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April 2023

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MPRA Paper No. 117130, posted 26 Apr 2023 00:14 UTC

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Abstract

This study develops a Malthusian growth model with heterogeneous agents and natural selection to explore the evolution of human brain size. We find that if the cognitive advantage of a larger brain dominates its higher metabolic costs, then the average brain size increases over time, which is consistent with the rising trend in human brain size that started over 2 million years ago. Furthermore, an improvement in hunting-gathering productivity gives rise to a larger optimal brain size in human evolution. Finally, as the average brain size increases, the average level of hunting-gathering productivity also rises, generating a positive feedback loop.

JEL classification: O13, Q56, N10

Keywords: Natural selection, brain size evolution, Malthusian growth theory

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[A]rchaic and early modern humans slowly but steadily acquired new skills, mastered the use of fire, developed increasingly sophisticated blades, handaxes, and flint and limestone tools, and created artworks. A key driver of these cultural and technological advancements, which came to define humankind and set us apart from other species, was the evolution of the human brain. Galor (2022, p. 13-14)

1 Introduction

As humans evolved, the volume of the human brain has increased. Over 2 million years ago, a dramatic increase in the growth rate of human brain size occurred, which coincided with the emergence of the earliest members of the human genus *Homo*.¹ *Homo habilis* is one of the earliest known humans and lived in Africa from roughly 2.4 million to 1.5 million years ago according to existing fossil evidence, and they had a brain size of about 550 cm³ to 690 cm³. *Homo ergaster* also lived in Africa from roughly 1.7 million to 1.4 million years ago and had a brain size of about 700 cm³ to 900 cm³. The well-known *Homo erectus* lived from roughly 1.6 million to 250,000 years ago in different parts of the world (including Africa, Asia and Europe) and had a brain size of about 600 cm³ to 1250 cm³. *Homo heidelbergensis* lived in Africa and Europe from roughly 600,000 to 200,000 years ago and had a brain size of about 1100 cm³ to 1400 cm³. *Homo neanderthalensis*, who is commonly known as the Neanderthals, lived in mainly Europe from possibly 430,000 to 40,000 years ago and had a brain size of about 1200 cm³ to 1750 cm³. Finally, *Homo sapiens* emerged in Africa roughly 300,000 years ago and has an average brain size of about 1400 cm³. Therefore, except for the Neanderthals who had an even larger brain size than modern humans,² human brain size has been increasing from early members of genus *Homo* to modern humans.³

In this study, we develop a hunting-gathering Malthusian growth model with heterogeneous agents to explore the evolution of human brain size driven by natural selection. Our results can be summarized as follows. If the cognitive advantage of a larger brain dominates its higher metabolic costs,⁴ then the average brain size of human population increases over time. This implication is consistent with the rising trend in brain size of archaic human species. We also find that an improvement in hunting-gathering productivity (e.g., the use of fire in hunting animals and cooking food) could give rise to a larger optimal brain size in human evolution. For example, Fonseca-Azevedo and Herculano-Houzel (2012) argue that the shift to a cooked diet may be an important reason for the rapid rising trend in human brain size. Ofek (2001, p. 73) also wrote that "the hunting-gathering feeding ecology [that led to an improvement in the quality and quantity of diet] facilitated a growing brain."

¹See DeSilva *et al.* (2021) for data on a rising trend in human brain size starting about 2 million years ago. They also find that there may have been a brain size reduction since 3000 years ago; however, a subsequent study by Villmoare and Grabowski (2022) questions the validity of this recent reduction in human brain size.

²Existing evidence suggests that both *Homo neanderthalensis* and *Homo sapiens* evolved from *Homo heidelbergensis*, rather than *Homo neanderthalensis* evolving into *Homo sapiens*.

³Another exception is *Homo floresiensis*, who lived in the island of Flores, Indonesia from possibly 190,000 to 50,000 years ago and had a small brain size of about 420 cm³, which was likely due to island dwarfism.

⁴See van Valen (1974) and Lynn (1990) for estimates of the cognitive advantage of a larger human brain size. See Gonzalez-Forero and Gardner (2018) for estimates of the metabolic costs of the human brain.

Furthermore, we find that as the average brain size increases over time, the average level of hunting-gathering productivity also rises over time, generating a positive feedback loop. This implication is consistent with Galor's (2022, p. 16-17) observation that "[t]he evolution of the human brain was the main impetus for the unique advancement of humanity, [...which] in turn, shaped future evolutionary processes, enabling human beings to adapt more successfully to their shifting environments and to further advance and utilise new technologies".

