Notably, humans purposefully ferment feed for livestock (sileage) in order to increase its digestibility and caloric value. Like starches and sugars, fibers are polysaccharide structures made up of bound glucose molecules and other small carbohydrates. Originating primarily in the cell walls of plants, fibers such as cellulose and pectin are resistant to hydrolyzation by human digestive enzymes and therefore pass through the small intestine unbroken (Messer et al. 2017; Nelms and Sucher 2015; Vanderhoof 1998). Once in the colon, these fibers are fermented by enzymes from gut flora, and the now-available sugars are fermented into acid/base conjugates. These are then further degraded by secondary microorganisms into short chain fatty acids (SCFAs) (Cummings and Macfarlane 1991; Bik et al. 2017; Battcock et al. 1998). Microbial fermentation of carbohydrates into SCFAs is estimated to contribute 2-10% of total dietary energy in humans (McNeil 1984; Livesey 1995; McBurney 1994). This is small compared to other mammals, which typically derive from 16% to over 80% of maintenance energy from the production of SCFAs in the gut (see **Table 1**).

These fermentation products have important biological functions. More than 80% of produced SCFAs take the form of either butyrate, proprionate, or acetate (Bik 2017). Butyrate is the preferred energy source for the cells making up the intestinal wall of the colon, and feeds the rapidly reproducing colonocytes while also producing Vitamin K and a variety of B vitamins for circulation (Vanderhoof 1998; Messer et al.

2017; Markowiak and Śliżewska 2017). Proprionate is absorbed into the bloodstream and provides a precursor for hepatic synthesis of glucose (Nelms and Sucher 2015). Acetate is also metabolized by the liver to synthesize cholesterol and other long chain fatty acids. Additionally, acetate provides energy to a number of organs and tissues including the heart, kidneys, muscle and fat (den Besten et al. 2013; Bik et al. 2017; Ramakrishna 2013; De Filippo et al. 2010).

Protein availability is also enhanced through fermentation, though to a lesser extent than carbohydrates. Fermentation of legumes hydrolyzes large structures into more easily digestible individual amino acids (Katz 2016). Proprionate, a SCFA and metabolite of carbohydrate fermentation, travels to the liver after absorption and acts as a substrate for protein synthesis (De Filippo et al. 2010). Free peptides, amino acids and ammonia-derived nitrogen are synthesized into microbial protein by yeast and fungi, and the availability of essential amino acids such as tryptophan, lysine, and methionine levels also increases as a result of microbial fermentation (Sandhu, Punia, and Kaur 2017; Mackie 2002; Holzapfel 2002).

Thus, fermentation provides increased macronutrient digestibility for both carbohydrates and proteins. These benefits have led public health scholars to recommend increasing the consumption of fermented foods in countries experiencing food insecurity and high infant mortality (Franz et al. 2014; Holzapfel 2002).

Fermentation promotes micronutrient absorption

Fermentation is also critical for the absorption of vitamins and minerals. One way this can occur is via actual synthesis of vitamins by bacteria. In the colon, vitamin K2 is synthesized by multiple genera of bacteria (Katz 2012; Ramezani et al. 2016; Ramakrishna 2013). B complex vitamins are produced from carbohydrate fermentation by alcohol-producing yeasts and Lactobacillus species - this can occur in the gut as well as in the environment (Katz 2012; Ramakrishna 2013; Priyodip et al. 2017). Notably, externally fermenting foods prior to consuming them can increase the amounts of B vitamins (thiamin, riboflavin, and niacin) by up to 10-fold (Sandhu et al. 2017; Battcock et al. 1998).

Another mechanism by which internal and external fermentation increase bioavailablity of micronutrients is through the breakdown of anti-nutritional factors (ANFs). ANFs are compounds found in staple cereals, grains, seeds, legumes and tubers that bind essential nutrients, preventing their absorption in the body.

One group of ANFs includes phytates and oxalates, which are are powerful chelating agents that form complexes with metal cations, preventing absorption of these minerals (Barakoti and Bains 2007; Humer and Schedle 2016; Nikmaram et al. 2017; El-Abasy et al. 2012; Morrison and Savage 2003). Phytate is a salt formed from plants' phosphorus storage compound, phytic acid. Oxalate is commonly found in leafy vegetation, nuts, and tubers; it forms chelates with essential nutrients iron, magnesium, and most importantly, calcium (El-Abasy et al. 2012; Morrison and Savage 2003). Iron, zinc, magnesium, and calcium are thus particularly impacted by ANFs found in raw plant matter (Bassiri and Nahapetian 1977), yet sufficient absorption of these is critical for life (e.g., Lopez et al. 2016; Rerksuppaphol and Rerksuppaphol 2018; DiNicolantonio et al. 2018). Interestingly, humans, unlike rodents, produce little phytase in their small intestine (Iqbal, Lewis, and Cooper 1994). The bioavailability of minerals is therefore greatly reduced in humans despite their abundance in raw material. Lactobacillus bacteria-driven fermentation is an alternative to phytase -- by lowering the pH, it provides a favorable environment for both bacterial and endogenous phytase within the plant material to hydrolyze the binding phytate and release the bound minerals (Humer and Schedle 2016; Katz 2016). Oxalate can also be degraded through Lactobacillus fermentations, either externally or internally (Bik et al. 2017; Wadamori, Vanhanen, and Savage 2014). Of note, degradation of phytate by external fermentation has been shown to be more effective than heat treatment or cooking due to the decreased phytase bioactivity at a temperature above 80°C (Gupta, Gangoliya, and Singh 2015; Mahgoub and Elhag 1998).

Another group of ANFs includes phenolic compounds like tannins that bind to proteins and enzymes, lowering their bioavailability (Nikmaram et al. 2017). Tannins also lower the overall digestibility of amino acids, minerals, and other macronutrients (Nikmaram et al. 2017). External fermentation by Lactobacillus reduces the concentration of tannins in plant foods rendering proteins, digestive enzymes, and important minerals easier to metabolize and absorb (Humer and Schedle 2016; Verni et al. 2017; El-Abasy et al. 2012).

