

Is Encephalization of the Genus of Homo Due to Ecological or Social Adaptation?

Wenqing Yue¹, Jordan Lucore[#] and Forest Malley[#]

¹Shenzhen College of International Education, China

[#]Advisor

ABSTRACT

Brain expansion of the early Homo has led to many debates surrounding the selective pressure that re-sulted in this evolution. Two of the primary arguments are the relative importance of ecological versus social factors. Also, why the other adaptive traits didn't evolve when the early Homo species were facing survival challenges such as variable environment, but chose the development of such an energy-consuming organ? Here, I will compare and contrast the social versus ecological intelligence hypotheses and determine which is more likely to have contributed to encephalization of the genu Homo. I conclude that both hypotheses contribute to explaining why Homo became emphasized. While the social intelli-gence hypothesis is better to explain specifically the case of the Homo encephalization compared to the other primates, the ecological intelligence hypothesis helps explain things such as the energy requirement of encephalization and the impact of the paleoenvironment.

Introduction

One of the biggest questions concerning the evolution of the genus Homo is the process of encephaliza-tion. The evolution of encephalization is relatively rare likely in part because the energy cost of the brain is huge. The brain evolution could occur only when the benefits it brings exceeded the huge cost on energy, and this factor limit the evolution towards encephalization (Parker, 1990). The finite energy that animals have means that there would be an "opportunity cost" when investing this energy, because the energy expenditure on encephalization not only includes developing the brain, but also sustaining it. In the case of the Homo genus particularly, there is a clear increase in the relative cranial capacity during the emer-gence of the early species, especially compared to the Australopithecus. Since the evolution of a larger brain is so expensive particularly in the energy level, there must be some certain selective pressure that pushes the hominins towards this devel-opment route. What the factors that drive this brain expansion process is has thus, been highly debatable. Cur-rently, there are several existing classes of hypotheses that may be put forward to justify this development in the genus,

Two of the classes are the ecological intelligence and the social intelligence hypothesis. The social intelligence hypotheses argues that the complex social structure is the key selective pressure that favors enceph-alization (Dunbar, 1998; Humphrey, 1976; Jolly, 1966). The complex social system of the primates in general requires computational demands, driving the brain to develop (Whiten & Byrne, 1997). In this case, the selective pressure that pushed the development is often the cognition needed to form a stable social group with members connected to each other.

The ecological intelligence hypotheses is concerned with selective forces related to ecology, and poses that brain expansion happened due to dietary change that required advanced cognitive skills for foraging (Rosati, 2017). Generally, the ecological intelligence hypothesis suggests that the large brain is developed to solve problems associated with food gathering and extractive foraging. Of course, the social and ecological intelligence hypotheses are not mutually exclusive, as much of the evidence are able to support both sides of

the argument, and some of the hypotheses are also overlapped. Regardless, the different focus of the two groups is significant.

Both the social and ecological intelligence hypotheses aim to explain overall patterns of encephalization, not just the genus *Homo*. However, there are also more extreme sub-hypotheses that focus specifically on humans, pointing out the “special” cognitions that humans, and potentially other *Homo* species have, compared to the other primates. These hypotheses can provide a better insight into the reason of the specific early *Homo* encephalization trend.

The task of this literature review is to consider the points on both sides. After that, I will compare between the two sides by assessing the evidence supporting them, and whether they can answer the question of the specific case of the *Homo* encephalization. In the end, I will draw out a conclusion to determine how successfully does the two sides of hypotheses answer the question of the *Homo* encephalization.

The Paleoenvironment During the Evolution of Early *Homo*

This environmental background of the period can provide more insights towards the ecological intelligence hypothesis as the shifting climate posed challenge to the survival of the species. The genus *Homo* originated approximately during the interval around 3.0 to 2.5 millions years ago (Grine & Fleagle, 2009). Geological studies of this time period show the high variability of the climate (Potts, 2012). The increasing variability of the environment during this time provides a noticeable context to the Pilo-Pleistocene *Homo* evolution. Moreover, the paleoenvironment background also provides insights into the ecological and social intelligence hypotheses, although the ecological aspects are connected more directly.

