# Human Brain Evolution in a Malthusian Economy

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**Abstract**

Why did the human brain evolve? 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 (e.g., the discovery of fire in hunting animals and cooking food) helps to trigger this human brain size evolution. As the average brain size increases, the average level of hunting-gathering productivity also rises over time.

[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 cm$^3$ to 690 cm$^3$. *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 cm$^3$ to 900 cm$^3$. 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 cm$^3$ to 1250 cm$^3$. *Homo heidelbergensis* lived in Africa and Europe from roughly 600,000 to 200,000 years ago and had a brain size of about 1100 cm$^3$ to 1400 cm$^3$. *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 cm$^3$ to 1750 cm$^3$. Finally, *Homo sapiens* emerged in Africa roughly 300,000 years ago and has an average brain size of about 1400 cm$^3$. 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 discovery of fire in hunting animals and cooking food) helps to trigger this human brain size 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." Furthermore,

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[1] See 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.

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

[3] Another 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 cm$^3$, which was likely due to island dwarfism.

[4] See 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.

we find that as the average brain size increases, the average level of hunting-gathering productivity also rises over time. 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] 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, Lagerlof (2007) on the selection of human body mass, Galor and Michalopoulos (2012) on the selection of entrepreneurial spirit, and Galor and Ozak (2016) on the selection of future-oriented mindset. A recent 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, who 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.

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[5]See 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 large number of families indexed by $i \in \{1, ..., m\}$. Each family $i$ has an adult population $N_{i,t}$ at time $t$. Therefore, the total adult population size at time $t$ is

$$N_t = \sum_{i=1}^{m} N_{i,t}. \tag{1}$$

Each family $i$ is endowed with an exogenous brain size denoted as $b_i \in [b^{\min}, b^{\max}]$, where $b_i$ is heterogeneous across families and follows a general distribution within the lower bound $b^{\min}$ and upper bound $b^{\max}$ on brain size.

Given the metabolic costs of the brain, a family with a larger brain size faces a higher subsistence requirement on per capita consumption denoted as $\kappa_i = \kappa(b_i)$, which is assumed to be an increasing function in brain size $b_i$.[6] 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 $t$:

$$u_{i,t} = (1 - \gamma)\ln(c_{i,t} - \kappa_i) + \gamma \ln n_{i,t+1}, \tag{2}$$

where $\gamma \in (0,1)$ is the degree of preference on fertility relative to consumption $c_{i,t}$. $n_{i,t+1}$ 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

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

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

$$c_{i,t} = (1 - \gamma)y_{i,t} + \gamma\kappa_i, \tag{4}$$

and the utility-maximizing level of fertility is

$$n_{i,t+1} = \frac{\gamma}{\rho}(y_{i,t} - \kappa_i), \tag{5}$$

where fertility cost $\rho$ is identical across families for simplicity. Equations (4) and (5) show that a family with a larger brain size $b_i$ allocates a larger amount of food output to consumption (due to the higher subsistence requirement $\kappa(b_i)$) at the expense of fertility. 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

$$N_{i,t+1} = n_{i,t+1}N_{i,t} = \frac{\gamma}{\rho}(y_{i,t} - \kappa_i)N_{i,t}, \tag{6}$$

which is decreasing in the subsistence requirement $\kappa_i$. The growth rate of $N_{i,t}$ at time $t$ is

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

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[6] Lagerlof (2007) also considers the case in which a higher body mass has a higher subsistence requirement.

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

$$\frac{\Delta N_t}{N_t} = \sum_{i=1}^{m} s_{i,t} \frac{\Delta N_{i,t}}{N_{i,t}} = \frac{\gamma}{\rho} \sum_{i=1}^{m} s_{i,t}(y_{i,t} - \kappa_i) - 1, \tag{8}$$

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 human brain, we assume that the level of hunting-gathering productivity denoted as $\theta_i = \theta(b_i)$ in each family $i$ is also increasing in its brain size $b_i$. The food production function of family $i$ is

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

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.