One of the best-documented examples of how external fermentation can render poisonous foods edible is the detoxification of cyanogenic glycoside in bitter cassava (aka yuca or manioc), a common staple for hundreds of millions of people living within the Tropical Belt (Battcock, Azam-Ali, and Food and Agriculture Organization of the United Nations 1998; Franz et al. 2014; Padmaja 1995). If consumed unfermented, the cassava releases dangerous amounts of hydrocyanic acid into the gut when cyanogenic glycosides are hydrolyzed by colonic microorganisms and absorbed as cyanide. Through inhibition of cellular respiration, cyanide poisoning can cause convulsions, hypotension, respiratory failure, and decreased heart rate that times may in death (Katz 2012; Padmaja 1995; CDC 2013). When processed properly, cell walls in the fibers of the cassava tuber are softened by Lactobacillus bacteria during soaking, allowing the endogenous enzymes normally sequestered from the cyanogenic glycosides to hydrolyze the toxin. The production of lactic acid during fermentation also acidifies the environment and provides a favorable mileu for other microorganisms to contribute to the hydrolysis of up to 95% of the toxin prior to consumption (Battcock, Azam-Ali, and Food and Agriculture Organization of the United Nations 1998; Padmaja 1995).

ANFs are present in the leaves, seeds, and other plant materials that make up a significant portion of many primate species’ diets, including hominoids. Foraging strategies of primates that consume plants as part of their diet suggest deliberate avoidance of plant species with high endogenous ANF content, as well as preference for younger leaves over mature leaves, as a strategy to reduce ANF burden and increase digestibility (Glander 1982), (Garber 1987)). Primates that have folivory-heavy diets have evolved gut specializations for fermentation - either through the evolution of a complex forestomach, as in colobine monkeys (Langer and Others 1988) or through the expansion of the hindgut (caecum and colon) (Cork 1996). Predictably, hindgut fermenters have caecum/colon volumes that correlate positively with the proportion of leaves that make up their total diet (Chivers and Hladik 1980). We propose that external fermentation may represent a parallel, alternative adaptation.

External fermentation supports gut fermentation

The third mechanism by which external fermentation supports digestion is by supporting and contributing to the gut microflora, which in turn contributes to ongoing enhanced nutrient absorption. It may effectively act as an external reservoir of bacteria necessary for internal fermentation. In other species, this reservoir function is supplied internally by the caecum (Palestrant et al. 2004; Swidsinski et al. 2005). Caecal size is larger in Old and New World monkeys and prosimians than in anthropoids, smaller in cercopithecoid monkeys, and reduced further in hominoids; of the great apes, humans have the most reduced caecum (Scott 1980). Humans and other apes, however, possess a vermiform appendix, located adjacent to the caecum (Scott 1980), which has been proposed to function as a reservoir for beneficial intestinal flora (Randal Bollinger et al. 2007), along with small crypts within the colon (Donaldson, Lee, and Mazmanian 2016).

Diets rich in plant material have been shown to increase beneficial bacteria in the human gut by supplying fermentable substrates to existing microorganisms (De Filippo et al. 2010; Markowiak and Śliżewska 2017). Fermented food provides the additional benefit of introducing probiotic compounds that are not present in unfermented, raw or cooked food. These ingested microflora colonize their new environment, contributing diversity to the host microflora and boosting the guts' ability to ferment more polysaccharides into energy and nutrients (Bik et al. 2017; De Filippo et al. 2010; Markowiak and Śliżewska 2017). Ingested probiotic bacteria can also support the health of endogenous microflora. For example, some species of Lactobacillales and Bifidobacteria bacteria produce bacteriocins, toxins that competitively inhibit pathogens (Ohland and Macnaughton 2010; Priyodip, Prakash, and Balaji 2017). Complete colonization is not necessary; in some cases, just transient contact with certain species of microorganisms to enough to beneficially alter existing colonies of bacteria or produce anti-pathogenic metabolites (Ohland and Macnaughton 2010).

External fermentation may provide additional immune benefits

By supporting the gut flora responsible for internal fermentation, external fermentation may also help protect the host from infection and disease. Once bound to colonic epithelial cells, probiotic bacteria prevent large amounts of pathogenic bacteria from colonizing the intestinal wall, reducing their ability to penetrate into the bloodstream and infect the host (Markowiak and Śliżewska 2017; Ohland and Macnaughton 2010). A rich microbiome producing large amounts of SCFA through the fermentation of indigestible carbohydrates is well-linked to decreased inflammation in the gut and a reduction in GI disorders (Bik et al. 2017; De Filippo et al. 2010; Markowiak and Śliżewska 2017; Priyodip, Prakash, and Balaji 2017; Katz 2016; Katz 2012). Certain orders of bacteria such as Lactobacillales and Bifidobacteriales and genera including *Bacteroides* and *Faecalibacterium* are known to contribute large amounts of SCFA across human populations, but studies have shown a richer microbiota containing novel bacterial species in diets containing relatively large amounts microorganisms also results in higher quantities of SCFAs (De Filippo et al. 2010; Priyodip, Prakash, and Balaji 2017). As previously discussed, colonic epithelial cells derive the majority of their energy from SCFAs resulting in a direct relationship between the health of intestinal lining and SCFA levels. Diets low in plant fiber force colonic microorganisms to rely on dietary fats and protein, substrates less than ideal for the microbes, resulting in decreased SCFA production. In the absence of adequate fiber, microbes can also degrade the epithelial mucus layer through digestion of mucins secreted by the host putting the consumer at increased risk of intestinal infection (Bik et al. 2017).

In summary, the ingestion of fermented foods provides four critical components to digestion and absorption. First, it increases the digestibility of foods; second, it increases the bioavailability of micronutrients; third, it supports gut fermentation by contributing to host microfloral diversity; and lastly, it supports immune function and resistance to disruption of the gut microbiome. These benefits would have been adaptive advantages for our early ancestors, and could have played a key role in human brain evolution, as we describe below.