This study relates to the literature on natural selection and Malthusian growth theory.⁵ Recent studies in this literature explore how natural selection of different traits affects the transition of an economy from pre-industrial stagnation to modern economic growth; see Galor and Moav (2002) and Galor and Klemp (2019) on the selection of child quality, Galor and Michalopoulos (2012) on the selection of entrepreneurial spirit, and Galor and Ozak (2016) on the selection of future-oriented mindset. A related study by Chu (2023) explores natural selection and the extinction of archaic human species in a Malthusian economy. Another related study by Chu and Xu (2023) explores the subsequent transitions of human society from hunting-gathering to agriculture and then from agriculture to industrial production also in a Malthusian economy. This study contributes to this literature by exploring natural selection of human brain size and its evolution in a Malthusian growth model.

This study also relates more broadly to the scientific literature on human brain size evolution; see Heldstab *et al.* (2022) for a survey. A recent study by Gonzalez-Forero and Gardner (2018) provides a quantitative analysis on the evolution of human brain and finds that ecological challenges for "finding, caching or processing food" are the main reason for human brain evolution. Robson and Kaplan (2003) provide an economic analysis on the development of human brain as health capital that is accumulated by bodily investment to reduce mortality. We contribute to this literature by also providing an economic analysis based on a microfounded Malthusian growth model, in which fertility decisions of heterogeneous agents give rise to natural selection and the underlying natural-selection mechanism for human brain evolution is also ecological in nature that is driven by the advantage of a larger brain in hunting-gathering and food production.

The rest of this study is organized as follows. Section 2 sets up the Malthusian model. Section 3 presents our results on human brain evolution. The final section concludes.

2 A Malthusian model with human brain evolution

The Malthusian growth model is based on the seminal work of Malthus (1798), who observed that population growth is limited by the availability of natural resources. In this section, we consider a canonical Malthusian growth model; see for example, Ashraf and Galor (2011). There is a group of humans, which may be *Homo sapiens* or any other archaic humans, such as *Homo erectus* or Neanderthals. The group engages in hunting-gathering within a fixed area of land Z . The novel element is heterogeneity in brain size, which in turn affects consumption and hunting-gathering productivity.

⁵See Hansson and Stuart (1990) and Rogers (1994) for early economic models of natural selection of agents with different time preferences and Robson (2001) for a survey.

2.1 Endogenous fertility and population dynamics

Within the human population, there is a continuum of families indexed by $i \in [0, 1]$. Each family i has an adult population $N_{i,t}$ at time t . Therefore, the total adult population size at time t is

$$N_t = \int_0^1 N_{i,t} di. \quad (1)$$

Each family i is endowed with a certain brain size that is heterogeneous across families. Given the metabolic costs of the brain, a family with a larger brain size requires a higher level of consumption per capita. We consider overlapping generations of agents, and each agent lives for two periods. Each adult agent of family i has the following utility function $u_{i,t}$ at time t :

$$u_{i,t} = \beta_i \ln c_{i,t} + (1 - \beta_i) \ln n_{i,t+1}, \quad (2)$$

where the degree of consumption preference β_i is assumed to be increasing in brain size due to the higher metabolic cost of a larger brain. $n_{i,t+1}$ is the agent's number of children, who then become adults at time $t + 1$. Raising children is costly, and the level of consumption net of the fertility cost is

$$c_{i,t} = y_{i,t} - \rho n_{i,t+1}, \quad (3)$$

where the parameter $\rho > 0$ determines the cost of fertility and $y_{i,t}$ is the per capita output of food production in family i .

The utility-maximizing level of consumption is

$$c_{i,t} = \beta_i y_{i,t}, \quad (4)$$

and the utility-maximizing level of fertility is

$$n_{i,t+1} = \frac{1 - \beta_i}{\rho} y_{i,t}, \quad (5)$$

where fertility cost ρ is identical across families for simplicity. Equations (4) and (5) show that a family with a larger brain size allocates a larger share of food output to consumption at the expense of fertility.⁶ Therefore, if a larger brain size does not carry a cognitive advantage, then families with larger brains would have an evolutionary disadvantage.