In the context of the evolution of early *Homo*, the paleoenvironment provided a selective pressure of the adaptive versatility instead of survival strategy towards specific environment is shown (Potts, 2012). A specific example might be the dietary expansion of the hominin species at the time. The adoption of animal food including protein and fat tissue would act as a buffer against the shifting templates of food resources across a range of habitats due to the instability of climate (Antón, Leonard, & Robertson, 2002). This feeding ecology also provided the background of the ecological brain hypothesis, from which encephalization occurred to support the increased cognitive skills required. More importantly, the dietary expansion provided enough energy to buffer the energetic cost of large brains.

While for the social hypothesis, although it may not seem to be directly linked to the environmental factors, the dietary shift in the context of the variable climate also led to important social implications. The transportation strategy of the food and stone tool would lead to repeated social encounters in certain places across the landscape and create conditions that further favored social-based strategies (Potts, 2012). From past excavations of sites of concentrated animal remain associated with the stone tools 2 to 13 km from their sources about 2.0 to 1.8 million years ago are found (Plummer & Bishop, 2016).

The Social Intelligence Hypothesis

The social intelligence hypothesis argues that the socio-cognitive skills that primates need to solve social problems acted as a selective pressure that drove the evolution of encephalization in *Homo* sp (Dunbar, 1998). (Johnson-Ulrich, 2017 There are a few variations of the social intelligence hypothesis that are mainly different on what specific abilities the organisms develop, or the reason why these skills are needed. The earliest form of social intelligence hypothesis (SIH) is the Machiavellian intelligence hypothesis emphasizes the need for advanced cognitive abilities living in a competitive social environment (Humphrey, 1976; Whiten & Byrne, 1997). Similarly, the Vygotskian intelligence hypothesis argues that the unique aspects of human cognition were driven by social cooperation (Moll & Tomasello, 2007). The social brain hypothesis proposed the term of

sociality needed for the primates to solve ecological problems (Dunbar, 1998). Finally, the cultural brain hypothesis is more specific to the evolution of cultural learning, a more specialized skill of social cognition that is observed mostly in humans only (Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007).

One of the things that is noteworthy is the scope of the hypotheses proposed. Since the purpose of this paper is to specifically explore the reason of encephalization occurred within the Homo genus, it is worthwhile to check the hypotheses involving examination of this case. Generally, the SIHs are mostly applying to the primates in general, but some of the hypotheses that fit under this category have a more specific approach. For the hypothesis of a more general approach such as the Machiavellian intelligence hypothesis or the social brain hypothesis, the same factors should also be applied in the case of the Homo genus specifically. However, to study this case we need to focus specifically on the encephalization that occurred during the time of the early Homo relative to the other members of the primate order (Whiten & Byrne, 1997). While the hypothesis can still be applied to this incident of brain expansion as well as to the order in general, there might be some other factors that drove this further encephalization. In the case of the SIHs, it might be some specific social cognition that is specifically needed by the Homo genus.

From the list of hypotheses listed before, the Cultural intelligence is one example with a rather exclusive scope because cultural learning is mostly observed specifically within humans rather than the other primates. The empirical evidence supporting the argument shows that humans are more capable in the aspect of the ability to learn and understand the causal forces that are unobserved previously compared to the apes. However, in the case of the earlier Hominins such as the Homo erectus, it is argued that this specific cognition had not occurred yet, mostly because there weren't many signs of this level of cultural differences between different groups, suggesting that the Homo erectus might not have mastered this kind of cultural learning skill (Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007). The evidence of cultural interactions of the extinct species is hard to find, and this lack of evidence doesn't necessarily mean that the other Homo species don't fit in the scope of this hypothesis. Still, humans are the only one species that has been tested to be supporting this hypothesis. Therefore, the Cultural intelligence hypothesis is more referred to as "species specific", but probably not applying to the brain expansion during the appearance of the early Homo.

