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Why did the human brain size evolve? A way forward

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Why the human brain size evolved has been a major evolutionary puzzle since Darwin but addressing it has been challenging. A key reason is the lack of research tools to infer the causes of a unique event for which experiments are not possible. We describe how the analogous problem of why there is day and night has been successfully addressed in physics and learning from that experience, we outline a strategy to address why the human brain size evolved: hypotheses are expressed in mechanistic models that yield quantitative predictions for evolutionary and developmental trajectories of brain and body sizes, the predicted trajectories are compared to data, and models are chosen by their ability to explain the data. By pursuing this strategy, we present results from one model that predicts evolutionary and developmental trajectories for six hominin species. We compare these predictions to data, finding that the model recovers multiple but not all aspects of hominin evolution and development. Counterintuitively, the human brain size evolves in this model as a spandrel, that is, as a byproduct of selection for something else, specifically, preovulatory ovarian follicles. Our analysis describes an alternative way forward to infer why the human brain size evolved.

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1. Introduction

Human evolution is characterised by a large brain expansion observed over the last 4 million years. Australopiths had a brain size about 2 times larger than expected for their body size, slightly larger than the brain size of chimpanzees. Over time, brain size tripled from australopiths to modern humans and became over 5 times larger than expected for the body size of *Homo sapiens* [1]. Evidence suggests that this brain expansion involved a concomitant increase in neuron number, as interspecific comparisons show that larger brains tend to have more neurons [2]. Increasing the number of neurons in artificial neural networks (typically described by increasing the number of synapses, which are called parameters) is key to increase their performance given a network architecture, and doing so has played a central role in the ongoing revolution of artificial intelligence [3], Fig. 22.7 in [4], [5]. These and multiple other lines of evidence suggest that hominin brain expansion underpinned large increases in cognitive abilities.

A longstanding question has thus been *why* such brain expansion happened. This is a "why" question in that it asks for causes of an event, rather than a "how" question that asks for descriptions of an event. This "why" question is particularly challenging and has been thought to be unanswerable [6–9]. Indeed, while "why" questions can be answered by studying the effects of interventions that are either human-made as in artificial selection experiments or natural as in comparative analyses, both types of interventions are largely infeasible for human brain expansion: human-made experiments are largely infeasible because of practical or ethical reasons and natural experiments because of the evolutionarily unique nature of human brain expansion. Consequently, the question asks about an effectively single data point corresponding to humans for which data must typically be observational, leaving the problem of why the human brain size evolved with a severe dearth of research tools.

An active yet problematic approach to the question is based on correlational analyses. In that approach, hypotheses are formulated, which often emphasize ecological [10–13], social [14–17], or cultural [18–22] factors as selecting for larger brains. Then, proxy variables are chosen as being relevant to each hypothesis, such as diet type [23,24], environment productivity and precipitation variability [25], group size [16], or social learning frequency [26], and they are tested for whether they correlate with brain size or the size of particular brain regions. Finally, if the proxy variable of a hypothesis correlates with the brain variable, or if it is more strongly correlated than the other proxy variables, then the correlations are interpreted as supporting the hypothesis. However, such conclusion does not necessarily follow from the analysis, including because those correlations do not imply selection as they may arise from myriad other reasons, the directions of causality may be reversed to the given interpretation, causal connections between the variables may not be evolutionary, and correlations may be spurious. Hence, these correlational analyses provide limited evidence for or against the hypothesis considered [27–29].

We outline an alternative way forward to infer why the human brain size evolved by borrowing ideas from physics. We discuss an application of such a strategy and its findings so far, which suggest that, counterintuitively, the human brain size could be an evolutionary byproduct of selection for another trait: in the words of Gould & Lewontin [30], the human brain size could be a spandrel. We discuss whether or not these findings are consistent with available data from fossil and living hominins. In addition, we briefly discuss potential risks of this strategy and possible ways to mitigate these risks.

2. Social learning from physics

Inferring why the human brain size evolved is particularly challenging because it asks about the causes of a unique event for which experiments are largely impossible. Despite this difficult combination, analogous challenges have been successfully tackled in physics. We consider the following example as a model to copy strategies that could help address why the human brain size evolved.

