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Dopaminergic systems expansion and the advent of *Homo erectus*

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A B S T R A C T

It is well accepted that a grade shift occurred in hominin evolution approximately 1.9 million years ago with the appearance of *Homo erectus*. With the challenges of complete terrestrial life, new cognitive abilities were selected for that allowed this species to thrive for the next million and a half years. It has also long been recognized that there was a change in diet with the advent of *Homo erectus*, that is, a greater reliance on meat. However, the relationship between additional meat and the cognitive abilities of *Homo erectus* has mostly remained unclear. The present paper proposes that an increase in dietary meat protein and fats may have led to an increase in dopamine and dopaminergic systems, a critical chemical neurotransmitter in the brain. This purported change in dopaminergic systems may have played a key role in many of the traits and abilities exhibited by *Homo erectus* at that time, including increases in body and brain size, dispersion, and a greater aptitude for spatial and social cognitions.

1. Introduction

Although the genus *Homo* semantically begins with the origins of habilines about 2.5 million years ago (Ma), there is a general consensus that a major grade shift occurred in hominin evolution beginning with *Homo erectus* about 1.9 Ma. The brain size of *Homo erectus*, about 900 cc to 1,000 cc, approaches the lower limits of modern *Homo sapiens*, about 1,000 cc to 2,000 cc (average = 1,350 cc). In addition, although the habilines are associated with the first stone tools, the stone tools of *Homo erectus* are thought to be more sophisticated technically, cognitively, and aesthetically (e.g., Wynn, 1989, 2002). Their bifacial and symmetrical design was to persist for the next million years and more. More critical, especially in terms of the evolution of modern cognitive abilities, may have been the full transition of *Homo erectus* to life on the ground instead of a life in trees. Coolidge and Wynn (2009) proposed that modern human cognitive abilities appear to have evolved in two major leaps (Coolidge and Wynn, 2006) with the first being the advent of *Homo erectus*, which is marked behaviorally by an expansion of territories, responses to ecosystem change, increased sociality, and increases in spatial cognition (e.g., Antón, 2003).

Explanations for Homo's increase in relative brain size and abilities have focused on the energetic costs of large brains (Pontzer, 2012). There is a direct relationship between number of neurons and caloric requirements (Fonseco-Azevedo and Herculano-Houzel, 2012), a link that could possibly be related to protein calorie nutrition, as a lack of dietary protein has been shown to lead to a decrease in brain weight and in the protein content of the brain (Lucas and Campbell, 2000). Thus, an evolutionary increase in brain size must have been accompanied by an increase in accessible calories, either by a change in dietary quality, an increase in time spent foraging, or a change in the way calories are stored. In 1995 Aiello and Wheeler (1995) made a strong case for the “expensive tissue hypothesis,” arguing that early *Homo* ‘paid for’ the increase in neurons via a dietary shift to meat, which is a higher quality food (more concentrated calories) than the plant foods that form the majority of the diet for most apes, including early hominins. They further argued that the dietary shift would have been accompanied by a decrease in the length of the gut; because the gut is also an “expensive tissue,” it would be difficult for hominin physiology to support both. Digesting meat requires shorter guts than digesting plants, and thus a reduction in gut length would naturally accompany the dietary shift or, a stronger version of the argument, require the dietary shift. The modern human gut also appears to be adapted to cooked foods (Wrangham

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et al., 1999; Wrangham, 2009). Wrangham argues that in the absence of cooking, the sheer amount of chewing time required to process meat would have limited its usefulness as a high-quality food. He argued that *Homo erectus* adopted fire for cooking; cooking both makes meat easier to chew and easier to digest. Earlier *Homo* processed meat by pounding (there is extensive evidence for pounding tools at the 1.75 Ma site of FLK (Mora and de la Torre, 2005)). Complicating the picture even further is the possible role of body fat, which is higher in humans than apes, as a buffer against dietary stress, and thus a possible factor in increased brain size (Anton and Snodgrass, 2012; Anton et al., 2014; Roberts and Thorpe, 2014). What seems clear is that the 30% increase in brain size over *Australopithecus* required some kind of dietary/adaptive shift. The contemporaneous archaeological evidence for butchery makes a strong circumstantial case that this dietary shift included meat.

This increase in consumption of meat also provided the precursors necessary to significantly increase dopamine, a chemical neurotransmitter in the brain, and when combined with ecological pressures could have led to an expansion of dopaminergic systems. Previc (1999), appears to be the first to propose that this change in the hominin diet was *the* critical precursor to the expansion of the dopaminergic system that may have led to a revolutionary cascade of changes in later *Homo* cognition. Evolution of the dopamine system has been sporadic since mammals first evolved, and may have also been an important part of the evolution of the *Homo* genus (Previc, 2009). Dopaminergic systems have been shown to be important to essential modern human behaviors, particularly motor movements and cognition. In particular, it systemically and neurologically allows for thermoregulation, novelty seeking, sociality, handedness, increases in REM sleep, goal achievement and reward, behaviors that are thought to have arisen or increased during the grade shift that led to *Homo erectus* (Fig. 1).