The other hypothesis that provides a possible trait that is more limited to humans is the Vygotskian intelligence hypothesis. Compared to the previous Machiavellian intelligence hypothesis, the Vygotskian intelligence hypothesis focuses more on the development of cooperation involving shared intentionality rather than the development of cognition that helps the primate to survive in competitive social environment. In other words, humans are more cooperative compared to all the other primates, and this led to further brain development. The focus point of this hypothesis, as a result, is more on humans specifically. Generally, while the skills of the non-human primates are still displayed more in a competitive context, the humans seem to have special skills and motivations to engage in activities that have a more cooperative nature (Moll & Tomasello, 2007). Still, the hypothesis acknowledges the more competitive nature of the non-human primates, and the cooperative skills are developed from the more competitive social group that many of the non-human primates have. As it is argued by Moll and Tomasello (2007), this derived ability to display a skill of cooperating with a shared interest probably emerged after the human's ancestors split from the great ape and began a new evolutionary path 6 million years ago. This time period, of course, includes the evolution of the whole Homo genus and led to the emergence of the Homo sapiens. This situation, like the cultural intelligence hypothesis, left out a space of discrepancy between the humans and the other non-human primates in this specific cognitive ability. Through this, a two-stage theory of the cumulative cultural evolution process is proposed by Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012 that attempts to explain the development of this cooperative ability. The first step is a decrease in the overall competitiveness, while the second step involves the key development of social cognition of forming shared goals, which drives the cooperative behavior. Although it is not entirely clear in what period these steps occurred, it is suggested that around 2 million years ago, a trend of global cooling and drying causes an expansion of the place that terrestrial monkeys spread. This competition of food resources

possibly caused the early Homo species to scavenge for large carcasses as food. This kind of scavenging skill requires multiple individuals to participate, and as a result, drove the selection of hom-inins that were more tolerant to their partners (Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012). It is suggested that the scavenging activity later developed into cooperative hunting, with evidence support-ing the fact that these hominins carried large prey back to their home base dated around 400-200 kya (Stiner, Barkai, & Gopher, 2009). The evidence does not entirely support this evidence. The argument as excavations of proof dated much later in the evolution of the Homo genus, which means it might not be entirely the reason for the brain expansion that happened throughout the genus. Still, it is highly likely that this is a continuous process that went on from the emergence of this genus.

In general, despite the difference in focus of the list of social intelligence hypotheses, they still hold an argument that the need for certain social cognition in a complex social system drives the en-cephalization in primates. Different scopes that the hypotheses provided also give more detailed explana-tions of the possible reasons that specifically caused the brain development within the Homo genus. Nev-ertheless, the theory of how and when certain social cognition developed during the interval of the earlier Homo genus is still not entirely clear, and the cognitions are more often considered as just exclusive to humans.

The Ecological Intelligence Hypothesis

Compared to the social intelligence hypothesis, the ecological hypotheses in general, answer an important ques-tion better: how is the energetic cost of the brain balanced by the benefits that encephalization pro-vides? Ac-cording to the ecological intelligence hypotheses, the dietary adaptations of the hominins can likely be an answer. Moreover, the favoritism of other ecological adaptations due to the paleoenviromental background is also a possible suggestion. Generally, the hypothesis is divided into frugivory and the extractive foraging hy-pothesis.

Just like the social intelligence hypothesis, we should also examine if the ecological intelligence hy-pothesis can explain the specific case of encephalization occurred in early Homo species. Here, the dis-crepancy between humans and other primates also exists, similarly as in the case of the social intelligence hypothesis. In the ecological intelligence hypothesis, human hunter-gatherers are often considered as an extreme case when it comes to the ecological aspect, compared to the other primates. Their foraging niche is by far the most compli-cated, the broad diet also drives for these special skills to acquire (Schuppli, Graber, Isler, & Schaik, 2016).

The frugivory hypothesis associate a correlation between a frugivorous diet and encephalization in the primates (DeCasien, Williams, & Higham, 2017). In one way it is associated with the energy invest-ment bal-ance between the gut and the brain. Having a fruit-based diet, of course, requires less digestion compared to a florivorous diet. Incorporating a fruit-based diet, therefore, means less energy investment needed in developing the guts. More energy can then be used on the brain (Aiello & Wheeler, 1995). Of course, frugivory is also, interconnected with the extractive foraging abilities required as mentioned in the next paragraph due the certain abilities needed to forage for fruit sources, which are often distributed more separately.

The extractive foraging hypothesis offers a more mutual correlative relationship between the cost and benefit. The complicated form of extractive foraging requires an expansion of the brain, while the increased quality of the food obtained in this form provides energy to maintain the enlarged brain (Schuppli, Graber, Isler, & Schaik, 2016). In some studies, the foraging niche complexity is also within a coevolution with the life history of developmental slowdown, as well as brain expansion. The needing-to-learn hypothesis, for example, suggests that the more complicated need to be attained later in life by learning and mastering the skills (Janson, 1993). This prolonged time that provides the organisms with more opportunities to master these complex skills is also connected with the increased brain size. The energy tradeoffs of developing a large brain will cause a slowdown in growth after all (Barton & Capellini, 2011).

