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Tool use, language & improved hunting/diet as the chief influences on the reorganization & growth of the brain between *Australopithecus* & *Homo*

Abstract

A relatively large brain is a defining characteristic of humans and its origins can be traced to ancient hominid ancestors who lived ~5 mya. From *Australopithecus* into *Homo*, adaptations such as tool use, improved diet and language have initiated rapid brain growth and significant reorganization of the cerebral cortex including the frontal and temporal lobes. This paper explores the large mosaic of mechanisms that spurred brain evolution. Evidence from preserved tissue is not to be found; therefore evolution of the brain must be studied from both direct and indirect evidence based on endocasts, statistical models and deduction.

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Mosaic Theory of Brain Evolution

Tables & Figures

Table 1: Body, Brain Sizes & Encephalization Quotient (EQ) Values

Species	Time Lived	Body Size	Brain Size	Average	Martin EQ
Pan troglodytes	Present	46 kg	275 – 500 cm^3	375 cm^3	2.38
A. afarensis	3.5 - 3.0 mya	37 kg	342-540 cm^3	434 cm^3	1.87
A. africanus	3.0 - 2.0 mya	35.5 kg	424-508 cm^3	448 cm^3	2.16
H. hablis	2.0 - 1.8 mya	34.3 kg	503-661 cm^3	601 cm^3	3.38
H. rudolfensis	2.0 - 1.8 mya	45.6 kg	736 cm^3	736 cm^3	
H. erectus	1.8 - 0.5 mya	57.8 kg	850-1100 cm^3	975 cm^3	3.34
H. sapiens	0.5 mya - Present	63.5 kg	1125 – 1390 cm^3	1257 cm^3	6.28

Sources: Martin 1984 78 & Halloway et al. 2009, 7

Table 2: Anatomical Terms & Summaries

Foramen Magnum – hole in the center of the skull where the spinal cord (vertebrae) attaches. If forward positioned (center of the skull), this indicates bipedalism and is the main anatomical evidence of locomotion adaptations between humans and other great apes.

Cerebral Cortex – the mammalian section of the brain that constitutes almost 90% of the total size. This is the advancing layer of gray and white matter in the brain that is responsible for all higher-level cognition. As humans have evolved there has been an increase in the cerebral cortex while a simultaneous decrease in the reptilian part of the brain. The cerebral cortex is divided into 4 major lobes (Frontal, Temporal, Parietal, Occipital) and the left and right hemispheres.

Neocortex – the subdivision of the cerebral cortex that makes up almost 90% of its total size. This area is shown to be larger in primates relative to social group size, with humans having the largest neocortex size. This is indicative of the complex social culture that humans now employ. The neocortex is responsible for language production, comprehension, and voluntary control of skeletal muscle and also thought, strategy and spatial planning.

Frontal Lobe – became enlarged during the first cerebral reorganization (3.2 mya) and its functions are responsible for higher cognition. The frontal lobe contains the premotor and primary motor cortexes, which are involved in executive control over skeletal muscles and thus precise movement. Executive control was required to manipulate the legs and feet for bipedal locomotion and also manipulate the hand for tool use and construction. The frontal lobe is also responsible for thought and the formation of mental images, something essential for tool creation. Broca's area is also contained majorly on the left frontal lobe through lateralization and is responsible for the formation of speech (see lateralization/handedness).

Broca's Area – located on the frontal lobe and separated from the temporal lobe by the central sulcus, this area is responsible for the formation of speech. This area was developed simultaneously as the rest of the cerebral cortex during *Australopithecus* and is widely influential in creating the rudiments of speech that were used in group cooperation for hunting and the transfer of tool making knowledge. Connects to Wernicke's area through the accurate fascillious.

Temporal Lobe – contains the centers for language and the primary auditory complex, which is responsible for comprehending and translating electrical signals sent from the cochlea in the ear. Development most likely began in *Australopithecus*, but is physically evident on endocasts in the transitional species *H. hablis/rudolfensis*.

Wernicke's Area – this area of the brain is responsible for the comprehension of speech from signal information. Interacts with the primary auditory cortex in the conversion of electrical impulses from the ear into comprehendible language. Connected to Broca's area through the accurate fascillous in the neocortex.

Acurate Fascillous – this bundle of neurons connects both Broca and Wernicke's areas through the neocortex. This helps facilitate the hearing, understanding, and response in language. Its evolutionary origin is impossible to determine

Lunate Sulcus - a landmark of the brain that is imprinted on the back of skulls and endocasts that is used to predict human-like organization of the cerebral cortex. While highly contested, it was recently proved *Australopithecus* had a human-like cerebral cortex, which refuted all previous held ideas that brain size increase predated cerebral reorganization.

Anterior Fontanel – fontanel located between the parietal and temporal bones that allows overlapping during delivery. Fontanels developed in response to bipedalism, as the birth canal was restricted at the same time as larger brains began to form. Fontanels allow the plates of the skull to slide over each other like tectonic plates and allow the birthing of larger brained offspring