For simplicity, the amount of land occupied by family $i$ for hunting-gathering is assumed to be proportional to its population share $s_{i,t}$:[7]

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

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

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

which is increasing in the family's brain size $b_i$ via its hunting-gathering productivity $\theta(b_i)$.

# 3  Natural selection and brain size evolution

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

$$g_{i,t} \equiv \frac{\Delta N_{i,t}}{N_{i,t}} = \frac{\gamma}{\rho}\left[\theta_i l^\alpha \left(\frac{Z}{N_t}\right)^{1-\alpha} - \kappa_i\right] - 1, \tag{12}$$

which is increasing in hunting-gathering productivity $\theta_i$ but decreasing in the subsistence requirement $\kappa_i$. Recall that both $\theta_i = \theta(b_i)$ and $\kappa_i = \kappa(b_i)$ are increasing functions of brain size $b_i$. Therefore, a larger brain size $b_i$ has a positive effect on fertility via a higher level of hunting-gathering productivity $\theta_i$ and also a negative effect on fertility via a higher

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[7]Alternatively, one can consider a more general allocation rule $Z_{i,t} = [(N_{i,t})^\phi / \sum_{j=1}^{m}(N_{j,t})^\phi]Z$ with $\phi \in [0,1]$, which gives rise to more complicated population dynamics across families.

subsistence requirement $\kappa_i$. If we were to assume $\kappa_i = \kappa$ to be homogeneous across families, then families with the largest brain size $b^{\max}$ would dominate the population by having the highest hunting-gathering productivity $\theta(b^{\max})$ and the highest population growth rate. Conversely, if we were to assume $\theta_i = \theta$ to be homogeneous across families, then families with the smallest brain size $b^{\min}$ would dominate the population by having the lowest subsistence requirement $\kappa(b^{\min})$ and the highest population growth rate. In general, families that have the highest population growth rate would dominate the population in the long run. For the rest of this analysis, we assume that $\theta(b_i)$ is weakly concave in $b_i$ whereas $\kappa(b_i)$ is weakly convex in $b_i$. We now examine the condition under which the average human brain size evolves towards $b^{\max}$.[8]

## 3.1 Expanding brain size in human evolution

If the positive effect of brain size $b_i$ on fertility always dominates its negative effect (i.e.,

$$\frac{\partial g_{i,t}}{\partial b_i} > 0 \Leftrightarrow l^\alpha \left( \frac{Z}{N_t} \right)^{1-\alpha} \frac{\partial \theta_i}{\partial b_i} > \frac{\partial \kappa_i}{\partial b_i} \tag{13}$$

for all $b_i \in [b^{\min}, b^{\max}]$ and $N_t \in [N_0, N^*]$ where $N^*$ is the steady-state level of total population),[9] then the population growth rate of family $i$ is increasing in its brain size $b_i$. In this case, the growth rate of the population share of family $i$ is also increasing in its brain size:

$$\Delta s_{i,t} \approx \frac{\Delta N_{i,t}}{N_t} = s_{i,t} g_{i,t} \Rightarrow \frac{\partial \Delta s_{i,t}/s_{i,t}}{\partial b_i} \approx \frac{\partial g_{i,t}}{\partial b_i},$$

which uses the approximation $N_{t+1} \approx N_t$.[10] As a result, families with the largest brain size would have an evolutionary advantage and eventually dominate the population. In the long run, $s_{i,t}(b_i = b^{\max}) \to 1$ because its population growth rate $g_{i,t}(b_i = b^{\max})$ is the highest among all families such that $s_{j,t}(b_j < b^{\max}) \to 0$. In this case, total population $N_t$ converges to the steady-state population level of the families with the largest brain size $b^{\max}$:

$$\lim_{t \to \infty} N_t \to N^* = \left[ \frac{\gamma \theta(b^{\max}) l^\alpha}{\rho + \gamma \kappa(b^{\max})} \right]^{1/(1-\alpha)} Z, \tag{14}$$

which is derived from (12) by setting $b_i = b^{\max}$.