Consider the question of why there is day and night. An answer was suggested by Ptolemy's hypothesis around 150 AD that the sun revolves around the earth, which was consistent with the evidence at the time, as the sun moves daily from east to west. An alternative hypothesis suggested by Copernico around 1543 was that, instead, the earth revolves around the sun, which Kepler found around 1609 to be more consistent with the evidence gathered with telescopes. Kepler also found that planets follow trajectories around the sun that are eliptical rather than circular as previously thought and used equations to describe the trajectories. So far these explanations are causally relatively shallow, as they do not explain why planets rotate around the sun. Around 1687, Newton proposed a causally deeper explanation, namely, the existence of a universal force of gravitation that pulls masses together. By writing this law of gravitation and his laws of motion in equations, he produced a mechanistic mathematical model for planetary motion, from which he derived Kepler's equations for the elliptical planetary trajectories. That is, Newton's mechanistic model predicted trajectories that matched observation. Later in 1859, Le Verrier found that Newton's model did not accurately predict Mercury's precession, that is, the rotation of the elliptical trajectory of Mercury around the sun. In 1915, Einstein proposed general relativity, which gave another mechanistic model for planetary motion, where gravity is no longer a force, but a fictitious force arising from the curvature of spacetime caused by large masses. Einstein's model was found to not only predict the eliptical trajectories of planetary motion but also to correctly predict Mercury's precession. This and all other evidence to date finds Einstein's model to better predict observations than Newton's. This process has thus converged on an causally deep answer to the question of why there is day and night: because the earth rotates around the sun due to the curvature of spacetime caused by the large masses of the sun and its planets.

This approach suggests a strategy that we can borrow to address the question of why the human brain size evolved. As with human brain expansion, the solar system was effectively unique until recent years as other solar systems could not yet be observed. Experiments are also impossible on the solar system. Thus, the solar system involves the basic combination of being effectively unique and unexperimentable, for which our available tools would have limited ability to infer causes. Despite this combination, physicists have converged to an answer by following the strategy: (1) determine the trajectories to explain; (2) formulate mechanistic models of the trajectories; (3) test the predicted trajectories; and (4) keep the model(s) that best explain the observed trajectories. For the physics example, these steps involved: (1) Kepler's determination of elliptical trajectories to explain; (2) Newton and Einstein's formulation of mechanistic models of the trajectories; (3) Le Verrier and others' tests of the predicted trajectories; and (4) the choice of Einstein's model given its more accurate predicted trajectories. The data used in this approach is not experimental but observational and the analysis is not correlational but mechanistic.

3. Applying the physics strategy

Recent work has sought to apply this strategy to infer why the human brain size evolved. The steps so far have involved: (1) choosing the trajectories to explain as being the evolutionary trajectories of brain and body sizes over hominin evolution and the developmental trajectories of brain and body sizes for various hominin species from birth to adulthood; (2) formulating a mechanistic mathematical model, hereafter the brain model [31–33], that yields quantitative predictions for the development and evolution of hominin brain and body sizes; and (3) testing the predicted evolutionary and developmental trajectories of hominin brain and body sizes. Step 4, which consists of comparing mechanistic models or model variations, has not been undertaken yet as only one model has been studied so far.

The brain model is based on energy conservation, which is commonly used in physics to derive mechanistic models. The brain model considers an individual's energy consumption at rest, partitioned into that due to growth and maintenance, taking into account the metabolic costs of tissue production and maintenance, including of the brain. The brain's energy consumption is assumed to be partly due to learning and memory of skills that enable the individual to obtain energy from the environment. The model considers only females, whose fertility is proportional to their pre-ovulatory ovarian follicle count. The model assumes that genes control the fraction of energy available for growth that is allocated to the growth of each tissue at each age. An individual's genotype thus modulates the growth rate of her tissues, whereas an individual's phenotype is her brain size, body size, follicle count, and skill level at each age.

This brain model yields a wide range of quantitative predictions, many of which correspond to observed patterns of development and evolution of human brain and body sizes, including the timing of human childhood, adolescence, and adulthood [31–33]. Yet, as step 4 has not been undertaken, this model only suggests why the human brain size *could* have evolved, and more models or model variations need to be studied before the strategy can converge on best causal explanations of why human brain expansion actually happened.

4. Testing the predictions

To illustrate the proposed strategy to infer why the human brain size evolved, we now qualitatively compare some of the model's predictions with empirical data observed in or inferred from the hominin fossil record and modern humans. We focus this assessment on three types of predictions, and we organize our evaluations from the most solid based on the fossil evidence, to the most speculative. These three types of predictions are: (a) evolutionary trajectories of adult brain and body sizes for six hominin species; (b) developmental trajectories over individuals' life span for these species; and (c) two key elements identified by the model as causing hominin brain expansion: time budgets for energy extraction and the effect that learning has on energy extraction efficiency.