Figure 1: Brain Structure

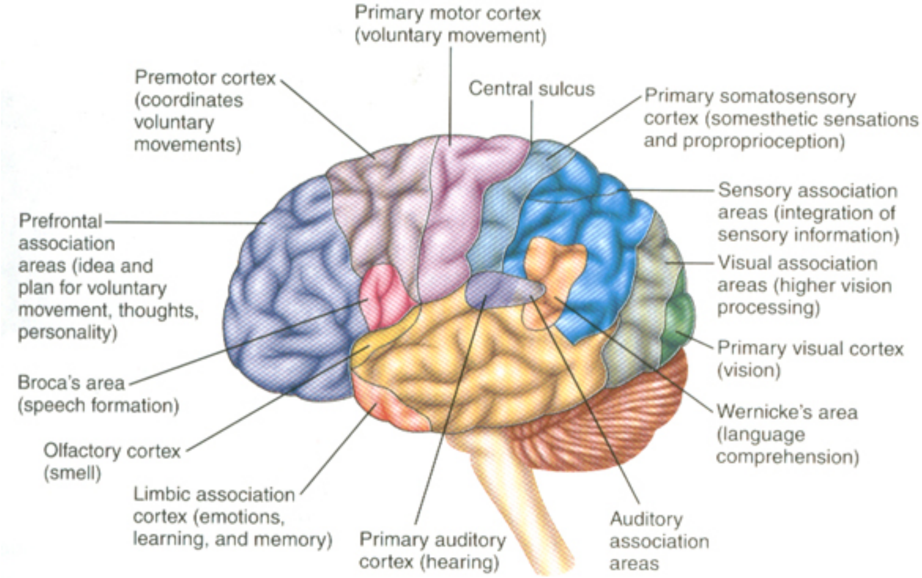


Figure 1: http://www.liquidarea.com/wp-content/uploads/2009/10/broca_area.jpg

Figure 2: Comparative Brain Anatomy

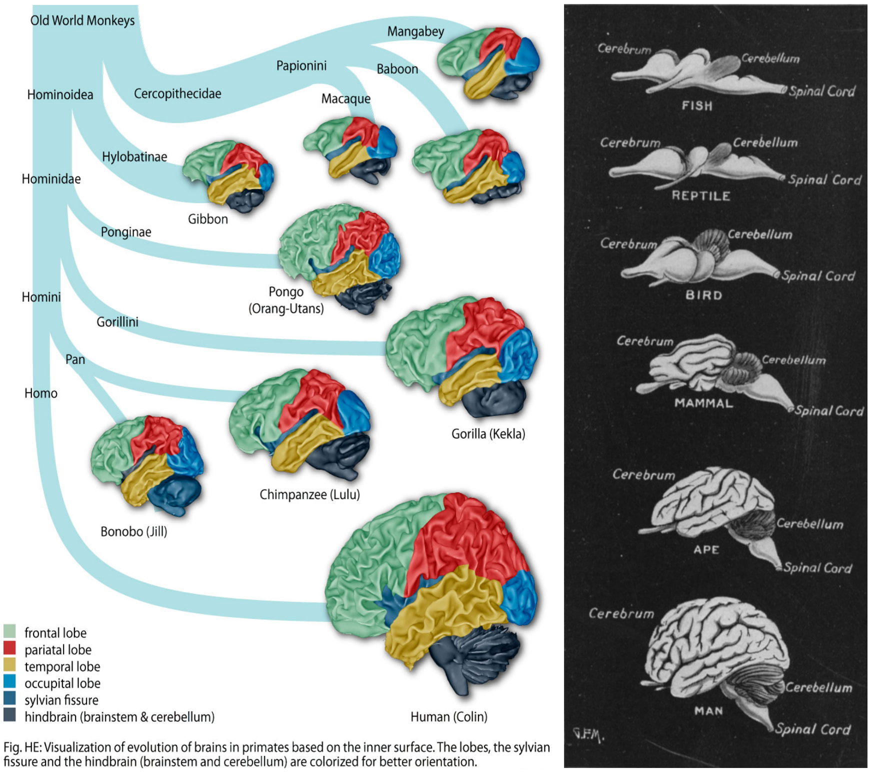
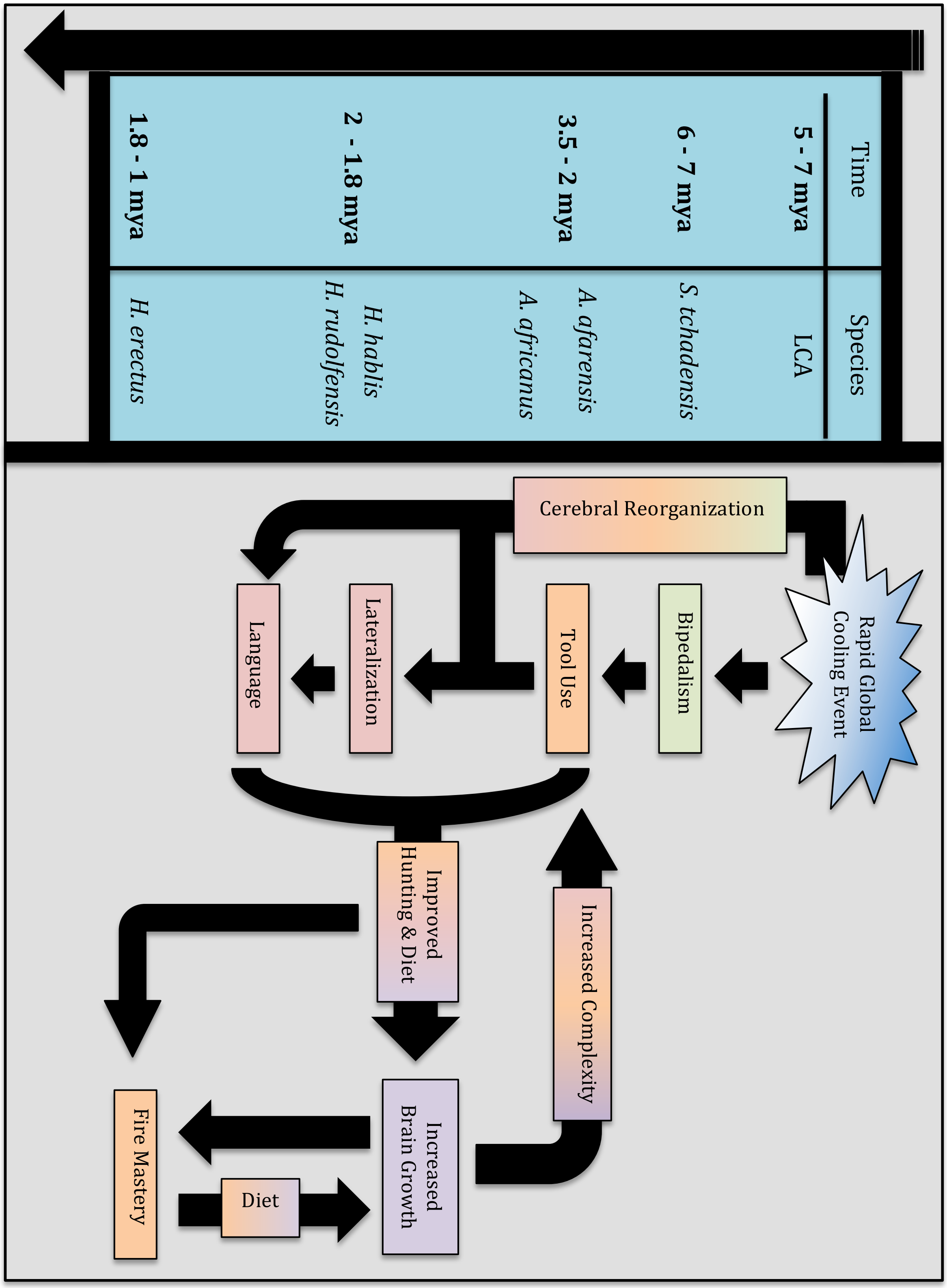