When talking about the case of the Homo encephalization, there is a chicken and egg problem. While asking the question of why encephalization happens, it is hard to identify if the extractive foraging skills drives the encephalization or the other way around. Within complex niches organisms are able to obtain diet with higher energy, thereby supporting the increase in brain size. However, the way to reach to the niches potentially lies under the precondition of an increase in brain size (Schuppli, Graber, Isler, & Schaik, 2016).

There are, of course, explanations of how this correlated evolution all started through evidence from the ecological aspect. Ultimately, the extractive intelligence hypothesis is connected to the wider environmental factors. While the environmental factors shape the ecology and caused certain cognitively challenging scenarios, the organisms need to adapt to this environment by solving these challenges. The discussion of hypotheses that the environment drove the brain expansion is beyond the scope of this paper, but the effect to the ecology of the habitat that the hominins are living in is very worth noting. As mentioned before, in such a variable environment, the adoption of a more carnivorous diet can provide the hominins with enough energy to survive when the herbivorous food that might be affected by the shifting climate. It is not that easy to access this higher quality diet. Scavenging already has a huge uncertainty, while hunting down living prey would be even harder. The hominins need more complicated extractive foraging skills in this case. This, in turn, became the driving force of the development of a larger brain. However, the other factor that limited the encephalization, which is the energy tradeoff, also needs to be balanced, and this is where the changes of life history happened. The Homo adopted an evolutionary delay in development, which allowed the brain to continue develop after individuals were born. From the previous study, monkey, apes and humans all have a high rate of brain growth in utero. However, only in humans the high brain growth rate continues into the postnatal interval. The study of earlier Homo like the Homo erectus also found that the juvenile samples of the species had a smaller cranial capacity, which means they required time to develop to reach the typical brain volume that the adults had (Stanley, 1992). It is when the factors limiting encephalization are solved, and the benefits are exceeding the cost of a larger brain, that selection began favoring this trait, making the Homo survive this period of variability and reach such a level of encephalization. At this point, it is difficult to separate the ecological aspect with the environment. Still, according to the argument, the larger brain is indeed developed to deal with challenges that exist in ecological sense.

In some ways, this kind of ecologically intelligent hypothesis has more connection with the different factors that are potentially causing brain expansion, such as, environment, nutrition requirement and so on, even the social intelligence hypothesis is connected in the argument. When the scope of the hypothesis comes to the specific case of the Homo genus, the context of the paleoenvironment also played a part in explaining the ecological challenges that the early Homo faced. Still, the hypotheses face the problem of over generalization. For example, there are many criticisms of frugivory. For example, according to Sayers (2013), frugivory hypothesis ignores different cases of the primate's adaptation. The correlative evidence also overlooks the adaptation, such as the case of the folivore primate gray langurs. Overall, when it comes to the aspect of ecology, the adaptation of the organisms can be affected by the environment they inhabited in. Still, through the study of the general relationship between primate brain development and the ecological background, the explanation of encephalization trend in the early Homo can be inferred. The correlations can provide a general view of the encephalization.

Discussion

Overall, from the reviewed materials, the conclusion I drawn is that while the social intelligence hypothesis does explain better why the early Homo evolved larger brains instead of other traits through the selection process, the argument isn't able to explain all the questions surrounding the early Homo encephalization. Problems such as the energy tradeoff of the brain, and the indication of environmental background are not answered

directly. This is where the ecological intelligence hypothesis fills up some of the gaps of the former through the explanations of more specific ecological adaptations.

To examine the argument, both groups compare the degree of encephalization between the different species with the possible factor listed in the hypothesis that acts as the selective pressure causing brain expansion. Generally, the concept of encephalization involves an increase in the size of the whole brain or neocortex size relative to body size, size of lower brain areas, or evolutionary time (Lefebvre, 2012). Of course, the absolute brain size cannot act as an accurate account for encephalization, because animals with larger body generally need a larger brain simply to maintain the somatic needs. When it comes to the evidence of the two hypothesis groups, they generally use different method to determine the brain expansion of certain species. Mainly, the ecological intelligence hypotheses tend to use the Encephalization Quotient, while the social intelligence use more of the neocortex ratio.