Each adult agent in family i has $n_{i,t+1}$ children, and the number of adult agents in family i at time t is $N_{i,t}$. Therefore, the law of motion for the adult population size in family i is

$$N_{i,t+1} = n_{i,t+1} N_{i,t} = \frac{1 - \beta_i}{\rho} y_{i,t} N_{i,t}, \quad (6)$$

which is decreasing in consumption preference β_i and fertility cost ρ . The growth rate of $N_{i,t}$ at time t is

$$\frac{\Delta N_{i,t}}{N_{i,t}} \equiv \frac{N_{i,t+1} - N_{i,t}}{N_{i,t}} = \frac{1 - \beta_i}{\rho} y_{i,t} - 1, \quad (7)$$

⁶If we were to modify (2) as $u_{i,t} = \beta_i \ln c_{i,t} + \gamma \ln n_{i,t+1}$ and assume γ to be identical across families, the term $1 - \beta_i$ would become $\gamma/(\beta_i + \gamma)$, which is still decreasing in the family's brain size via β_i .

and the growth rate of total adult population N_t at time t is

$$\frac{\Delta N_t}{N_t} = \int_0^1 s_{i,t} \frac{\Delta N_{i,t}}{N_{i,t}} di = \frac{1}{\rho} \int_0^1 s_{i,t} (1 - \beta_i) y_{i,t} di - 1, \quad (8)$$

where $s_{i,t} \equiv N_{i,t}/N_t$ and $\Delta N_t/N_t$ will be simply referred to as the population growth rate.

2.2 Hunting-gathering

To capture the cognitive advantage of a larger brain, we assume that the level of hunting-gathering productivity θ_i in each family i is increasing in its brain size. The food production function of family i is

$$Y_{i,t} = \theta_i (lN_{i,t})^\alpha (Z_{i,t})^{1-\alpha}, \quad (9)$$

where $lN_{i,t}$ and $Z_{i,t}$ are respectively the amount of labor and land devoted to hunting-gathering by family i . Individual labor supply $l > 0$ is exogenous, and the parameter $\alpha \in (0, 1)$ measures labor intensity of the hunting-gathering process.

The amount of land occupied by family i for hunting-gathering is proportional to its population share $s_{i,t}$:

$$Z_{i,t} = s_{i,t} Z = \frac{N_{i,t}}{N_t} Z. \quad (10)$$

Substituting (10) into (9) yields the level of food output per capita in family i as

$$y_{i,t} \equiv \frac{Y_{i,t}}{N_{i,t}} = \frac{\theta_i (lN_{i,t})^\alpha (Z_{i,t})^{1-\alpha}}{N_{i,t}} = \theta_i l^\alpha \left(\frac{Z}{N_t} \right)^{1-\alpha}, \quad (11)$$

which is increasing in hunting-gathering productivity θ_i and the brain size of family i .

3 Natural selection and brain size evolution

Substituting (11) into (7) yields the population growth rate of family i as

$$\frac{\Delta N_{i,t}}{N_{i,t}} = (1 - \beta_i) \theta_i \frac{l^\alpha}{\rho} \left(\frac{Z}{N_t} \right)^{1-\alpha} - 1, \quad (12)$$

which is increasing in $(1 - \beta_i) \theta_i$ (i.e., the product of fertility preference $1 - \beta_i$ and hunting-gathering productivity θ_i). Recall that both the degree of consumption preference β_i and the level of hunting-gathering productivity θ_i are increasing in brain size, which is now denoted as $b_i \in [b^{\min}, b^{\max}]$ where b_i follows a general distribution across families within the lower bound b^{\min} and upper bound b^{\max} on brain size. A larger brain size b_i has a positive effect on hunting-gathering productivity θ_i and a negative effect on fertility preference $1 - \beta_i$.⁷ If the positive effect always dominates (i.e., $(1 - \beta_i) \theta_i$ is monotonically increasing in b_i), then

⁷Recall that even if we have $u_{i,t} = \beta_i \ln c_{i,t} + \gamma \ln n_{i,t+1}$, the term $(1 - \beta_i) \theta_i$ simply becomes $\theta_i \gamma / (\beta_i + \gamma)$, where $\gamma / (\beta_i + \gamma)$ is still decreasing in b_i via β_i .