Fig. HE: Visualization of evolution of brains in primates based on the inner surface. The lobes, the sylvian fissure and the hindbrain (brainstem and cerebellum) are colorized for better orientation.

Figure 2: http://dbm.neuro.uni-jena.de/research/evolution-and-development/

Figure 3: Positive Feedback Loop for Mosaic Evolution



Time	Species
5 - 7 mya	LCA
6 - 7 mya	S. tchadensis
3.5 - 2 mya	A. afarensis A. africanus
2 - 1.8 mya	H. hablis H. rudolfensis
1.8 - 1 mya	H. erectus

Introduction

Unique from the rest of the animal kingdom, *Homo sapiens* have the most complex and largest relative brain on the planet. This however, was not always the case and there are many morphological changes that occurred from early hominid ancestors to make this possible. Between *Australopithecus* and *Homo erectus* the human brain was significantly enlarged and reorganized. Over this evolutionary period there was a trend towards increasing relative brain size, executive control over voluntary movement and the development of language. Coupled with increased use and complexity of tools, early hominid ancestors improved hunting techniques and managed fire, which ultimately led to an increase in diet, and brain growth through improved nutrition.

Overall, the evolutionary tract of the brain cannot be understood as a simple linear process. It is multifaceted and extremely convoluted. There are many different hominids discovered, however for the sake of scope each will be referred to on a macro level. This accounts for nuances between fossils by accepting extreme levels of sexual dimorphism and variation present at the time. A mosaic theory of evolution is examined in order to holistically understand the delicate interplay of ecology, behavior, biology, morphology and genetics that all spurred human brain growth and cognitive development. Since direct fossil evidence is spotty and not initially available, the evolution of the brain between *Australopithecus* and *Homo erectus* must be understood through the context of environment and anatomical development.

Climate Shift Catalyst

Adaptations usually occur in response to an ecological stimulus. Beginning around 16 mya the Earth began to experience a global cooling trend (Zachos et al. 2001, 686). This cooling was not steady, and came in flares like the one that occurred 7-9 million years ago at the Miocene-Pliocene boundary (Kennett in Elton 2008, 382). At this time early primate ancestors had to either adapt or face extinction. A drastic global cooling between 10-20° F swept across the globe and the advancing arctic glaciation created thousands of miles of open grasslands. Following this was multiple waves of extinction and species radiation (California Academy of Sciences 2009). The change was measured through ocean core analysis and contextual understanding of flora (pollen & dendrochronology) and fauna contemporary with early primates (Zachos et al. 2001, 687-9). By understanding the context in which the climate change affected the rest of the animal kingdom, the adaptations of primates slowly emerge.

The global cooling trend had dire consequences for the normal habitat of primates as the dense North African jungle began to retreat and was replaced by open savannah in a process called aridification (Elton 2008, 377-9). Coincidently, North Africa is where a lot of the earlier hominid fossils are found. The loss of jungle forced normally arboreal primates out of the secure canopy and onto the more bare grasslands and woodlands. This exposed them to new predators and ecological challenges which initiated a chain of evolutionary adaptions that culminated in increased cognition and intelligence.

Bipedalism

In order to conquer these new environmental problems bipedalism developed, which was a morphological change that allowed early hominids to walk up right on two feet. This freed the hands for tool use and grasping. A morphological change is any physical alteration in a species due to the reciprocal effects of ecology and genes. Bipedalism started a ripple effect, which caused other anatomical changes in the hands, legs and pelvis as a result (Wheeler 1991, 107-8). Bipedalism was fully developed in *Australopithecus* but it is difficult to trace direct ancestry due to many competing origin theories and species.

A limitation of trying to understand early brain evolution is that the fossil record of Africa for the Late Miocene is very poor, with only a few species recovered. Attempts to define one true habitat and species is misleading as early hominids occupied a large array of habitats and biomes around Africa (Elton 2008, 381). This limits the sample size, for which undiscovered species would mostly likely shed new developments on brain growth (Jablonski & Kelly in Elton 2008, 378). All of the early hominid samples recovered are suitable candidates for the last common ancestor (LCA), which is why it easier to view this process as macroevolution instead of microevolution.