As their population share $s_{i,t}(b_i = b^{\max})$ rises over time due to their higher population growth rate, the average brain size $b_t \equiv \sum_{i=1}^{m} s_{i,t} b_i$ of human population also increases over time, which is consistent with the rising trend in human brain size that started over 2 million years ago. Eventually, the average brain size converges to the upper bound (i.e., $b_t \to b^{\max}$ as $s_{i,t}(b_i = b^{\max}) \to 1$). As the average brain size increases over time, the average

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[8]To conserve space, we relegate the case in which the average brain size evolves towards an interior steady state $b^* \in (b^{\min}, b^{\max})$ to the appendix.

[9]Here, we assume that the initial level of population is below the steady-state equilibrium level.

[10]This approximation implicitly assumes that the brain size of an individual family has a negligible effect on the total population growth rate $g_t$. In general, $\Delta s_{i,t}/s_{i,t} = (g_{i,t} - g_t)/(1 + g_t)$.

level of hunting-gathering productivity $\theta_t \equiv \sum_{i=1}^{m} s_{i,t} \theta_i$ also rises over time and converges to $\theta(b^{\mathrm{max}})$.[11]

When does this expanding brain size in human evolution occur? To explore this question, we substitute $N^*$ from (14) into $N_t$ in (13) to derive

$$\frac{\rho + \gamma \kappa(b^{\mathrm{max}})}{\gamma \theta(b^{\mathrm{max}})} \theta'(b^{\mathrm{max}}) > \kappa'(b^{\mathrm{max}}). \tag{15}$$

Recall from (13) that the positive effect of $b_i$ is decreasing in $N_t$. So, if the inequality in (13) holds for $N^*$, it would also hold for $N_t \in [N_0, N^*]$. In the following section, we consider a parametric example to demonstrate when (15) holds.

### 3.1.1 A parametric example

Suppose $\theta(b_i)$ and $\kappa(b_i)$ take the following functional form: $\theta(b_i) = 1 + \bar{\theta} b_i$ and $\kappa(b_i) = \bar{\kappa} b_i$, where $\bar{\theta} > 0$ and $\bar{\kappa} > 0$ are productivity and cost parameters, respectively. Then, (15) simplifies to

$$\bar{\theta} > \frac{\gamma}{\rho} \bar{\kappa}. \tag{16}$$

In this case, in order for human population to evolve towards a larger average brain size, the parameter $\bar{\theta}$ needs to be sufficiently large.[12] In other words, a high level of hunting-gathering productivity $\bar{\theta}$ (e.g., the discovery of using fire in hunting animals and cooking food or the development of "increasingly sophisticated blades, handaxes, and flint and limestone tools") helps to trigger the emergence of an expanding brain size in human evolution.[13]

## 3.2 Summary of results

Proposition 1 summarizes all our results in this section.

**Proposition 1** *The population growth rate of family i is increasing in its hunting-gathering productivity $\theta_i$ but decreasing in its subsistence requirement $\kappa_i$. If the positive effect of a larger brain size $b_i$ on hunting-gathering productivity $\theta_i$ always dominates its negative effect (via a higher subsistence requirement $\kappa_i$) on fertility, then families with the largest brain size $b^{\mathrm{max}}$ have an evolutionary advantage, and the average brain size in human population increases over time. As the average brain size $b_t$ increases, the average level of hunting-gathering productivity $\theta_t$ also rises over time. Suppose $\theta(b_i) = 1 + \bar{\theta} b_i$ and $\kappa(b_i) = \bar{\kappa} b_i$. Then, a large hunting-gathering productivity parameter $\bar{\theta}$ helps to trigger the emergence of an expanding brain size in human evolution.*

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[11]See for example, Galor (2022, p. 16-17).