III. External Fermentation as a Driver of Hominin Brain Expansion

The development of external fermentation technology represents a plausible metabolic mechanism leading to brain expansion beginning at our ancestors' divergence from the australopiths. The importance of considering metabolic costs in brain evolution was famously outlined in the Expensive Tissue Hypothesis, in which the reduction of gut tissue in the human lineage permits the reallocation of metabolic resources towards brain tissue, which is metabolically expensive (Aiello and Wheeler 1995). The obvious paradox here is that gut tissue, while metabolically expensive as well, is the site of caloric uptake for the organism. Thus, reduced gut sizes could only evolve if our ancestors were able to exploit a more nutrient-dense and easily-digestible food source. Following mixed results in empirical tests of the Expensive Tissue Hypothesis, Isler and Van Schaik (2014) expanded and elaborated this framework to include tradeoffs between multiple constraints and drivers in brain size evolution, of which metabolic costs and dietary changes are one component. Importantly, while there is debate and disagreement on the extent to which a gut-brain tradeoff is a causal mechanism in brain enlargement in animals generally or in humans specifically, there is widespread agreement that the evolution of larger brains is closely tied to changes in the budget of energy costs and expenditures.

Aiello and Wheeler examined the relative proportion of the most metabolically expensive tissues outside of the brain: the heart, liver, kidneys, and gastrointestinal tract. This led them to observe that the gastrointestinal tract - stomach, small, and large intestine - was 60% smaller than predicted for a primate of our size (Aiello and Wheeler 1995). But if we take a closer look at the gastrointestinal tract, we find that the reduction in size is not equal across organs. The volume of large intestine in non-human great apes is twice that of the small intestine (in gorillas, close to five times the volume); whereas in humans, the ratio is reversed, with the colon having approximately one-third the volume of the small intestine (Katharine Milton 1987; Katharine Milton 1999). Aiello and Wheeler compared the expected organ proportions for a primate of our size (using chiefly great apes for comparison) with the observed proportions and found a large difference - however, this difference was not broken down by subcomponents of the gastrointestinal tract.

Using estimations from Milton (K. Milton 1986; Katharine Milton 1987; K. Milton and Demment 1988) on differences between the proportions of small intestine and colon in humans and apes, we calculated the approximate masses of these subcomponents by taking the midpoint values given by Milton (1999) and applying them to the total gastrointestinal tract values from Aiello and Wheeler (1995). **Table 2** shows these calculations; **Figure 2** shows the relationship between different organ sizes in a hypothetical 65 kg human with ape-like organ sizes (expected) and the actual proportions of these organ sizes in modern western humans (actual). While total gut reduction is impressive (a reduction of over 41%), when we look at subcomponents, it's clear that the reduction is not consistent across the board. Small intestine proportion actually increases, from approximately .4 kg to .62 kg in modern humans, an increase of 58%. The subcomponent which accounts for the largest share of the reduction is the colon. With a predicted ape-like value of 0.85 kg, a typical human instead has an estimated mass of .22 kg, a reduction of 74% - the largest reduction of any of the gut subcomponents and any of the other major organs analyzed (**Table 2**).

What permitted the drastic reduction in colon size in the human lineage? Milton has implicated meat-eating (Milton 1999). It is reasonable to postulate that a smaller colon would reflect a reduction of dependence on fibrous plant material, given that a major function of the colon is to house bacteria that aid in the breakdown of carbohydrates to SCFAs, as described above. This idea is supported by the fact that humans and members of the order Carnivora share small colon size. However, the gut transit time in Carnivora is much faster than in humans. Milton postulates that this difference is due to our evolutionary history as plant eaters, and that meat-eating is nonetheless the most likely candidate for providing the greater nutrient density needed as gut size reduced.

An equally or perhaps more probable explanation is that colon reduction does indeed follow from reduced need to break down fibrous plant material within the digestive tract, but that this reduced need is due not to an increased dependence on meat, but rather to an increase in bioavailability of nutrients *before* food is consumed -- i.e., external fermentation (**Figure 1**).

Plausibility in early hominin lifestyles

Is this scenario realistically plausible for our australopith ancestors? In our view, the major hurdle is that it requires a cache of food to be stored in a location conducive to fermentation, and remain there for a duration sufficient for it to occur. Notably, the transport and caching of food is something that separates human ancestors from our closest extant primate relatives. Early hominins appeared to have carried food resources to specific locations, as evidenced by concentrations of animal bones in larger than expected quantities; further, evidence suggests stone tools were carried large distances as well, up to 10 kilometers (Potts 1984; Toth and Schick 2009). Combined with the accumulating evidence that stone tools were likely knapped prior to the emergence of *Homo* (Lewis and Harmand 2016), it has been argued that australopiths were already knapping tools, butchering animals, and carrying and caching both food and tools (Toth and Schick 2009). By contrast, although chimpanzees do occasionally transport tools, distances are frequently less than 500 meters and rarely reach a kilometer (Luncz et al. 2016). Food transport is limited to the transport of meat across short distances; most other food sources are eaten in the location they are acquired (McGrew and McGrew 1992).

Notably, forethought and mechanistic understanding are *not* requirements for the initial emergence of external fermentation. Our early ancestors may have simply carried food back to a common location, left it there, and intermittently eaten some and added more. Re-use of a consistent storage location could have promoted the stability of a microbial ecosystem conducive to fermentation. As new food items were brought back and added to the cache, they could have become inoculated with the microorganisms already present in the location (or on the hominids themselves). Importantly, fermenting microorganisms can persist in a local environment even through the intermittent absence of a substrate. Thus, over time, the fermentation of stored foods could have become quite stable and self-sustaining, and may have even been unavoidable.

External fermentation may have occurred for a protracted period of time in this manner - as an epiphenomenon of pre-existing adaptive habits of food transport and storage. Socially-transmitted practices such as the re-use of the same containers or tools would have further promoted the initiation of fermentation and the stability of ongoing ferments. As time went on, additional facilitation may have come from culturally-reinforced norms, such as superstitions about where food must be stored or how long it must rest before being eaten. As brain size and cognitive capacity increased, understanding of the proximate causes and consequences of fermentation could have progressed in a gradual fashion. Over time, strategic control and manipulation of fermentation practices would have become increasingly complex, leading to the modern day, where cumulative culture has led to a remarkable diversity of fermentation practices (see **Table 3**).