An example of one of the few earliest bipedal species recovered in the archaeological record is *Sahelanthropus tchadensis* from Chad, which dates between 6-7 mya. The forward position of the foramen magnum provides evidence of bipedalism (Brunet et al. 2002, 146 & 2005, 752). This species is suggested to be a viable example of the last common ancestor (LCA), a hypothetical species from which hominids diverged from chimpanzees about 6-8 mya. This coincides with the global cooling trend and a transformation of jungles into grasslands (Steiper & Young 2006, 384-5). These species of hominid were not shown to have a large brain, however cerebral reorganization most likely occurred to compensate for the morphological changes of the body. Being able to walk on two feet gave early hominids an evolutionary advantage. As such they were able to use tools and communication in order to obtain access to better food, the positive feedback loop for brain development began (Figure 3). A positive feedback loop is a complex chain of reciprocal interactions and causations that amplifies the impact and effect of the original antagonist.

It must be noted however, that the development of bipedalism and larger, complex brains are two separate evolutionary processes. While the processes intersect in some aspects, bipedalism is important because it freed the hands for tool use and caused significant reorganization of the cerebral cortex in the brain. This reorganization occurred before significant brain growth and was due to the fact that the body had to adapt to the precise movements of new adaptions such as opposable thumbs and the coordination of walking upright on two feet. Other than opening the door for the mosaic of influences, bipedalism didn’t directly cause brain growth or intelligence. However, by 3.2 mya the earliest *Australopithecus* hominids were not only walking on two feet, but also displaying larger relative brains and increased tool use.

Australopithecus

The two major species of gracile *Australopithecus* that have been found are *Australopithecus afarensis* and *africanus*. These two species are occasionally combined into simply *Australopithecus* for the purposes of this argument based on being characteristically similar and accounting for human-like levels of sexual dimorphism present at the time (Reno et al. 2003, 9404). Gracile *Australopithecus* is known to be the species most anatomically related to genus *Homo* (Strait & Grine 1999, 1210). Much of the assumptions made about brain evolution stem from the idea that contemporary phylogenies accurately represent the evolutionary tract of human beings (Harvey & Pagel 1991, 36). There are more species and many yet to be discovered but analysis of these lies outside the scope of the argument.

Since evolution and adaptation takes many generations and millions of years to produce notable effects, it wasn't until 3.6 mya that the first *Australopithecus afarensis* began to appear in the fossil record. The most notable among these being the mostly complete skeleton of Lucy found in Ethiopia (Johanson, et al 1982, 37). *Australopithecus* while still displaying many ape-like characteristics also featured a forward positioned foramen magnum and modified hand (Kimbel et al. 2004, 59-71). The foramen magnum dictates bipedal locomotion while the hand indicates that there was increased tool use affecting the morphological development of the body. More species of *Australopithecus* such as *africanus* were found and noted to be also gracile and small, with brains, measuring about a third of what an average human has today (Table 1). Despite having a small absolute brain compared to later ancestors, *Australopithecus* had a larger relative brain than chimpanzees, even if it was only marginal. During this time, there was an increased consumption of meats and weather by scavenging or small hunting and gathering of plants (Wrangham 2009, 51). Some researchers suggest scavenging was not an option however, because that requires food to be cooked, and fire wasn't controlled until much later (Klein 1999, 186).

Regardless, diet improved and a relatively larger brain allowed for the construction of the first rudimentary stone tools and biological items that resemble ones currently employed by chimpanzees (McGrew 1992, 311). Based on the morphology of *Australopithecus* and the multitude of likenesses with chimpanzees, it can be inferred they were behaviorally similar. Chimpanzees also until very recently occupied many similar habitats alongside humans until being confined in modern times (McBrearty & Jablonski in Elton 2008, 382). There is no indication of linguistic ability in *Australopithecus* however there may have been communication through gesture and grunting comparable to modern chimpanzees (De Heinzelin 1999, 625). *Australopithecus* does display a human-like brain and increased frontal lobe that suggests cerebral reorganization occurred (Falk et al 2012, 1-2). Despite the small advances of *Australopithecus*, a relatively larger brain and bipedalism provided an evolutionary advantage that increased survivability in a time of climate change. Around 2.0 mya, *Australopithecus* was replaced by various transitional species.

First Cerebral Reorganization – Frontal Lobe

The best means to examine hominid cerebral reorganization and brain growth is through endocasts and contextual analysis. Fossil evidence and preserved tissue is very rare to come by as all tissue evidence decomposes shortly after death. However, endocasts model the interior of the skull and display external structures (petalias) of the brain imprinted on the cranium upon fossilization (Holloway 2009, 353). There are three kinds of endocasts. The first, natural, is formed by sediments compacted in the skull that crystallizing over time such as the Taung Child endocast (Dart 1925, 197). The second is a man-made endocast using latex or silicon rubber (Holloway et al. 2009, 2-4). The last, most accurate model comes from laser scanning the inside of the skull to create a virtual model that picks up on the tiniest imperfections (Falk & Clarke 2007, 529-30). There is estimated to only be about one endocasts for every 235,000 years of human evolution (Halloway et al 2009, 6). While endocasts reveal a lot of evidence they also lack internal structures, which are not imprinted upon the cranium after death. Despite limitations, endocasts provide the best available direct physical evidence needed in order to study human brain evolution.