families with larger brain size have an evolutionary advantage (i.e., their population share $s_{i,t}$ rises over time due to their higher population growth rate). Specifically, families that satisfy the following condition experience a rise in their population share $s_{i,t}$ at time t :

$$\Delta s_{i,t} > 0 \Leftrightarrow \frac{\Delta N_{i,t}}{N_{i,t}} > \frac{\Delta N_t}{N_t} \Leftrightarrow (1 - \beta_i)\theta_i > \int_0^1 s_{i,t}(1 - \beta_i)\theta_i di.$$

As a result, the average brain size $b_t \equiv \int_0^1 s_{i,t} b_i di$ of the human population increases over time, which is consistent with the rising trend in human brain size that started over 2 million years ago. As the average brain size increases over time, the average level of hunting-gathering productivity $\theta_t \equiv \int_0^1 s_{i,t} \theta_i di$ also rises over time.⁸ In the long run, families with the largest brain size will dominate the population (i.e., $s_{i,t}(b_i = b^{\max}) \rightarrow 1$).

If $(1 - \beta_i)\theta_i$ is instead an inverted-U function in brain size b_i , then there exists an optimal brain size $b^* \in (b^{\min}, b^{\max})$ from an evolutionary viewpoint. In other words, families with this optimal brain size b^* will dominate the population in the long run (i.e., $s_{i,t}(b_i = b^*) \rightarrow 1$), and the average brain size b_t rises towards b^* .⁹ For example, suppose $(1 - \beta_i)\theta_i$ takes the following functional form:

$$(1 - \beta_i)\theta_i = (1 - b_i)(1 + \bar{\theta}b_i), \quad (13)$$

where $\bar{\theta} > 1$ is a hunting-gathering productivity parameter. Then, the brain size that maximizes $(1 - \beta_i)\theta_i$ is given by $b^* = (\bar{\theta} - 1)/(2\bar{\theta})$, which is increasing in $\bar{\theta}$. Therefore, an increase in hunting-gathering productivity $\bar{\theta}$ (e.g., discovering the use of fire in hunting animals and cooking food) raises the optimal brain size b^* .¹⁰ Furthermore, continuous improvement in $\bar{\theta}$, such as the development of "increasingly sophisticated blades, handaxes, and flint and limestone tools", leads to a continuous increase in the optimal brain size b^* ; in this case, the average brain size b_t keeps rising until reaching a stationary b^* in the long run.

Proposition 1 summarizes all our results in this section.

Proposition 1 *The population growth rate of family i is increasing in $(1 - \beta_i)\theta_i$. If the positive effect of a larger brain size b_i on hunting-gathering productivity θ_i always dominates its negative effect on fertility preference $1 - \beta_i$, then families with larger brain size have an evolutionary advantage, and the average brain size in human population increases over time. As the average brain size increases, the average level of hunting-gathering productivity also rises over time. If $(1 - \beta_i)\theta_i$ is an inverted-U function in b_i , then there exists an optimal brain size b^* , and families with $b_i = b^*$ will dominate the population in the long run. Suppose $(1 - \beta_i)\theta_i = (1 - b_i)(1 + \bar{\theta}b_i)$. Then, an increase in hunting-gathering productivity $\bar{\theta}$ raises the optimal brain size b^* . Given an initial value, the average brain size b_t rises towards b^* .*

⁸See for example, Galor (2022, p. 16-17).

⁹Here we assume that the average brain size at time 0 is below b^* .

¹⁰See Fonseca-Azevedo and Herculano-Houzel (2012), Galor (2022, p. 17) and Ofek (2001, p. 73).

4 Conclusion

In this study, we have developed a hunting-gathering Malthusian growth model with heterogeneity in human brain size, which gives rise to natural selection and brain size evolution. We find that if the cognitive advantage of a larger brain dominates its higher metabolic costs, then the average human brain size increases over time, which is consistent with the rising trend in brain size of archaic human species. Furthermore, we have used our growth-theoretic framework to show how an improvement in hunting-gathering productivity (e.g., the discovery and use of fire) could give rise to a larger optimal brain size in human evolution.

Finally, we conclude with the following discussion. Our growth-theoretic analysis assumes that the range of human brain size is exogenous. It is the population share that changes endogenously over time, which in turn gives rise to an endogenous evolution of the average brain size. One can endogenize the range of brain size, for example, by assuming that the average brain size has a spillover effect on its range, such that each family's brain size in the next generation grows by the same proportion as growth in the average brain size across families in the current generation. We leave this extension to future research.

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