From the past research there also proofs using these two standards that contradicts the other hypothesis group (DeCasien, Williams, & Higham, 2017; Dunbar, 1998), so it is worthwhile to compare the two measuring methods themselves to see which one is better to support the hypothesis.

The Encephalization quotients (EQ) is one useful way to study the brain size comparatively and determine the extent of encephalization of organisms. It is calculated through the actual brain mass divided by the predicted brain mass for body size (Foley & Lee, 1991). The encephalization quotient method is very straightforward because it directly uses the actual brain mass compared to the relative brain mass in the calculation, which is linked to the very definition of encephalization. The EQ also contains the comparison between the predicted brain size that is calculated with the measurement of the body mass, which can act as a good criterion to be compared between different species.

Due to the data availability of the EQ, the ecological intelligence hypothesis is often able to provide a wider range of EQ value of mammals compared to the social intelligence hypothesis, which the data is often only available across certain species.

When it comes to the study of the Homo, the EQ can provide a rough trend of encephalization of the extinct species to show the pattern of evolution of the brain, making the comparison not exclusive to humans and the non-Homo primates.

From the EQ calculating method, it is shown that the data correlates more with the claims of the ecological intelligence hypothesis such as cognitive foraging and frugivory as mentioned before. However, when it comes to the measuring of group size and the EQ, there are departures of the two values that contradicts what the social intelligence hypothesis predicts. The gibbons, for example, exhibits a drop in their groups size and increased relative brain size. There are also cases where the organisms exhibit an increase relative brain size without an enlarged group size, such as the rebids and the aye-aye (Antón, Leonard, & Robertson, 2002). This might either imply that these cases are driven more by the ecological factors, or it is just that the social brain hypothesis specifically fails to explain these cases, and some other social factors cause the deviations.

Also, when it comes to the Homo genus, through the EQ prediction of extinct species, the deviation is not clearly shown. The deviation of gibbons is only shown after they diverge from the common ancestor of apes (Antón, Leonard, & Robertson, 2002). Furthermore, the rough correlation of EQ can make the more specific brain development be ignored. While the absolute size of the brain does matter, the different composition can cause much difference between species, which can provide very different insight into either the organism's adaption to the ecology or social cognition developed. The cognition that the hominids harness, either ecological or social, are after all the result of a change in the specific brain structures.

This is where the neocortex ratio comes into place. The neocortex ratio, as the name suggests, is calculated through the size of the neocortex divided by the whole brain size (Dunbar, 1998). The expansion of the neocortex does accounts for the human brain expansion to a large extent. More importantly, the neocortex development is directly connected to many of the cognitions developed as this region of the brain plays a major

role in the information processing (Dunbar, 1998; Stiles & Jernigan, 2010). The problems of this type of measurement is, as mentioned before, the lack of data. The brain development of Homo is often drawn between the comparison of Homo sapiens and other non-human primates. Therefore, the neocortex ratio can act as a more helpful standard when it comes to determining the brain development. Of course, the development of other parts of the brain, such as the cerebellum and hippocampus, but the significant increase in the relative size of the neocortex is still able to correlate with the cognition to an extent.

There's another way to test the hypotheses which is to use species that has readily measured encephalization degree and test their performance in certain aspects either ecological or social. The social intelligence hypothesis compares different social cognitions between primate species (or other mammals), and sometimes separate humans as a special case for certain cognitive abilities that seems to be mastered by humans exclusively, forming the more extreme flavors of the hypothesis group. On the other hand, the ecological hypotheses also conduct similar experiment, testing between primates (also sometimes for other mammals) with different diet or foraging niches while comparing these to their degree of encephalization. Humans are again, being viewed as an extreme case. The study of modern hunter-gatherers group is also included (Leonard & Robertson, 1997).

It is hard to directly compare the two groups of hypotheses based on the evidence alone. While they do show certain trends that supports the argument, it only shows the correlation between possible encephalization and other factors but didn't fully prove that these factors are the very reason that cause brain expansion, as they can also just be a consequence of the already enlarged brain. More importantly, the conclusion of the brain development of the early Homo genus can't be drawn simply by focusing on humans, or the other primates along. Of course, studying the trend of the primates can indeed provide insights into the specific case of the Homo genus, but the deviations of the argument also can't just be ignored.