Finding their natural habitat shrinking due to climate change, early hominids adopted walking on two feet instead of retreating south in Africa. In order for locomotion to adjust many morphological changes in the brain, pelvis, legs, hands and feet needed to occur. To manipulate limbs in a new manner required rewiring of the brain to allow executive control of skeletal muscle. The region of the brain responsible for this is the cerebral cortex, which forms the outermost layer and accounts for a large percentage of the brain. It is divided into 4 distinct lobes (Frontal, Temporal, Parietal, Occipital), covering the left and right hemispheres (Figure 1). A major subdivision is the neocortex, which forms about 90% of the cerebral cortex. This relatively advancing layer of the brain is where complex functions such as strategic planning, executive motor commands, thought, and language occur (Holloway 2009, 7). The neocortex is highly functional in social communication and is enlarged in all primates who live in larger social groups (Dunbar 1992, 470-1). Cerebral reorganization and the internal structure of the brain however is what ultimately differentiate humans from the rest of the great apes.

While evolution is a gradual process over time, there are two major cerebral reorganizations noticed in hominids. The first cerebral reorganization possibly occurred 5-7 mya in tandem with changes to the body and brain as hominids adapted to anatomical developments in the legs, hands and feet due to bipedalism. However current physiological evidence definitively places this at 2-3 mya (Holloway et al 2009, 1). Proof for cerebral reorganization lies with the lunate sulcus, a structure imprinted on the back of the skull upon fossilization. Raymond Dart first speculated the lunate sulcus to be human-like in the Taung child endocast (*A. africanus*), which was later confirmed by contemporary researchers (Holloway et al. 2009, 5). This caused a paradigm shift as it was assumed before this that brain enlargement preceded cerebral reorganization.

An analysis of *A. africanus* endocasts also displayed increased frontal lobe width compared with earlier species, showing a development of the cerebral cortex (Falk et al 2012, 1-2). The frontal lobe functions in higher cognition and is responsible for voluntary control over muscles, strategy, mental image formation and the production of language. There are three major anatomical divisions of the frontal lobe, which are (from anterior to posterior location) the prefrontal, premotor and primary motor cortexes. The prefrontal cortex is involved in the idea formation and planning of voluntary action, such as constructing tools from autocued mental plans (Figure 1). The primary motor and premotor cortexes are responsible for all executive voluntary movement such as the precise use of hands required to manipulate objects or the skeletal muscle in the legs in order to walk on two feet from adapted locomotion (Figure 1). Consequently, based on understanding anatomical changes in the body and the archaeological record it seems logical these areas saw rapid increase in *Australopithecus*, a trend that would continue into *Homo.*

Cerebral reorganization granting improved executive muscle control over the arms, hands, legs and feet originally occurred in order to aid the body in adopting bipedalism. However, it also led to improved dexterity, control and manipulability of the hand in the use and formation of tools. While *Australopithecus* did not have complete manipulation of the characteristic opposable thumb, the framework for its construction was being laid during his time. The premotor cortex prepares and executes limb movements and integrates information from the senses to make proper movements. The premotor cortex is also involved in learning by imitation, and social cognition. This fits with the idea that tool use and language are integrally connected as early hominid ancestors most likely diffused tool making schemes through social learning and imitation, much like chimpanzees. This motif of tool use and the development of the brain are not isolated to just these two areas of the frontal lobe.

Also involved in movement is the primary motor cortex which is critical in executive control over movement. However it is important to note that the neuron surface area density mapped for each area of the body is different. For example, areas representing the arm and hand motor areas occupy the greatest portion of the primary motor cortex (Meier et al. 2008, 1805-9). In addition, the brain will rewire itself throughout life based on training and usage of certain areas (Meier et at. 2008, 1810). It has also been physiologically shown that the primary visual cortex size has decreased while the primary motor cortex has increased from other great apes showing increased use and selection (Holloway & deLaCoste-Lareymondie 1982, 105-7). This represents an increased reliance on voluntary manipulation of skeletal muscle and less on processing constant visual stimuli (Frey 2008, 1953-4). Overall, the changes in the primary motor and premotor cortexes of the frontal lobe have a great emphasis placed on the development of the brain to grant increased executive control over limb movement, especially the arms and hands which likely follows from an increased reliance on tools.

The frontal lobe also contains Broca's area, responsible for the production of language. While not definitely displayed in the fossil record until the transitional species, it is located majorly on the left frontal lobes in modern humans due to lateralization. Since lateralization potentially occurred before the LCA due to handedness in chimpanzees, Broca's area could have theoretically developed much before. A lowering of the hyoid bone eventually enabled spoken language but anatomical evidence suggests this had not occurred yet (Vilkman & Karma 1989. 142-3). However it is likely that early *Australopithecus* cooperated in small groups for hunting and did have a basic form of communication such as grunting and gesturing used by modern chimpanzees (De Heinzelin 1999, 626) So while it was not imprinted on endocasts until much later, the development of Broca's area most likely occurred during *Australopithecus* or long before.

Although most evolutionary researchers believe the enlarged frontal lobe is characteristically human, contemporary research suggests this be revisited. With a study done with the largest sample size it was discovered great apes had a comparable relative frontal cortex size to contemporary *Homo sapiens* (Semendeferi 2002, 273-4). In this case the absolute volume of the cerebral cortex or increasing neuron density could account for something the relative value fails to explain as it allows for simply more neural connections to be made and thus increasing on the capabilities already existent. Either way, it suggests that human cognition is not limited to just one single variable.

Tool Use Influences

The first cerebral reorganization was caused by the duality of bipedalism and tool use in *Australopithecus* and previous hominids. The first tools used were likely very similar to those employed by chimpanzees currently. It is debated however, which tools exactly fall into modern chimp intelligence (Gibson 1990, 261). These tools are perishable and made from locally available materials such as wood, bone or stone (Toth 1985, 106-7). In fact most of the early stone tools found show no evidence of retouching once created, and early hominids were not selective about the quality of tools used (Semaw 2000, 1197-99). Comparing chimpanzee and *Australopithecus* behavior also shows chimps never intentionally modify tools in the wild either (Mercador et al. 2002, 1452). Due to a lack of sophistication early are most likely looked over in the archeological record. This does not mean however that tools were not being increasingly used however as reflected in anatomical changes in the hand and brain.