IV. Explanatory power compared to other hypotheses

We propose that the offloading of fermentation to the extra-somatic environment can provide explanations for evolutionary changes in the human lineage: the increase in brain size as well as the reduction in gut size, particularly the large intestine. The emergence of meat-eating, tuber-harvesting, and cooking have all also been proposed to account for these changes; why should our just-so story be given any additional credence? Below, we consider several explanatory advantages of the external fermentation hypothesis versus other current hypotheses.

Less brainpower required

In searching for an initial trigger to the upward spiral of human brain expansion, it is important to recognize that it would have to occur in organisms with brains roughly the size of a chimpanzee. The cognitive capacities of chimps may arguably be inferior to those of australopiths, particularly later, larger-brained australopiths. At a minimum, though, we can reason that behaviors which are well within the chimp repertoire were likely to have been attainable by australopiths, and that behaviors which are beyond the chimp repertoire may have at least been challenging for australopiths.

Chimpanzees display a variety of complex, socially learned, instrumental behaviors oriented toward food, such as “fishing” for termites or honey using sticks, and fashioning spears to hunt monkeys. Notably, among apes, behavioral adaptations to increase net caloric gain are not limited to chimpanzees; for example, gorillas fold leaves in complex ways which increase the efficiency of consumption (Byrne and Byrne, 1993). Perhaps the most well-studied example, though, is chimpanzee nut cracking. Juvenile chimpanzees spend years learning to accomplish this using a hammer stone and anvil stone. During this time, they make errors like banging the hammer stone on the anvil stone while the nut is left resting on the ground nearby (Hirata, Morimura, and Houki 2009). This suggests that chimpanzees have difficulty understanding the underlying causal mechanism – i.e., that the nut's shell is opened *because* it was struck. Despite nut-cracking occurring in a social context with multiple expert and novice crackers in the same location, using the same tools, at the same time, understanding of the *causal relationship* between percussion and a cracked shell is not socially learned. Instead, each chimpanzee independently "re-discovers" this causal relationship for itself. The social context merely contributes a scaffold in which independent learning can occur (Tennie et al., 2009).

Chimpanzee stone tool use has continued substantially unchanged for at least 4,300 years, as indicated by the discovery of fossil stone tools (Mercader et al., 2007). Thus, animals with brains similarly sized to australopiths are capable of socially transmitting instrumental behaviors which are stable over long periods of time in the absence of underlying causal understanding about how the specific details of the action are related to its end goal. Aspects of behavior that *are* easily socially transferred by chimpanzees include memory for the objects, tools, and locations that are involved in achieving a particular goal. We propose that this is all that is required for social transmission of fermentation to take hold.

In comparison with fermentation, the means-ends dependencies between objects, actions, and outcomes in cooking are considerably more constrained and complex. Cooking requires comprehension of causal mechanisms between multiple interacting objects - i.e., a chain of sequential, dependent interactions between fuel, flames, and raw food. This is precisely the type of means-ends dependency that is challenging for chimpanzees. Thus, we propose that external fermentation poses less of a cognitive hurdle than control of fire, and was thus more likely than cooking to impact the gut-brain tradeoff at an earlier point in evolution.

Notably, one experiment did address whether chimpanzees might have some of the cognitive skills necessary for cooking. Warenken and Rosati (2015) presented chimps with a device which, via unseen experimenter manipulation, “transformed” raw food to cooked food, and showed that chimps deliberately used the device to obtain the latter. Beran et al (2016) argue that this experiment reveals more about chimps’ food preferences and capacity for bartering or exchange behavior than it does about their capacity for cooking. We propose an alternative but not necessarily mutually exclusive view, namely, that these results provide evidence that chimp-sized brains are capable of understanding and performing the steps required to ferment food: put food in a particular place, wait for it to become transformed, and then enjoy an improved version.

Why is it, then, that nonhuman apes *don’t* engage in external fermentation? A potential explanation may be that despite having the basic cognitive mechanisms, chimps lack other, prerequisite, psychological mechanisms required for food caching to occur. One of these may be the ability to delay gratification. Other possibilities include increased social tolerance, food-sharing, and the existence of cultural norms about ownership. These mechanisms are uniquely developed in humans, which are the only ape species known to store food, and may be necessary for the continued existence of a cache of communally accessible food.

No lightbulb moment required

While the utility of fire and fermentation for food processing could both be discovered accidentally, we argue that this discovery was more probable for fermentation. Naturally-occurring fire is not a daily incident. Opportunities for our ancestors to spontaneously observe fire or notice its potential for cooking must have been sporadic. It is conceivable that accidental cooking may have occurred (for example, the action of wildfire on animal carcasses or buried tubers), but this seems likely to have been infrequent. More importantly, the transition from opportunistic, infrequent access to accidentally-cooked food to a long-term and stable source of extra calories would require a “lightbulb moment:” recognition of the effects of the accidental process, and intentional, deliberate actions to reproduce their causes. In contrast, naturally-occurring fermentation *is* a daily incident. Bacteria and fungi are everywhere, all the time, and spontaneously colonize food that isn’t consumed or otherwise preserved. Moreover, no “lightbulb moment” is required to transform unintentional external fermentation into a stable, ongoing source of extra calories.

Environmental stability

Fires require ongoing active effort to maintain, whereas fermentation is largely a passive process. Once started, an ongoing fermentation does not extinguish, and does not require tending or restarting, as fire does. Moreover, this environmental persistence offers more chances for social learning, further supporting the longevity of the practice across generations.