(a) Evolutionary change in adult brain and body sizes

We begin our qualitative testing of the model by comparing adult brain sizes predicted by the brain model [33] with adult brain sizes (proxied by endocranial volumes) observed in the hominin fossil record. The model has been shown to accurately recover the evolution of adult brain and body sizes for all major species of the genus *Homo* and less accurately for *Australopithecus afarensis* at the final points of the predicted evolutionary trajectories [32,33]. We here analyse the correspondence of the model predictions along the complete evolutionary trajectories rather than only at their end.

To understand the predictions, first consider some methodological aspects. The model predictions are found to depend on the ancestral conditions, which means that there are hard phylogenetic constraints that are typically absent in evolutionary models ignoring development [33]. Thus, to start the model from a realistic point, the model is run under conditions, that is, parameter values, that yield the evolution of *Australopithecus*-like brain and body sizes (such parameter values are described in the bottom gray box of Fig. 1a, which yields the bottom trajectory in Fig. 1a; the computer code used to generate all figures uses that of [33] and is available online as Supplementary Information). Organisms with the resulting genotype (at yellow circle in the bottom trajectory in Fig. 1a) are then exposed to different conditions (top gray box of Fig. 1a and gray boxes of Fig. 1b-f), which yields an immediate plastic response in the phenotype (the start of the top trajectory of Fig. 1a, and of the trajectories in Fig. 1b-f). Depending on such conditions, subsequent evolution then converges to adult brain and body sizes of *H. sapiens*, *H. neanderthalensis*, *H. heidelbergensis*, *H. erectus*, *H. ergaster*, and *H. habilis* (the top trajectory of Fig. 1a, and the trajectories in Fig. 1b-f). These are the predicted evolutionary trajectories that we test. Each evolutionary time step (τ) lasts the time it takes for rare mutants to fix; to illustrate how our predictions may translate to real time, we use the yardstick that mutant fixation takes 11.5 kyrs (calculated by assuming that mutant fixation takes 500 generations and one generation for females is 23 years [34]). This is only for illustration, as a better approach is to calculate time to fixation from the selection coefficient [35], but we leave that for future work as the parameter (η_1) controlling evolutionary speed in the model has not yet been calibrated with data.