The first tool group is called the Oldowan Industrial Complex and is associated with the change from *Australopithecus* to the transitional species *H. hablis* and *rudolfensis.* Conservative estimates for stone tool use are around 2.5 mya based on physical archeological evidence (Mercader et al. 2002, 1453). However, it is also shown by 3.2 mya morphologically the hand of *Australopithecus afarensis* allowed for human-like grip even if it still lacked the mobility of the opposable thumb which limited tool making (Marzke 1997, 93). These anatomical and morphological changes in the hand could have come from genetic alteration, most likely impacted by repeated use of more primitive tools by previous ancestors. As the morphological changes occurred, the brain was rewired to improve control over voluntary movement and aided in the formation of mental plans. Creating even simple stone tools is a complex mental process. The ability to conceive and create a tool requires a mental model of the finished product, which is then translated into a series of voluntary actions by muscle manipulation of the hands. This process involves two key attributes, technology and technique. Technique consists of the specific series of skeletal muscle motions required to produce a tool. Technology is a categorized body of accrued knowledge such as scientific concepts, mathematics and information about general geography that would aid in tool construction and conceptualization (Gibson 1990, 256). Together, techniques and technology provide fundamental framework for all tool making.

This process of tool making most likely occurred primarily in the frontal lobe as this is the seat of voluntary executive motion, mental planning and also located next to the limbic cortex in the temporal lobe, responsible for learning and memory (Figure 1). Coincidently, the frontal lobe is the area of the brain first seen affected by cerebral reorganization. It has been noted that habitually right-handed individuals made early stone tools and this handedness trend even exists in chimpanzees (Hopkins & Cantalupo 2004, 424 & Lonsdorf & Hopkins 2005, 12634). This shows tool use likely predated the LCA, however physical evidence of this is hard if not impossible to come by.

Lateralization & Handedness

The overall structural organization of the brain is asymmetrical and was formed through a process called lateralization. Lateralization causes the hemispheres to specialize for example, in modern humans brain activity related to tool use and language generally occurs on the left hemisphere of the brain. The left hemisphere corresponds to the right side of the body. It is noted that almost 90% of the modern human population has a preference for right-handedness based on cerebral petalias (projections) on the crania (LeMay & Galaburda et al 1978, 852-3). This increased lateralization could only have come from the combined effects of tool use and language use having a prolonged and sustained impact on the development of the brain and body over the course of many millions of years. Humans are not the only species that experience lateralization either. Recent studies have shown that chimpanzees also experience a trend of right-handedness and show remarkable tool use previously thought impossible (Lonsdorf 2005, 12637). This new evidence potentially pushes the idea of another major cerebral reorganization and tool use back before the time of the LCA.

Evidence definitively shows however by the time the transitional species *Homo hablis* and *rudolfensis* appeared, brain size had increased and Broca's area was present (Gibson 1990, 262). Since lateralization and handedness are linked, it only makes sense language and tool use are also linked. Widespread uniform tool use required language to have developed in order to convey both the techniques and technology required to make the tools. Language allows the passage of individually acquired knowledge to be shared with others, something distinct from chimpanzees as researchers note that large bodies of culturally accumulated knowledge are routinely passed down through linguistic means in human societies (Gibson 1990, 256). The ability to recreate increasingly complex tools coupled with the ability to cooperate, strategize and work as a group made early hominid ancestors masters of their ecological niches relatively quickly. This explains why tool use and language seem to be centered on the left side of the brain as it most likely interacted together.

Transitional Species: *Homo hablis & rudolfensis*

Everything within anthropology resides on a spectrum. This creates a multifaceted problem as fundamental semantic debates such as lumping and splitting or gradual and burst evolution complicate theories further. In this regard, the two species *Homo hablis* and *Homo rudolfensis* that lived between 2.0 and 1.8 mya are treated as transitional species between *Australopithecus* and *Homo erectus.* This is based on the short period present in the fossil record and accounting for sexual dimorphism and variation. While both species display advanced cognitive structures, they still have many ape-like characteristics such as small bodies (Table 1). The classification of these species is constantly subject to debate, for example some argue they be removed from *Homo* altogether (Wood & Collard 1999, 66). These hominids however, were remarkably superior and more human-like than previous *Australopithecus* ancestors.

These two species were the first to display marked improvements in the key indicator areas of anatomic change between *Australopithecus* and *Homo erectus*. During this time Broca's area was enlarged and defined, modifications to the hand including use of the opposable thumb occurred along with a definitive enlarged brain (Aiello & Dean 2006, 112). *H. hablis* is most closely associated with the overlapping Oldowan Industrial Complex, and featured increasingly complex tools than that of *Australopithecus*. The lifestyle of *Homo hablis* involved hunting, for which a bigger brain proved highly useful in strategizing and cooperation among hominids along with making deadlier tools. Improved hunting allowed for higher quality food, a fundamental requirement of relative brain growth, as brains are energetically expensive. There was also an increase in body size during this time.

It has been noted (& contended) that *H hablis* learned to control fire and begin rudimentary cooking despite a lack of physical evidence such as hearths (Wrangham 2009, 109). In addition to this certain anatomic features in the hand and wrists suggest *Homo hablis* had the ability to grasp tools with the opposable thumb with dexterity and manipulability not seen before in hominid ancestors (Aiello & Dean 2006, 123). The influence of cooking was highly visible though as *H. hablis* to *H. erectus* saw an exponential brain size increase coupled with a reduction in gut size based on a much more nutritionally efficient diet (Pennisi 1999, 2004-5). At this point hominids had established fledgling dominance in their ecological niche and evolution began to favor a larger brain above all else.