Stable food preservation - a caloric buffer

Because brain tissue is so energetically expensive, and is intolerant of reduced energy availability, organisms with larger brains are more susceptible to fluctuating availability of food (van Schaik). The evolution of increased adipose tissue in humans is a proposed adaptation to ameliorate this risk; fat provides an “internal buffer” for survival through lean times (Leonard et al., 2003; Navarette et al., 2011). External fermentation practices may have provided a secondary, “external buffer.” Fermentation can preserve food for *years.* Food spoilage is caused by microorganisms, and some of the best inhibitors of microorganisms are other microorganisms. Fermentation allows for the proliferation of non-harmful or beneficial strains which out-compete harmful strains; for example, by-products of fermentation include alcohol and acid, which inhibit further microbial growth, effectively preserving the food. There are other food storage techniques whose effective timescales are within that of fermentation, such as smoking, drying, freezing, and salting (notably, often used in combination with fermentation). However, compared to these other methods, we propose that fermentation may have been accomplishable more easily, across a wider range of environments, and by earlier, smaller-brained, less cognitively-complex ancestors.

Summary of explanatory power of the External Fermentation Hypothesis

Unlike other proposed dietary modifications, a transition to eating fermented foods does not require great leaps in cognitive ability. It does not require advanced planning, as hunting, particularly hunting in groups, would. It does not require the acquisition of a difficult technology, as in fire for cooking. And it can more directly explain, than tubers, meat, or cooking, how colon fermentation could be replaced through dietary changes.

Fermentation accounts for all the benefits that cooked food offers: softer food, higher caloric content, greater bioavailability of nutrients, and protection from pathogenic microorganisms. Fermentation solves several problems. It does not require special materials beyond a place to store food (a hollow, a cave, or a hole in the ground work). It does not require overcoming fear - there is a low barrier to entry. It can be stumbled upon rather than requiring planning and tool use. And it does not require, initially, long-term planning, focused attention, or sophisticated social coordination.

In all likelihood, for most of human history, it was nearly impossible to store food for any length of time *without* bacterial or fungal growth. Life-threatening illness is a risk of some food-borne microbes (e.g., *E. coli*, *salmonella*). Thus, it would have been necessary to either keep *all* microbial growth below potentially toxic levels (via e.g., drying, salting, smoking, or freezing), or encourage high levels of "good" microbial activity to out-compete the bad. The latter seems clearly easier.

Contemporary Human Fermentation Practices

We can look to current fermentation practices for insight into its role in our past. We have created a detailed list of examples that provide a sense of the widespread scope and impact of fermentation technology on the human diet worldwide (**Table 3**). Humans deliberately ferment foods of nearly every kind, including fruits, vegetables, grains, legumes, animals (muscle meat, organs, fat and bones), dairy, fish, and shellfish. Fermentation is practiced successfully in a diversity of climatic contexts, from tropical humid conditions to arctic environments. It is accomplished with a wide variety of microorganisms, including bacteria, filamentous fungi, and yeasts. Moreover, fermentation works on a range of timescales from hours to years; it can effectively act as a short-term flavor enhancer or a long-term storage technique.

We present this aggregation of examples as evidence supporting three points. First, given the incredible range of food types and environments that can lead to successful fermentation, it is plausible that this was also possible for the food types and environments of early human ancestors. Second, it seems that fermentation is ubiquitous across extant cultures and can be considered a human universal. This is consistent with fermentation having a very early emergence. Third, while cultural practices for fermenting food vary across the globe, it seems clear that humans in general have a taste for fermented food. This preference may be an evolved mechanism which emerged because an attraction to these flavors was adaptive in our shared past. Notably, many fermented foods listed in **Table 3** such as fish sauce, soy sauce, and vinegar, are *condiments* - i.e., substances added to other food items mainly for the purpose of improving palatability.

V. Testing the External Fermentation Hypothesis

Are preferences for fermented foods innate?

If our hypothesis is correct, then we might expect to find evolved innate preferences for beneficial fermentation products, or evolved innate aversions to dangerous byproducts of “off” fermentation. Interestingly, it appears that many of the most disparately-regarded foods - seen by some as prized delicacies, and by others as supremely unappetizing - are fermented: for example, thousand-year eggs, natto, and Limburger cheese. These preferences appear to be highly culturally-specific, which might be adaptive given the high cultural diversity of fermentation practices and the risks of consuming a ferment gone awry. The same flavors or odors which might signal “good” food in one culture could emanate from “off” ferments in another. Future research could address the extent to which preferences for fermented products are innate, cultural, or may be the product of gene-culture coevolution (Henrich and McElreath 2003). Are they more susceptible to cultural learning than other food preferences? Are they more sensitive to experience in a developmental critical period, and/or less flexible after this period closes? Are they heritable, either genetically or epigenetically (Dias et al. 2015)?

Do the risks of external fermentation outweigh the benefits?

A potential argument against our hypothesis concerns the potential for fermented foods to be colonized by pathogenic microbes. This must certainly have been a risk, but the more relevant question is, how did the risks and benefits of external fermentation compare to the risks and benefits of other potential solutions to the of balancing the metabolic budgetary increase associated with brain enlargement? Hunting, scavenging from large carnivores, and use of fire certainly carry their own risks; perhaps the risks of fermentation were more predictable and thus more reliably mitigable through individual and cultural learning. In the environments and time periods relevant for our hypothesis, what kind of situations might have caused a fermentation to go “off”? How easy would it have been for a hominid with a chimpanzee-sized brain to avoid these risks, either deliberately or via socially-learned canalization of practices? How often would “off” fermentation have catastrophic results versus temporary illness, and how would this have compared to injuries sustained during hunting, scavenging, or fire use? Potential answers to these questions might come from food microbiology investigations where fermentation products are studied under varying environmental conditions, or from field research with existing hunter-gatherer populations.

Is the human microbiome adapted for consuming fermented food?