Some aspects of the dopaminergic system, as well as complex traits that arise from such systems are only possessed by *Homo sapiens.* When comparing the human genome to the chimpanzees, the D5 dopamine receptor in humans has an unusually large number of DNA sequence changes, pointing to adaptive evolution (e.g., Somel et al., 2013). Given D5 receptors co-localization with known dopaminergic pathways, it is thought to play an active role in dopaminergic neurotransmission (e.g., Khan et al., 2000). It has also been amply demonstrated that dopamine is found in high concentrations in the dorsal lateral prefrontal cortices and the anterior cingulate cortices. There is substantial empirical evidence that these regions play critical roles in working memory and its executive functions, attention, and goal-directed behavior, traits long thought to contribute to human intelligence. Furthermore, these cognitive processes are known to serve a foundational basis for higher human reasoning, such as fluid intelligence (the ability to solve novel problems).

2. Meat eating and Plio-Pleistocene *Homo*

Sometime about 1.35 Ma, a group of *Homo erectus* butchered a number of large mammals at a site at Olduvai Gorge, including an elephant, a hippopotamus, a rhinoceros, a Sivatherium (related to modern giraffe), and two Pelorovis (related to Cape Buffalo). There is no evidence that the hominins killed the animals, and scavenging was the likely means by which they accessed the carcasses. Remains at the site (BK) also include bones from small and medium sized mammals, which may have been hunted. Percussion and cut marks on the bones confirm extensive butchery of all of the remains. Clearly, meat had come to be an important part of the *Homo erectus* diet (Dominguez-Rodrigo et al., 2014).

Homo erectus was not the first hominin to butcher animals for meat. 400,000 years earlier another group of hominins butchered animals at Olduvai Gorge. The site at FLK has famously yielded evidence for butchery of small to medium sized mammals, with an especially distinct focus on extracting marrow from long bones (Bunn and Kroll, 1986; Bunn et al., 2010; Dominguez-Rodrigo et al., 2011). Here the taxon of the butchers is not clear; the one fossil hominin recovered from the site was the skull of a *Paranthropus,* but many consider it to have been not the butcher, but one of the butchered. An early form of *Homo, Homo habilis,* occurs in deposits of the same age at Olduvai, and thus was the presumed butcher at FLK (Wood, 2014). *Homo habilis* used sharp flakes struck from lava cores to butcher meat from the scavenged carcasses, and the cores themselves to break open the long bones for marrow.

Stone tools such as cores, flakes, and hammer stones allow paleoanthropologists to trace presumed butchery even further back in time than the examples from Olduvai Gorge. Recently archaeologists have pushed back the oldest known tools to the 3.3 million-year-old site of Lomekwi 3 in northern Kenya (Harmand et al., 2015). There was no butchered bone at Lomekwi, but the slightly older site of Dikika in Ethiopia has yielded possibly cut marked bone, but no artifacts (McPherron et al., 2010). The 2.6 million-year-old site of Gona (Semaw et al., 2003), and the 2.3 million-year-old site of Lokalalei (Roche et al., 2003; Delagnes and Roche, 2005) have yielded both stone tools and cut marked bone. It thus appears as if butchery was a component of hominin adaptations prior to the first appearance of *Homo erectus* 1.8 Ma (Anton and Snodgrass, 2012; Anton et al., 2014). The hominin evident at Dikika was *Australopithecus afarensis,* and the nearest time/space associated hominin for Lomekwi was *Kenyanthropus platyops*, another smaller brained form (Harmand et al., 2015). Thus, *Australopithecus* grade hominins were the first to develop knapped stone technology, and also the first to make a shift toward reliance on meat from scavenged carcasses.

Brain expansion is the primary anatomical criterion that distinguishes the genus *Homo* from earlier hominins such as *Australopithecus*, yet the picture of when and where early *Homo* evolved is far from clear. Fossil evidence indicates that there were at least three different varieties of early Pleistocene *Homo* living in East Africa between 2.5 and 1.5 Ma. The two seemingly earlier varieties, assigned by some to *Homo habilis* and *Homo rudolfensis*, had brain sizes that were on average 30% greater than pene-contemporaneous *Australopithecus* and *Paranthropus*. These two *Homos* differ from one another in regard to facial characteristics and body size (Anton et al., 2014). However, because the sample sizes are so small, other paleoanthropologists take a more cautious approach to this variability and lump all of these remains into a single, polytypic taxon (Anton and Snodgrass, 2012). *Homo erectus* itself is often divided into an African variety, *Homo ergaster* and an Asian variety, *Homo erectus sensu stricto* The 1.85 Ma site at Dmanisi in the Caucasus Mountains complicates taxonomy even more, with five quite variable individuals, some of which are *erectus*-like and others more similar to *habilis* (Anton et al., 2014). While all of the above had larger brains than *Australopithecus*, it is not clear which were responsible for the butchery at Gona and FLK. For purposes of this discussion, then, we will lump all of them together into a single evolutionary grade of early Pleistocene, large brained, hominins — early *Homo sensu lato*.

3. How meat could have led to dopamine expansion

The brain is known as one of the most expensive tissues metabolically, as evidenced by the fact that the human brain makes up only 2% of its mass, yet it consumes approximately 20%–25% of its energy expenditure. Given that larger brains require more