Second Cerebral Reorganization - Temporal Lobe

The second cerebral reorganization occurred between *Australopithecus* and *Homo erectus* and created an even more human-like brain structure. Key characteristics of this allowed for language production and even more executive control over voluntary actions such as new grip techniques with the modified hand and opposable thumb. While the first cerebral reorganization occurred with marginal change in brain growth and impacted the frontal lobe, the second one affected the temporal and frontal lobes and ran parallel with major brain size increases between *Australopithecus* and *Homo erectus*. This second cerebral reorganization also saw the development of the major language centers and increased lateralization of the brain based on a preference for right-handedness in humans showing improved tool use and communication through the beginnings of language.

The development, production and comprehension of language occur because of the connected nature of the two language centers in the brain. Broca's area is involved the production of language and also since it is located in the frontal lobe. Wernicke's area is related to the understanding of written and spoken language. These two areas work in unison to allow human beings to ability to speak and understand communication between one another Broca's area associates with Wernicke's area through the arcurate fasciculus, a complex bundle of neurons connecting them through the neocortex (Figure 1). The temporal lobe is also the location of the primary auditory cortex, which interprets data sent from the cochlea in the ear (which interpret sound waves to electrical impulses to be sent to the brain). This shows integration of the center of language, from the process of interpreting; producing and comprehending language to the voluntary control over mechanical processes that affect the ability to communicate. Modern human forms of Broca and Wernicke areas are first seen in *H. rudolfensis* and *H. hablis* respectively about 2.0 – 1.8 mya. This suggests that this species was fully capable of understanding and forming rudimentary human-like language (Finley 2001, 269). Previous evidence also suggests that the development of Broca's area possibly began with *Australopithecus*, it just was not until this time that it had grown enough to make an imprint on the outer cranium of the skull. Regardless of when it occurred, by this time not only where major structural changes occurring, but the overall size of the brain was also increasing exponentially.

Brain Volume Increase

To better understand brain development and cognition it is important to note that absolute brain size is irrelevant as many mammals have larger brain volumes than *Australopithecus* or even *Homo*, but would not be considered more intelligent. For this means the encephalization quotient (EQ) was developed to relate brain size to body size to produce relative brain size. Increased encephalization is associated with greater behavior complexity (Martin 1983, 78). In taking into account the two important *Australopithecus* species *africanus* and *afarensis,* it can be noted that they have a similar EQ values of 2.79 and 2.44

respectively, and also have a similar average brain size between 434 and 448 cm^3 (Table 1). *Australopithecus* likely had a brain similar to a chimpanzee's according to a comparison between *A. africanus* EQ value of 2.79 and the *Pan troglodytes* EQ value of 3.01 (Table 1). According to researchers, *Australopithecus* communicated much like the great apes today and lived in small groups, a stark contrast to the normal hunter-gatherer groups of *Homo erectus.* However, by at least 3 mya *Australopithecus* was noted to have a larger absolute and relative brain (Kimbel et al. 1994, 449 & Falk et al. 2000, 696). Regardless of when it occurred, there was exponential brain growth between *Australopithecus* and *Homo erectus.*

The characteristic enlarged brain of humans first began to show in *Homo hablis*, and was associated with the ability to make and manipulate tools. (Brown etl al 2013). This large brain would have been highly beneficial to *H. hablis* and would have allowed more complex tool making skills, cooperation through language and the ability to hunt and strategize more effectively. All of these would have provided a more beneficial diet and led to increased nutrition. The increased nutrition would enable better survivability and led the early transitional species to even more so master their environment. It must be noted that while *H. erectus* had a larger brain than its ancestors, relative brain size stayed partially the same because of increased body size (Table 1). Overall, the trend of brain evolution was originally slow and then exploded exponentially as the positive feedback loop between tool use, language and brain growth and reorganization created greater survivability based on increasing complexity.

Language Influences

Language provided a necessary advantage in hominid evolution. It allowed the production and passing on of information for tool production and usage. It also allowed cooperation and increased group size, which increased survivability in the harsher environment. All of these adaptations allowed hominids to move up the food chain using superior intelligence, complex tools and strategy to conquer both prey and the environment. In fact language is so important the neocortex is noted to be larger in all-social primates. Even within a high social society such as humans, the ones living in larger social groups have larger neocortex than those that live in small groups (Dunbar 1992, 470-1). While conceptualization of language initially occurs in the brain, it is not just the brain that needed to develop in order for speech to occur.

While current linguistic evidence puts the date and developments of language back much later in human history, it is impossible to ignore the physiological and anatomical evidence. Based on the development and distinction of the main language centers of the brain, it can be interpreted that language played a vital, interconnected role with tool use in developing the modern human brain. The development of language was extremely important because it allowed hominids to work together and cooperate in a larger context. As discussed, earlier neocortex size is related to social group, so must be no coincidence that humans have the largest relative neocortex, and also have the largest society on the planet. In order to facilitate communication between mass amounts of people, language developed. Language enables communication not just within the ethnic social circles, but also with every other cultural group.

The development of language was an evolutionary advantage because it allowed early hominids to work together in groups and share ideas and strategies. This was cooperation led to increased survivability and the ability to transmit the ideas of tools between larger amounts of people led to more even more tools being created. One small *Australopithecus* or *Homo erectus* might not have been enough against mega fauna predators, however a unified group of 10-20 brandishing complex spears and tools would be a formidable opponent.