Another opportunity to find evidence for or against the External Fermentation Hypothesis may come from examinations of the human microbiome. Interestingly, a comparative analysis with chimpanzees, bonobos, and gorillas indicates that the human microbiome has undergone accelerated deviation from the ancestral ape state, and now shows reduced diversity (Moeller et al., 2014), which may be consistent with increased reliance on external microbial communities. If early humans really offloaded internal fermentation to the external environment, we should expect to see changes in the internal microbial community, and potentially evolutionary cross-talk between internal and external fermenters of human food. Would internal species associated with a particular food become less abundant over time, while the external species proliferated? Would humans' internal flora adapt to now specialize in the post-fermentation product, perhaps with evolved adaptations for tolerating higher levels of fermentation by-products like acid or ethanol? Can we trace the co-evolution of gut flora and external fermentation flora as human populations have moved around the globe? Could phylogenetic analyses of human gut microbes provide a window onto the onset of fermentation practices in human evolution?

Conclusions

We have proposed that the acquisition of fermentation technology by early hominins - the external fermentation hypothesis - is a good candidate mechanism for human brain expansion and gut reduction. The offloading of gut fermentation into an external cultural practice may have been an important hominin innovation that laid out the metabolic conditions necessary for selection for brain expansion to take hold. While the potential importance of fermentation in the evolving human diet has recently been postulated (Dunn et al., 2020), and the reduction in human colon size has long been known (Milton, 1999), to our knowledge, the possibility that external fermentation served as the initial trigger in the human lineage for the expansion of brains and the reduction of the gut – specifically, the colon – has so far been unnoticed. We have discussed the adaptive benefits of this hypothesized scenario, its realistic plausibility, and its explanatory power relative to other hypotheses. We invite commentary and experimental tests from the broader academic community.

Tables and Figures

Table 1

Species	Latin name	Diet	Total % of energy	Citation
Cattle	*Bos taurus*	Ruminant herbivory	72%	(Siciliano-Jones and Murphy 1989)
Sheep	*Ovis aries*	Ruminant herbivory	84%	(Bergman et al. 1965; Gray et al. 1967; Faichney 1969)
Pony	*Equus ferus caballus*	Monogastric herbivory	30%	(Glinsky et al. 1976)
Rabbit	*Oryctolagus cuniculus*	Monogastric herbivory	32%	(Hoover and Heitmann 1972; Marty and Vernay 1984; Parker 1976)
Beaver	*Castor canadensis*	Monogastric herbivory	19%	(Hoover and Clarke 1972)
Porcupine	*Hystrix dorsata*	Monogastric herbivory	16%	(Johnson and McBee 1967)
Pig	*Sus scrofa*	Omnivory	36%	(Imoto and Namioka 1978; K. I. Kim, Benevenga, and Grummer 1978; Rérat et al. 1987)
Rat	*Rattus norvegicus*	Omnivory	5%	(M. G. Yang, Manoharan, and Mickelsen 1970)
Mantled howler monkey	*Alouatta palliata*	Monogastric herbivory	30%	(K. Milton and McBee 1983)
Gorilla	*Gorilla gorilla gorilla*	Monogastric herbivory	57%*	(Popovich et al. 1997)
Human	*Homo sapiens sapiens*	Omnivory	2-10%	(McNeil 1984; Livesey 1995; McBurney 1994)

Legend: Percentage of maintenance energy derived from the production of short-chained fatty acids (SCFAs) via gut fermentation. Information adapted chiefly from (Bergman 1990). Values for gorillas were estimated from diet composition and human colonic fermentation rates.

Table 2

	Heart	Kidney	Liver	Other Gut	Small Intestine	Colon	Brain
Expected	0.32	0.238	1.563	0.63	0.404	0.846	0.45
Actual	0.3	0.3	1.4	0.26	0.616	0.22	1.3
% change	-6.3%	26%	-10.4%	-58.1%	52.3%	-74.0%	188.9%

Legend: Expected masses in kg and percentage difference for major organs in a hypothetical 65 kg human based on great ape values (expected) and observed (actual) measurements in western humans. Data based on Aiello and Wheeler's (1995) compilation of data from Stahl (Stahl 1965), Stephan et al. (Stephan, Frahm, and Baron 1981), and Chivers and Hadlick (Chivers and Hladik 1980). Gastrointestinal tract weights were subdivided based on ratios from Milton (K. Milton 1986; Katharine Milton 1987; K. Milton and Demment 1988).

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Table 3. The Ubiquity of Fermentation Technology