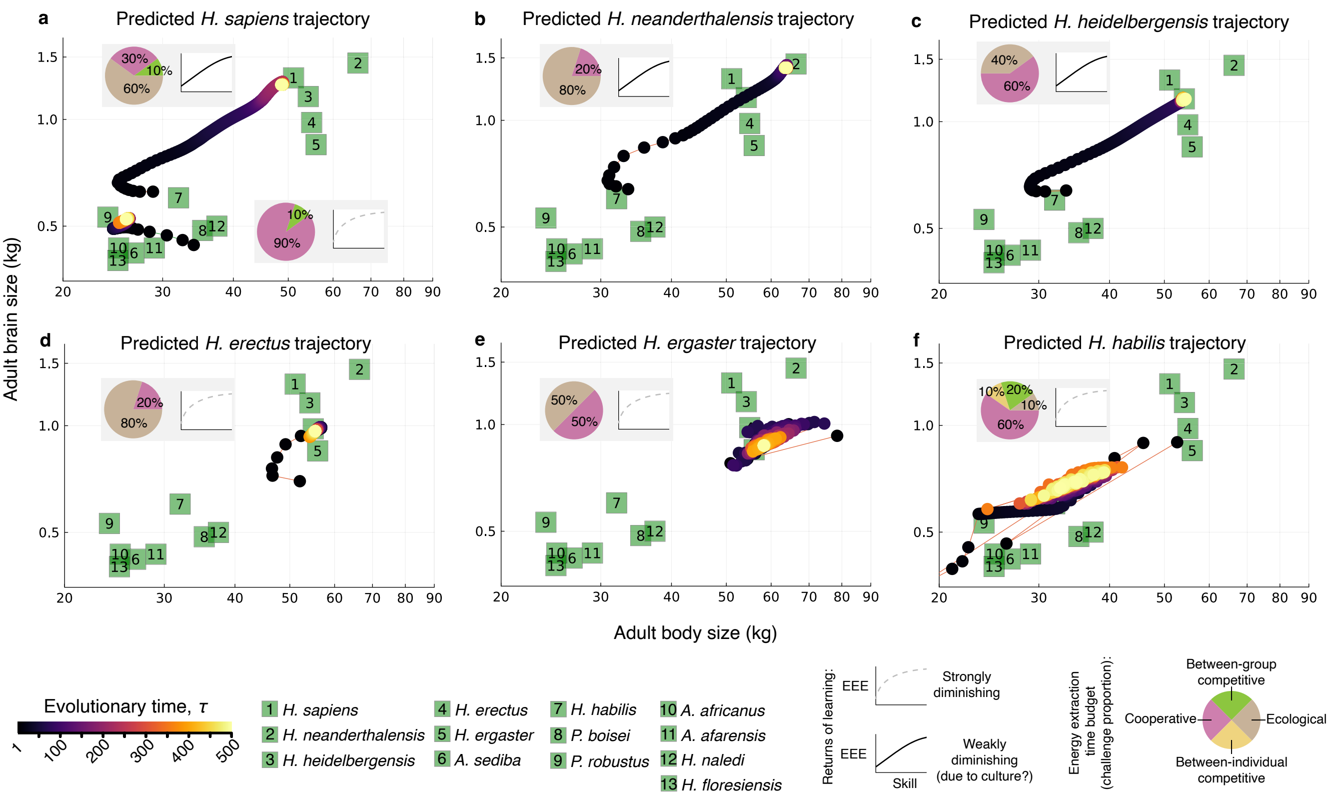

Figure 1. Predicted evolutionary trajectories. Each small circle shows the predicted adult brain and body sizes at a given evolutionary time. Gray boxes describe the used parameter combinations, which represent energy extraction time budgets and returns of learning. Green squares show the observed adult brain and body sizes in several hominin species (data from refs. [36–47] using only female data when possible). **a,** The bottom trajectory uses parameter values such that starting from a chosen initial condition the model converges to brain and body sizes that are of *Australopithecus* scale. The top trajectory starts with the evolved genotype of the bottom trajectory but uses different parameter values, which yields an immediate plastic change in brain and body sizes and the evolution of adult brain and body sizes of *H. sapiens*. **b-f,** Repeating the same procedure of changing parameter values starting from the *Australopithecus*-like genotype yields the evolution of adult brain and body sizes of *H. neanderthalensis*, *H. heidelbergensis*, *H. erectus*, *H. ergaster*, and *H. habilis*. Panel **a** is taken with modification from [33]. EEE: energy extraction efficiency.

The predicted evolutionary trajectories for later *Homo* species have a better correspondence with fossil data, whereas the predicted evolutionary trajectories for earlier and smaller brained species more poorly correspond to fossil data (Fig. 1). The predicted *H. sapiens* trajectory corresponds relatively well with the values observed in the fossil record (Fig. 1a). This *H. sapiens* trajectory involves an increase from *H. habilis*-like values to brain and body sizes that are typical of *H. sapiens* over approximately 250 evolutionary steps, which would correspond to the approximately 2.8 Myrs from the origin of the genus *Homo* [48] with our yardstick that each evolutionary time step is 11.5 kyrs. The *H. sapiens* predicted trajectory corresponds to a certain extent to the strong increase in brain size attributed to late Pleistocene *H. sapiens* and the subsequent recent decrease in brain size experienced by Holocene modern humans [49] (Fig. 2a). Regarding the latter, empirical data indicate that brain size in modern humans has reduced from an average value of approximately 1450-1500 cc to an average value of approximately 1350 cc, and that this change has occurred over the last 3000 years [50]; however, the timing and reasons for this recent brain size decrease, and even if this decrease in brain size existed at all, remain controversial [50–52]. The brain model does recover a brain size decrease (of about 20 g, Fig. 2a), but this is of a smaller magnitude than that inferred from empirical data, as the model does not reach the very large brain sizes typical of late Pleistocene modern humans. With our time yardstick of 11.5 kyrs per evolutionary time step, this decrease in brain size would be predicted to occur earlier than indicated by the fossil record (from a brain size peak at evolutionary step 234 to step 250, there would be 184 kyrs). The late Pleistocene values we have just referred to correspond to mixed-sex samples whereas the brain model refers to females, which may account for some of the discrepancy given the differences in average brain size between males and females [49]. As for body size, given the vast variation in body size across different human populations and given that the brain model so far gives predictions for means rather than distributions, comparing the predicted body sizes with empirical data remains particularly preliminary. Indeed, the female body size achieved by the brain model (51 kg) is lower than the body mass reported by some studies for different groups of modern humans (58 kg for contemporary modern humans [41];

62 kg for Holocene foragers, 68 kg for Upper Palaeolithic modern humans, and 63 kg for early *H. sapiens* [53]), but similar to more recent estimates for present-day modern humans (49 kg [46] and 51 kg [38]).