The case of the folivore primates, or the social groups size that doesn't fit into expectation with certain species all suggests that the rough trend and correlations can't explain all of the things that happened. Ultimately, the direct study of the extinct Homo species should also be involved through studying the archeological records. It is certainly harder to gather accurate information of the extinct Homo species, making this part of the hypothesis very hypothetical often. Still, this doesn't mean that there is no concrete evidence of the trend of development. The most noticeable is the stone technology. The stone tools appeared more frequently in sites dating around 2 million years, which is the time that the earliest Homo such as the Homo habilis appeared, suggesting an increasing reliance on these tools compared to the previous Australopithecus (Shook, Nelson, Aguilera, & Braff, 2019). The traces of certain behavior, while reflecting possible social development within the hominids, can also imply the attempt of the early Homo to increase their adaptive zone and exploit a larger diversity of environment. The trace of processed food also reflects the extended diet of the hominids, as well as their foraging and food processing cognition (Shook, Nelson, Aguilera, & Braff, 2019). Overall, the archeological evidence can support either side of the claims, it is just based on the different interpretations of the discovered materials and the correlation with the skeletons of these species.

The ecological intelligence hypothesis also answers the question of energy investment in a better sense compared to the social intelligence hypothesis. To develop a larger or more complex brain, there shouldn't not only be a selective pressure that favors this development, but also adaptations to provide more energy support for the organisms to grow and maintain such an energy consuming organ. The ecological intelligence hypothesis is more connected to this discussion of the balance of energy, especially when it comes to the discussion of the expanding diet of the early Homo. On the other hand, the social intelligence hypothesis seems to be less connected to this aspect of discussion, at least on the surface level. However, the more complicated social structure does also ensure more opportunity of obtaining food that are harder to get and more nutritious.

Although the two groups of hypotheses are discussed separately in the paper, it is noticeable that they are they are not two entirely different groups but have some features in common. There is a very important

detail that blurs between the 2 groups of hypotheses: the fact that the exterior ecology did encourage the formation of such social system of the primates. The trait of the social system that primates proposed is, after all, caused by ecological factors to a certain extent (Schaik, 1996). The further increase of social cognition is also thought to relate to ecological challenges posed during specific period. Ultimately, evolving into larger and more complex groups can increase the chance of survival. In some ways, the forming of social groups itself can be seen as an adaptation to the ecology. Take one specific case as an example, the behavior of scavenging can be seen in the sense of the social intelligence hypothesis as a process of the early hominins developing more cooperative social cognition, and it proceeds later into cooperating hunting (Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012). While this kind of activity does encourage cooperative skills in the social aspect, it is also considered as a typical way of extractive foraging method mentioned in the ecological intelligence hypothesis. Indeed, in this way the two kinds of hypotheses are not mutually exclusive, and it almost seems like the social domain is included in the ecological domain of the organisms. It can also be the case where the ecological and social factors both contributed to the ultimate result of brain expansion, although the different point of focus that the two groups posed make them seem to be in a more opposing situation.

There is one question that both sides of the hypotheses attempt to answer: why did the primates, and especially the species in the Homo genus, evolve in the direction of brain expansion to solve problems either ecologically or socially (although arguably sociality is driven by ecology), different compared to the other animals. Both groups of hypotheses are meant to be also applying the rule to the non-primates. Of course, some flavors of hypotheses, specifically the Vygotskian intelligence hypothesis and the cultural intelligence hypothesis, that took a more specific scope that focus on humans. The social intelligence hypothesis is more limited within the primates, although there are also some correlations shown in the testing of other animals, such as bats.

The ecological intelligence hypothesis provides a broader view of the encephalization trend, while the social intelligence hypothesis might act better to answer this very question. In conclusion, the social intelligence hypothesis explains the reason of the evolution trend of encephalization better due to its measurement and specific focus on explaining why the certain factors drives the brain expansion. However, the hypothesis can't explain the whole image without deviations from the correlations. This is where the energy and ecological intelligent hypothesis fills out the gap. It provides the ecological background of the emergence of the early Homo as well as the energy balance condition.

Acknowledgments

I would like to thank my advisor for the valuable insight provided to me on this topic.