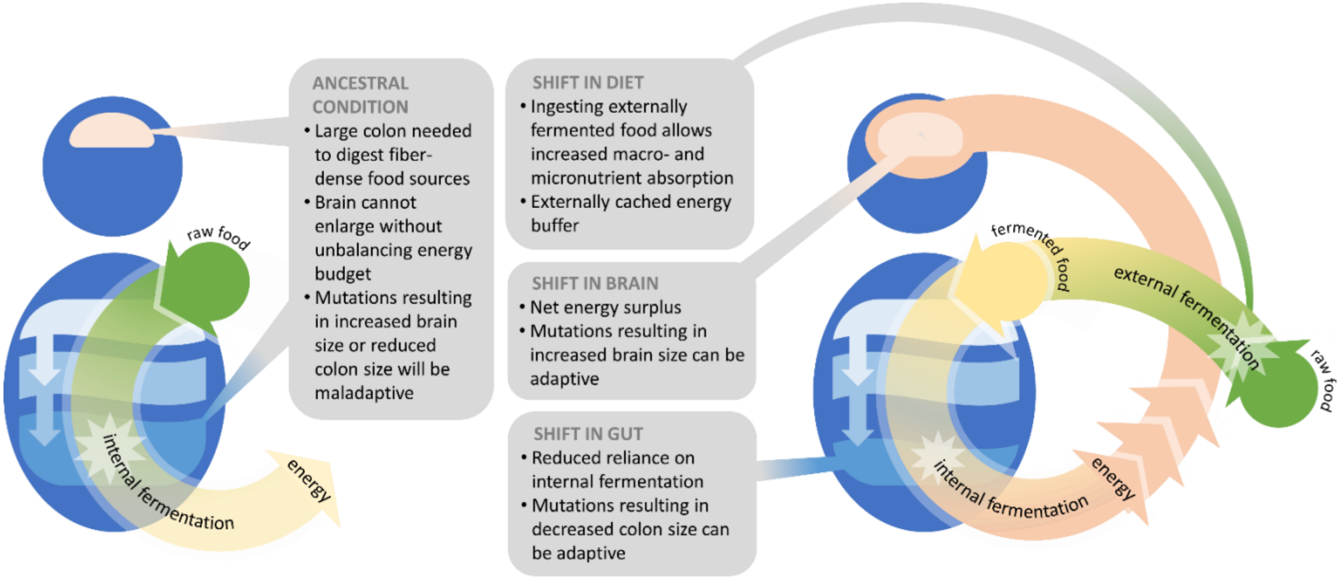
Food Name	Food Type	Fermentation Type	Origin	Incubation Time	Medium	Microflora	Source
kimchi	vegetable (many kinds)	acid	Asia	1 month	underground pots	Lactic acid bacteria (LAB)	Lee et al., 1986
sauerkraut	vegetable (leaves)	acid	Europe	weeks to months	salted and packed in jars with brine	Enterobactericiae, LAB, yeasts	Fleming et al., 1988; Stamer et al., 1971
puerh (aged black tea)	vegetable (leaves)	acid	Asia	weeks to months	dried and compressed	Aspergillus, Penicillium, Rhizopus, and Saccharomyces spp.	Wang et al., 2011; Lv et al., 2013
grape leaves	vegetable (leaves)	acid	Europe/Middle East	weeks to months	soaked	LAB	Basoglu et al., 1996; Kosar et al., 2007
sinki	vegetable (tuber)	acid	India, Nepal	weeks	dried and packed in jars	LAB	Tamang and Sarkar, 1993
gari	vegetable (tuber)	acid	West Africa	several days	grated and placed in knit bags in a trench	LAB, yeasts, fungi	Westby and Twiddy, 1992; Ray and Sivakumar, 2009
sapal	vegetable (tuber)	acid	Papua New Guinea	several days	grated, boiled, placed in covered jars	Leuconostoc, LAB, yeasts	Gubag et al., 1996
poi	vegetable (tuber)	acid	Hawaii	several days	steamed, ground, placed in barrels	LAB, Streptococcus	Gubag et al., 1996, Bilger and Young, 1935
tocosh	vegetable (tuber)	acid	South America	months	water immersion	LAB	Werge, 1979; Jimenez et al., 2018
fufu	vegetable (tuber)	acid	West Africa	several weeks	water immersion	LAB	Ray and Sivakumar, 2009; Oyedeji et al., 2013
nattō	vegetable (legume)	alkaline	Japan	1 day	steamed, water immersion	Bacillus subtilis natto	Saono et al., 1986; Murooka et al., 2008
kinema	vegetable (legume)	alkaline	Nepal	1-3 days	soaked, boiled, wrapped	Bacillus, yeasts	Odunfa 1981, Sarkar and Tamang, 1994, Sarkar et al., 1994
idli	vegetable (legume) + grain	acid	India	20 h	ground, mixed with water	Leuconostoc mesenteroides, yeasts	Padhye and Salunkhe 1978;
tempeh	vegetable (legume)	alkaline	Indonesia	1-2 days	soaked, boiled, wrapped	Rhizopus fungi, Bacillus	Steinkraus et al., 1995; Nout and Kiers 2005
soy sauce	vegetable (legume)	alkaline + acid	Asia	1 year	soaked and boiled, then brined	Aspergillus, then LAB and yeasts	Yong and Wood, 1974; Chou and Ling 1999
oncom	vegetable (legume)	alkaline	Indonesia	days to years	soaked, boiled, packed in layers	Rhizopus, Mucor, Neurospora spp. fungi	Sastraatmadja et al., 2002
dawadawa	vegetable (legume)	alkaline	West Africa	days	boiling, pounding, packed in pots	LAB	Dakwa et al., 2005; Deshpande 2000
coffee	vegetable (seed)	acid	Africa	~ 20 hours	pulped and placed in tanks with water	LAB, Bacillus, yeasts and fungi	Avallone et al., 2001
cocoa	vegetable (seed)	acid	Central America	~ 5 days	placed in heaps or depressions with drainage	LAB, Bacillus, yeasts and fungi	Schwan and Wheals, 2014; Schwan and Fleet, 2014
pulque	sap	alcohol	Mexico	12-24h	pulp is placed in closed containers	Zymomas mobilus, LAB, yeasts, proteobacteria	Escalante et al., 2008; Escalante et al, 2011; Valadez-Blanco et al., 2012
mead	honey	alcohol	Africa, Asia, Europe	months to years	diluted, placed in sunlight in open container	yeasts	Iglesias et al., 2014; McGovern et al., 2004; Ramalhosa et al., 2011; Sroka and Tuszynski, 2007; Teramoto et al., 2005
fruit wines	fruit	alcohol	Widespread	days to weeks	placed in sealed containers	yeasts	Battcock et al., 1998
vinegar	fruit or cereals (rice)	acid	Widespread	months	after alcohol fermentation, placed in sealed containers	Acetic acid bacteria, LAB	Solieri and Giudici, 2009; Vegas et al., 2010; Wu et al., 2012
dried sausage	meat	acid	Europe	weeks to months	chopped, placed in casings (some), hung in cool areas	LAB, yeasts, molds	Campbell-Platt, 1995; Danilovic and Savic, 2017; Feiner 2016
country ham	meat	acid	Asia, Europe	several months	salted, dried over time, hot or cold-smoked	LAB, Micrococcus, Staphylococcus, fungi	Bamforth 2008; Campbell-Platt, 1995
satchu	meat	acid	Himalayas	weeks	cut into strips and hung indoors to dry	LAB, Bacillus, Micrococcaceae, yeasts, molds	Rai et al., 2010; Sharma and Sarkar 2015
pemmican	meat	acid	North America	days	dried, chopped, and sealed with fat	*	Campbell-Platt, 1995
twini-digla	internal organs	*	Africa (Sudan)	*	sun- dried, ground, mixed with potash and pressed	*	Campbell-Platt,1995; Dirar 1992
dodery	animal bones	acid	Africa (Sudan)	1-2 weeks	soaked in water, then ground and mixed with potash	Bacillus, Staphylococcus, Micrococcus, LAB, yeasts, proteobacteria	Campbell-Platt,1995; Dirar 1992; Elnabi, 2008
tiroi	shellfish	acid	Oceania	weeks to months	boiled, packed in jars	*	Hudson et al., 2001
kina	shellfish	alkaline	Oceania	weeks to months	buried underground or water immersion	LAB	Hudson et al., 2001
hákarl	shark	alkaline	Iceland	months	packed underground, then hung outdoors	Moraxella, Acinetobacter	Skara et al., 2015; Jonsdottir and Leifsdottir, 2009
ngari	fish	acid	India, Himalayas	months to a year	dried and packed in jars	LAB, Bacillus, Micrococcus, yeasts	Thapa et al., 2004; Jeyaram 2009
surströmming	fish	acid	Europe	months to a year	immersed in brine, packed in barrels	LAB, Haloanaerobium	Skara et al., 2015, Kobayashi et al., 2000
nam-pla	fish	acid	Southeast Asia	18 months	salted and packed in jars	Bacillus, Pseudomonas, Micrococcus, Staphylococcus, Halobacterium	Rattagool et al., 1985; Lopetcharat et al., 2001; Park et al., 2001, McIver et al., 1982
ale	cereal grain	alcohol	Europe	weeeks to months	soaked in water and boiled, then stored in kegs	Yeasts (Saccharomyces spp.)	Lodolo et al., 2008
sake	cereal grain	alcohol	Japan	weeks	soaked, steamed, and left in open containers	Yeast (Saccharomyces) and molds	Uno et al., 2009; Yoshizawa 1999
makgeolli	cereal grain	alcohol	East Asia	1-2 weeks	steamed, stored in containers with inoculated rice starter	Yeast, LAB, fungi	Nile 2015; Kang et al., 2014
chicha	cereal grain	alcohol	Central America	1 week	chewed or malted (soaked,germinated), heated with water	LAB	Cutler and Cardenas, 1947, Elizaquivel et al., 2015
injera	cereal grain	acid	East Africa	several days	ground, mixed with water	LAB, Bacillus, Enterobacteriaceae, yeasts	Fischer et al., 2014; Yetneberk et al., 2004; Stewart and Getachew 1962
kenkey	cereal grain	acid	West Africa	several days	soaked, ground, packed in troughs	LAB, yeasts	Halm et al., 1993
pozol	cereal grain	acid	Central America	hours to days	cooked with lime, ground, wrapped in leaves	LAB, mesophilic bacteria, enterobacteria, molds, yeasts	Wacher et al., 2000; Omar and Ampe, 2000
kumis	dairy	alcohol	Central Asia, S. America	days	loosely covered, occasionally stirred	LAB, yeasts	Kabak and Dobson, 2011; Chaves-Lopez et al., 2011
yogurt	dairy	acid	Middle East	weeks	loosely covered, occasionally stirred	LAB	Innocente et al., 2016; Robinson et al., 2002
cheese	dairy	acid	Europe, Central Asia, N. Africa	days to years	heated, strained, sealed	LAB, mesophilic bacteria, yeasts, molds	Seifu, 2013; Şengül 2006