[12]If the inequality in (16) is reversed, then brain size would eventually converge to $b^{\mathrm{min}}$ instead. However, if initial population $N_0$ is sufficiently small, then the positive effect of $b_i$ may still dominate but only initially.

[13]See 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 an expanding 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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## Online Appendix

In this appendix, we examine the case in which the average brain size $b_t$ evolves towards an interior steady state $b^* \in (b^{\mathrm{min}}, b^{\mathrm{max}})$. If there exists a certain level of population threshold $\widetilde{N}$ under which

$$l^\alpha \left( \frac{Z}{\widetilde{N}} \right)^{1-\alpha} \frac{\partial \theta(b^*)}{\partial b_i} = \frac{\partial \kappa(b^*)}{\partial b_i}, \tag{A1}$$

then there exists an interior optimal brain size $b^* \in (b^{\mathrm{min}}, b^{\mathrm{max}})$ from an evolutionary viewpoint. To determine this optimal brain size, we also need the steady-state population level:

$$N_i^*(b_i = b^*) = \left[ \frac{\gamma \theta(b^*) l^\alpha}{\rho + \gamma \kappa(b^*)} \right]^{1/(1-\alpha)} Z = \widetilde{N}, \tag{A2}$$

where $\widetilde{N}$ and $b^*$ are determined jointly by (A1) and (A2). In other words, families with the optimal brain size $b^*$ have the highest steady-state population growth rate and dominate the population in the long run (i.e., $s_{i,t}(b_i = b^*) \to 1$ because its steady-state population growth rate $g_i^*(b_i = b^*) = 0$ is the highest among all families such that $g_j^*(b_j \neq b^*) < 0$).

Combining (A1) and (A2) yields the following condition that determines $b^*$:

$$\frac{\theta'(b^*)}{\kappa'(b^*)} = \frac{\gamma \theta(b^*)}{\rho + \gamma \kappa(b^*)}. \tag{A3}$$

The left-hand side of (A3) is weakly decreasing in $b^*$ because $\theta'' \leq 0$ and $\kappa'' \geq 0$. As for the right-hand side of (A3) defined as $\Phi(b^*) \equiv \gamma \theta(b^*)/[\rho + \gamma \kappa(b^*)]$, it can be shown that (A3) implies $\Phi'(b^*) = 0$. Therefore, we need to assume that at least one of $\theta'' \leq 0$ and $\kappa'' \geq 0$ is a strict inequality to ensure the existence of a solution $b^*$. If $b^*$ falls within the range of brain size $b_i \in [b^{\mathrm{min}}, b^{\mathrm{max}}]$, then families with the optimal brain size $b^*$ will dominate the population in the long run and have a steady-state level of population that is equal to the threshold $\widetilde{N}$ in (A2). In this case, given an initial value $b_0$, the average brain size $b_t \equiv \sum_{i=1}^m s_{i,t} b_i$ rises towards $b^*$ as $s_{i,t}(b_i = b^*) \to 1$.[14]

For example, suppose $\theta(b_i)$ and $\kappa(b_i)$ now take the following functional form: $\theta(b_i) = 1 + \overline{\theta} b_i$ and $\kappa(b_i) = \overline{\kappa} b_i^2$, where $\overline{\theta} > 0$ and $\overline{\kappa} > 0$ are parameters. In this case, the optimal brain size $b^*$ from (A3) is determined by the following quadratic equation:

$$(b^*)^2 + \frac{2b^*}{\overline{\theta}} = \frac{\rho}{\gamma \overline{\kappa}}, \tag{A4}$$

in which the solution $b^* > 0$ is increasing in the hunting-gathering productivity parameter $\overline{\theta}$. If $\overline{\theta}$ becomes sufficiently large, it is possible for $b^*$ to even exceed the upper bound $b^{\mathrm{max}}$, in which case the average brain size $b_t$ converges to $b^{\mathrm{max}}$ as in Section 3.

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[14] Here, we assume that the average brain size at time 0 is below $b^*$.