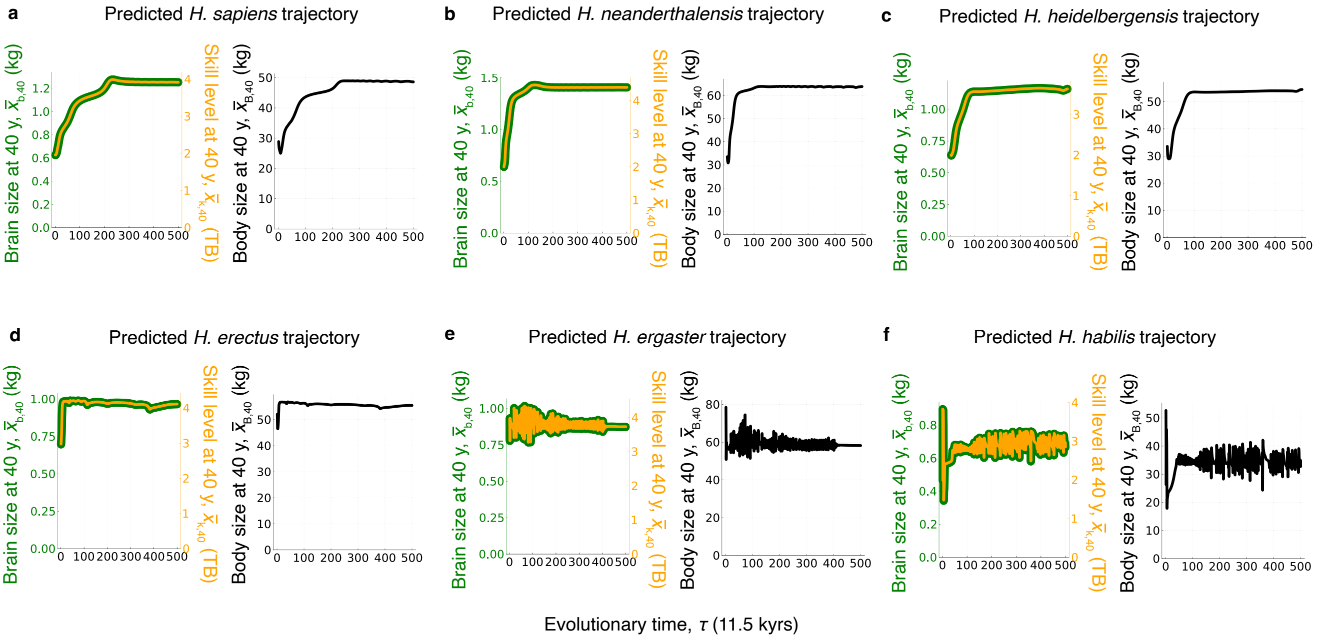

Figure 2. Predicted evolutionary trajectories over time. Plots show the predicted adult brain size, adult skill level, and adult body size over evolutionary time corresponding to the trajectories in Fig. 1. Panel **a** is taken with modification from [33].