* Unavailable information

Where possible, descriptions are based on non-commercial/non-industrialized methods

Location origin descriptions are more or less geographically specific depending on available information

Figure 1



ANCESTRAL CONDITION

- Large colon needed to digest fiber-dense food sources
- Brain cannot enlarge without unbalancing energy budget
- Mutations resulting in increased brain size or reduced colon size will be maladaptive

SHIFT IN DIET

- Ingesting externally fermented food allows increased macro- and micronutrient absorption
- Externally cached energy buffer

SHIFT IN BRAIN

- Net energy surplus
- Mutations resulting in increased brain size can be adaptive

SHIFT IN GUT

- Reduced reliance on internal fermentation
- Mutations resulting in decreased colon size can be adaptive

Figure 1 Legend: The External Fermentation Hypothesis

Figure 2

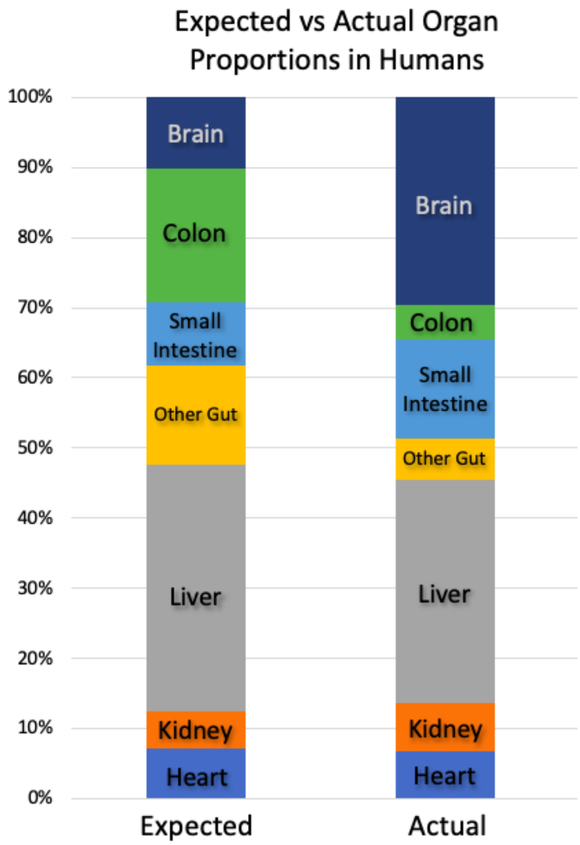


Figure 2 Legend: Proportions of major organs in a hypothetical 65 kg modern Western human using data from Table 1. “Expected” represents the ratio of organ masses expected if humans had proportions in line with other great apes. “Actual” represents an estimation of the ratios in a typical modern Western human.

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