References

- Aiello, L. C., & Wheeler, P. (1995). The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Current anthropology*, 36(2), 199-221.
- Antón, S. C., Leonard, W. R., & Robertson, M. L. (2002). An ecomorphological model of the initial hominid dispersal from Africa. *Journal of Human Evolution*, 43(6), 773-785.
- Barton, R. A., & Capellini, I. (2011). Maternal investment, life histories, and the costs of brain growth in mammals. *Proceedings of the National Academy of Sciences*, 108(15), 6169-6174.
- CH, J. (1993). Ecological risk aversion in juvenile primates: slow and steady wins the race. *Juvenile primates*.

- DeCasien, A. R., Williams, S. A., & Higham, J. P. (2017). Primate brain size is predicted by diet but not sociality. *Nature ecology & evolution*, 1(5), 0112.
- Dunbar, R. I. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, 6(5), 178-190.
- Foley, R. A., & Lee, P. C. (1991). Ecology and energetics of encephalization in hominid evolution. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 334(1270), 223-232.
- Grine, F. E., & Fleagle, J. G. (2009). The first humans: a summary perspective on the origin and early evolution of the genus *Homo*. In *The First Humans—Origin and Early Evolution of the Genus Homo: Contributions from the Third Stony Brook Human Evolution Symposium and Workshop October 3–October 7, 2006* (pp. 197-207). Springer Netherlands.
- Herrmann, E., Call, J., Hernández-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *science*, 317(5843), 1360-1366.
- Humphrey, N. K. (1976). The social function of intellect.
- Johnson-Ulrich, L. (2017). The social intelligence hypothesis. *Encyclopedia of evolutionary psychological science*, 1-7.
- Jolly, A. (1966). Lemur Social Behavior and Primate Intelligence: The step from prosimian to monkey intelligence probably took place in a social context. *Science*, 153(3735), 501-506.
- Lefebvre, L. (2012). Primate encephalization. *Progress in brain research*, 195, 393-412.
- Leonard, W. R., & Robertson, M. L. (1997). Comparative primate energetics and hominid evolution. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, 102(2), 265-281.
- Moll, H., & Tomasello, M. (2007). Cooperation and human cognition: the Vygotskian intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1480), 639-648.
- Parker, S. T. (1990). Why big brains are so rare: Energy costs of intelligence and brain size in anthropoid primates. *Language and intelligence in monkeys and apes: Comparative developmental perspectives*, 129-156.
- Plummer, T. W., & Bishop, L. C. (2016). Oldowan hominin behavior and ecology at Kanjera South, Kenya. *Journal of Anthropological Sciences*, 94.
- Potts, R. (2012). Environmental and behavioral evidence pertaining to the evolution of early *Homo*. *Current Anthropology*, 53(S6), S299-S317.
- Rosati, A. G. (2017). Foraging cognition: reviving the ecological intelligence hypothesis. *Trends in cognitive sciences*, 21(9), 691-702.
- Sayers, K. (2013). On folivory, competition, and intelligence: generalisms, overgeneralizations, and models of primate evolution. *Primates*, 54, 111-124.
- Schuppli, C., Graber, S. M., Isler, K., & van Schaik, C. P. (2016). Life history, cognition and the evolution of complex foraging niches. *Journal of Human Evolution*, 92, 91-100.
- Shook, B., Nelson, K., Aguilera, K., & Braff, L. (Eds.). (2019). *Explorations: An Open Invitation to Biological Anthropology*. Arlington VA: American Anthropological Association.
- Stanley, S. M. (1992). An ecological theory for the origin of *Homo*. *Paleobiology*, 18(3), 237-257.
- Stiles, J., & Jernigan, T. L. (2010). The basics of brain development. *Neuropsychology review*, 20(4), 327-348.
- Stiner, M. C., Barkai, R., & Gopher, A. (2009). Cooperative hunting and meat sharing 400–200 kya at Qesem Cave, Israel. *Proceedings of the National Academy of Sciences*, 106(32), 13207-13212.
- Whiten, A., & Byrne, R. W. (Eds.). (1997). *Machiavellian intelligence II: Extensions and evaluations* (Vol. 2). Cambridge University Press.

Van Schaik, C. P. (1996, January). Social evolution in primates: the role of ecological factors and male behaviour. In Proceedings-British Academy (Vol. 88, pp. 9-32). OXFORD UNIVERSITY PRESS INC..