The three predicted trajectories corresponding to the latest and largest-brained hominin species (*H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*) are relatively in line with what we would expect based on their evolutionary relationships (Fig. 1a-c). The early part of the three predicted trajectories is similar, starting from roughly similar phenotypic values that would correspond with a *H. habilis*-like ancestor (with predicted brain and body sizes respectively of 625 g and 28.8 kg, 639 g and 33.5 kg, and 639 g and 33.5 kg). In the three trajectories, brain and body size increase until they reach those corresponding to each species. For the predicted trajectories of *H. heidelbergensis* and *H. neanderthalensis*, and using our yardstick of 11.5 kyrs per evolutionary time step, the model reaches final values exceedingly fast, with the final values for brain and body size attained within the first 100 evolutionary time steps, which would correspond to approximately 1.1 Myrs from the beginning of the trajectory at *H. habilis* values (Fig. 2b,c). This abrupt increase in brain size is not supported by data from the fossil record, as *H. heidelbergensis* typical brain size is not attained until approximately 600 kya [54]. Empirical data indicate that *H. neanderthalensis* shows a fast increase in brain size from a *H. heidelbergensis*-like average brain size of 1241 cc in the early Neanderthals from Sima de los Huesos [55], dated to approximately 400 ka [56], to values of 1600-1700 cc in late Neanderthals dated to less than 100 ka, such as those from Le Moustier [57], La Ferrassie [58], Amud [59] or Shanidar [60]. However, as with *H. heldelbergensis*, *H. neanderthalensis* typical brain size values are attained earlier by the brain model than indicated by these empirical data. Body size within *H. heidelbergensis* shows a slight increasing temporal trend based on data from [25], but no clear trend is observed within the Neanderthal lineage, with early Neanderthals from Sima de los Huesos showing an average body size of 69 kg at 400 ka, already very similar to the average body mass of 70.5 kg estimated for classic Neanderthals [53]. The brain model does predict an early attainment and subsequent stability of Neanderthal typical body size, but, as with brain size, this is attained at an unrealistically early time point of approximately 100 evolutionary steps (1.15 Myrs) from a *H. habilis* typical body size.

The predicted *H. erectus* trajectory starts at values of approximately 700 cc, which is slightly below the range of variation observed in most Asian *H. erectus*, but rapidly stabilises at values of approximately 1000 cc (Fig. 2d), which are common for this sample [61,62]. Body size is also predicted to start off at values of approximately 45 kg, and to quickly stabilize at around 55 kg. Empirical data indicate a slower increase in brain size during the evolution of Asian *H. erectus* [63,64] rather than the rapid change predicted by the brain model.

The predicted evolutionary trajectory for *H. ergaster* is unrealistic, oscillating back and forth and eventually stabilising at combinations of brain-body sizes that are consistent with the values observed in this species. This trajectory starts off at relatively high brain and body size values, caused by a large plastic change induced by the change in parameter values. Both the abrupt change in parameters and the large plastic response of brain and body sizes to change in those parameters are likely unrealistic, the former because parameters may change more gradually in nature than the abrupt parameter change implemented, and the latter because developmental robustness probably limits strong plastic responses in brain and body sizes. Brain sizes for the *H. ergaster* trajectory move between 750 cc and more than 1000 cc, which is on the high side of the level of variation observed in *H. ergaster* specimens. Similarly, the predicted trajectory of body size for *H. ergaster* shows strong fluctuations in the initial part of the trajectory, which is unlikely to correspond to real evolutionary change. The initial segment of this trajectory shows body sizes between 50 kg and 80 kg, which exceed the range of variation estimated for *H. erectus* (43.4-60.9 kg), and it is largely above the estimated average value of 51.4 kg [46].

Likewise, although the brain model accurately recovers the average adult brain size of *H. habilis*, it does so through an even more unlikely evolutionary trajectory that moves back and forth between brain sizes of 400 cc to almost 1000 cc, and between body sizes of 20 kg to more than 50 kg, possibly also due to the unrealistically strong plastic response obtained at the starting time. A broad range of brain sizes has been suggested for *H. habilis*, particularly if this species is interpreted *sensu lato* and including *H. rudolfensis* [65], but the actual range of variation in brain size ranges from approximately 500 cc in KNM-ER 1813 [62,66] to approximately 800 cc in OH 7 [67]. Unlike later hominin species, *H. habilis* does not show a strong trend of overall increase in brain size during its evolutionary history [64], so, to some extent, the oscillations obtained in the brain model might correspond to the lack of a clear temporal trend within this species. As for body size, some studies calculate a quite low body size for *H. habilis* (32.6 kg, with a wide confidence interval from 22.5 to 47.5 kg [46]). While there is high uncertainty associated with these data, a clear increase in body size during the evolution of *H. habilis* does not appear likely, which would be again consistent with the results of the brain model [33].

(b) Species-specific developmental trajectories

We now seek to qualitatively test the predicted developmental trajectories for different hominin species. This test is limited, as empirical data on developmental trajectories is substantially more limited than for adult sizes. We focus on analysing predictions regarding the age at which adult brain size is attained across species.