Hunting, Gathering & Improved Diet Influences

Another one of the most important advances of *Australopithecus* and early *Homo* was the improvement of diet and nutrition based on increased hunting and potentially fire mastery. *Australopithecus* most likely hunted and consumed small game in small hunting parties, much like chimpanzees have been known to do (McGrew 1992, 234). In order for a large brain to develop, a higher quality diet was needed, as the brain is a very energetically expensive organ. At only 2% of the body's mass it requires 20% of its oxygen intact and a significant caloric intake in order to operate (Raichle & Gusnard 2002, 10237-8). While there was also a simultaneous increase in body size between *Australopithecus* and *Homo erectus*, a sacrifice had to be made. This occurred in the energetically expensive tissue of the gastrointestinal tract, which saw a reduction in size. In fact the mass of the gastrointestinal tract is only 60% of the expected size for a primate of similar size (Wrangham 2009, 87). The fact that the gut was reduced while brain size and body size increased provide a seeming paradox. This paradox is resolved however upon the acquisition of a higher quality nutritional diet as it led to less food being consumed but more of a beneficial gain metabolically.

While some researchers believe this advancement was caused solely by the introduction of meat into the diet, this does not account for the tremendous male/female cooperation, which assisted in the "stir-fry" hypothesis where both plants and meats equally (and sometimes more so plants) were the result of the improved diet (Aiello & Wheeler 1995, 201-5). Some plant food, such as tubers are known to have populated the known habitats of hominids and are proven to be and high-energy foodstuff (Pennisi 1999, 2004). Tubers populated the savannah woodlands as evidenced by the increased presence of tuber eating pigs and mole rats, which are often, found among hominid remains 2.0 mya (Wrangham 2009, 69). In fact it has also been shown that modern hunter-gatherer groups do not rely heavily on meat and other species eat meat without significant increases in brain size (Pennisi 1999, 2004-5). After calculating the caloric intake value of a diet of cooked tubers and no meat it was shown to have more value than a mostly meat diet (Wrangham 2009, 76). This shows that a holistic combination of meat and plant food was essential in providing the nutritional framework needed to supply an energetically expensive brain.

Most of brain growth occurs during the adolescent and formative years which shows that the trend for brain enlargement actually began with neonatal brain increases. Modern chimpanzees also have a small repertoire of available biological tools to use in aid of hunting and finding food, suggesting early hominids simply expanded upon this in order to gain access to a higher quality diet. Some researchers suggest that cooking emerged 1.9-1.8 mya based on a comparative study of taxonomy during transformation from *H. hablis* to *H. erectus*. This is contradictory as others argue the first evidence of human built hearths only dated to 250,000 ya (Pennisi 1999, 2004). However, based on microwear analysis, these early tools were also used in cutting meat from bones and using percussion techniques to gain access to marrow suggesting a early adaptation to hunting and scavenging (Mercader et al. 2002, 1453-55). Some researchers suggest scavenging was not an option because that requires food to be cooked, and fire wasn't controlled until much later (Klein 1999, 186). Other studies also show a marked decrease in BMI and a chronic energy deficiency in raw meat diets along with a 50% infertility rate (Wrangham 2009, 89). Both of these are detrimental to group survival so highly dependent on successful reproduction. This showed an increase in nutritional quality and might be responsible for the slight increase in body weight and brain size between *Australopithecus* and *Homo hablis/rudolfensis.*

The use and control of fire by *Homo erectus* displays an incredible adaptation to the environment and could single handedly be one of the biggest contributors to a larger brain. Before fire mastery and cooking, *Australopithecus* and other hominids were forced to scavenge and search for raw food to eat.

However, raw food takes much longer to digest and contains far less nutritional content than cooked food sources. Cooking changes both the physical and chemical make up of food. For example, cooking breaks up long glucose strains that allow for easily absorption through the small intestine, as the enzymes have to do less work to break the chain down to its constituent parts. In order to maintain an average human brain, up to 9 hours of foraging and eating must be done just to meet the nutritional demands (Wrangham 2009, 121). The invention of fire and cooking changed all of this. As hominids had to spend less time foraging and finding food, they could expand upon areas such as tool making, communication, and social structure to help develop the rudiments of civilization. This effect is also twofold. Women who had an improved diet saw an increase in neonatal brain size, which means birthing bigger brain babies.

Homo erectus

The anatomical blueprint for modern man began to emerge around 1.8 mya with *Homo erectus* who featured more cranial complexity, increased brain and body size. *Homo erectus* was a very advanced hominid, with sophisticated tools, and able to use and control fire. The best known African *Homo erectus* were found at Lake Turkana and Olduvai Gorge in Northern Africa (Brown, Harris, Leakey, Walker 1985, 788). These bodies had brain sizes that overlap with modern *Homo sapiens*, proving brain size was relatively modern at this point (Table 1). *Homo erectus* was also the first hominid group to organize themselves into hunter-gatherer societies; a feature mostly likely brought on by increased brain size due to communication, a feature proved anatomically possible at this point. This sophisticated level of social interaction is distinct from all other primates at this point. *Homo erectus* was able to control and master fire, along with increased efficiency of hunting and cooking. These advances in diet enabled a more energy efficient body with a smaller gut and a larger brain. This is evidenced as the body size of *Homo erectus* increased from transitional species, which accounting for increases also in brain size represents a much improved diet and caloric intake.

Conclusion

Brain evolution is very difficult to discuss because of a lack of physical evidence and a small sample size. The fossil record only contains a fraction of the vast amount of hominids that lived and died, and it is their information the field is based on. The evolution of the brain is not a linear process and involves a interplay of selection pressures, species migration, genetic drift, bottle neck events, genetic mutations and environmental changes that caused morphological adaptations in the body. Brain evolution is multifaceted and involves the interaction between social, material and cultural influences of various hominids. To accept anything as linear or singular in human behavior is to be remarkably simple minded. To understand the human brain presently, science must look to the past for fundamental evolutionary factors and selection processes that influenced the myriad of adaptations in early hominid ancestors.

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