Estimates for the age at which adult brain size is attained differ even in present day species. Classic studies indicate that 90-100% of adult brain size is attained at 5-7 years in humans [68,69], but more recent and extensive MRI-based analyses, which include some longitudinal datasets, indicate that total brain volume peaks at approximately 12 years in humans [70]. Adult brain size is estimated to be attained at between 2 and 5 years in chimpanzees [71,72] and at 3-4 years in mountain gorillas [73]. Given the association between adult brain size and time needed to reach it [74,75], it is expected that earlier smaller-brained hominin species will reach adult brain size earlier than later and larger brained hominin species. This trend is recovered by the brain model, with Neanderthals and modern humans being predicted to attain adult brain sizes beyond 12 years (Fig. 3a,e), *H. heidelbergensis* around 11 years (Fig. 3i), *H. erectus* at 7-8 years (Fig. 3m; see also refs. [76–78]), *H. ergaster* at 3-4 years (Fig. 3q), and *H. habilis* at 2-3 years (Fig. 3u).

Starting from *H. heidelbergensis*, the brain model predicts growth trajectories that are stepped with different brain growth spurts, the strongest one being that corresponding to the first year of postnatal life, although later than observed in smoothed cross-sectional curves [68,82,83]. A later and weaker pre-adolescent brain growth spurt is predicted by the brain model before the attainment of adult brain size at 10-12 years, whereas the intermediate childhood period shows a slower rate of growth. These brain growth spurts are not observed in human aggregated data [70], but more longitudinal datasets are needed to test the extent to which individual growth curves are smooth or stepped with different spurts. The brain model predicts a gradual evolution to this stepped trajectory (coloured dots in Fig. 3a; Supplementary Video 1 of [33]), with *H. heidelbergensis* showing an incipient version of the stepped trajectory, and Neanderthals and modern humans showing more clearly the separation between a fast postnatal brain growth, slow childhood brain growth, and fast but short pre-adolescent brain growth spurt. As with brain growth, body growth as predicted by the brain model also shows increasingly marked spurts in later hominin species. Attainment of adult body size happens at approximately 20 years of age in the model, which is slightly protracted with respect to empirical data [84–86].

Perhaps unrealistically although possibly insightfully, the evolved adult skill level predicted for most species within the genus *Homo* is very similar, at approximately 4 TB (Fig. 3d,h,l,p,t,x). The *A. afarensis* trajectory does result in a lower skill level of approximately 2 TB ([33] Extended Data Fig. 2d). The *H. habilis* trajectory recovers an initial increase in skill level that is followed by a strong reduction, after which it reaches a value of approximately 3 TB (Fig. 3x). All the other species are predicted to stabilize at an adult skill level that is close to 4 TB regardless of their different average brain sizes. For example, while the predicted difference in brain size between *H. erectus* (0.97 kg) and Neanderthals (1.41 kg) is 0.44 kg (45% larger brain in Neanderthals), the difference in skill level is only 0.3 TB (4.11 TB in *H. erectus* vs 4.40 TB in Neanderthals, so only 7% more skill in Neanderthals). The reason for the similar predicted adult skill level is that the model predicts, using a preliminary manual parameter fitting [31], that *H. sapiens*, *H. neanderthalensis*, and *H. heidelbergensis* had larger metabolic costs of memory ($B_{\mathrm{k}} = 50$ MJ TB^{-1} y^{-1}) than the other species ($B_{\mathrm{k}} = 36$ MJ TB^{-1} y^{-1}) [32]. Higher memory costs developmentally diminish adult skill level because the two are inversely proportional, as shown by a formula that relates adult skill level and brain size (resp. $\hat{x}_{\mathrm{k}}$ and $x_{\mathrm{bt_a}}$, where $\hat{x}_{\mathrm{k}} \propto x_{\mathrm{bt_a}}/B_{\mathrm{k}}$ [31]). The discrepancy between the strong increase in brain size and the weak increase in skill level seems inconsistent with the expectation of large increases in cognitive abilities over human brain expansion, but the transition to higher memory costs might indicate more complex skills being learned. This suggests that a transition might have occurred not so much in the quantity of skills but in their quality.

(c) Species-specific time budgets and returns of learning

The brain model predicts that changes in only two sets of conditions can yield the evolution of brain and body sizes of six major hominin species: the energy extraction time budgets and returns of learning (gray boxes in Fig. 1). First, we assess whether the energy extraction time budgets predicted by the brain model correspond to what is known or hypothesized regarding

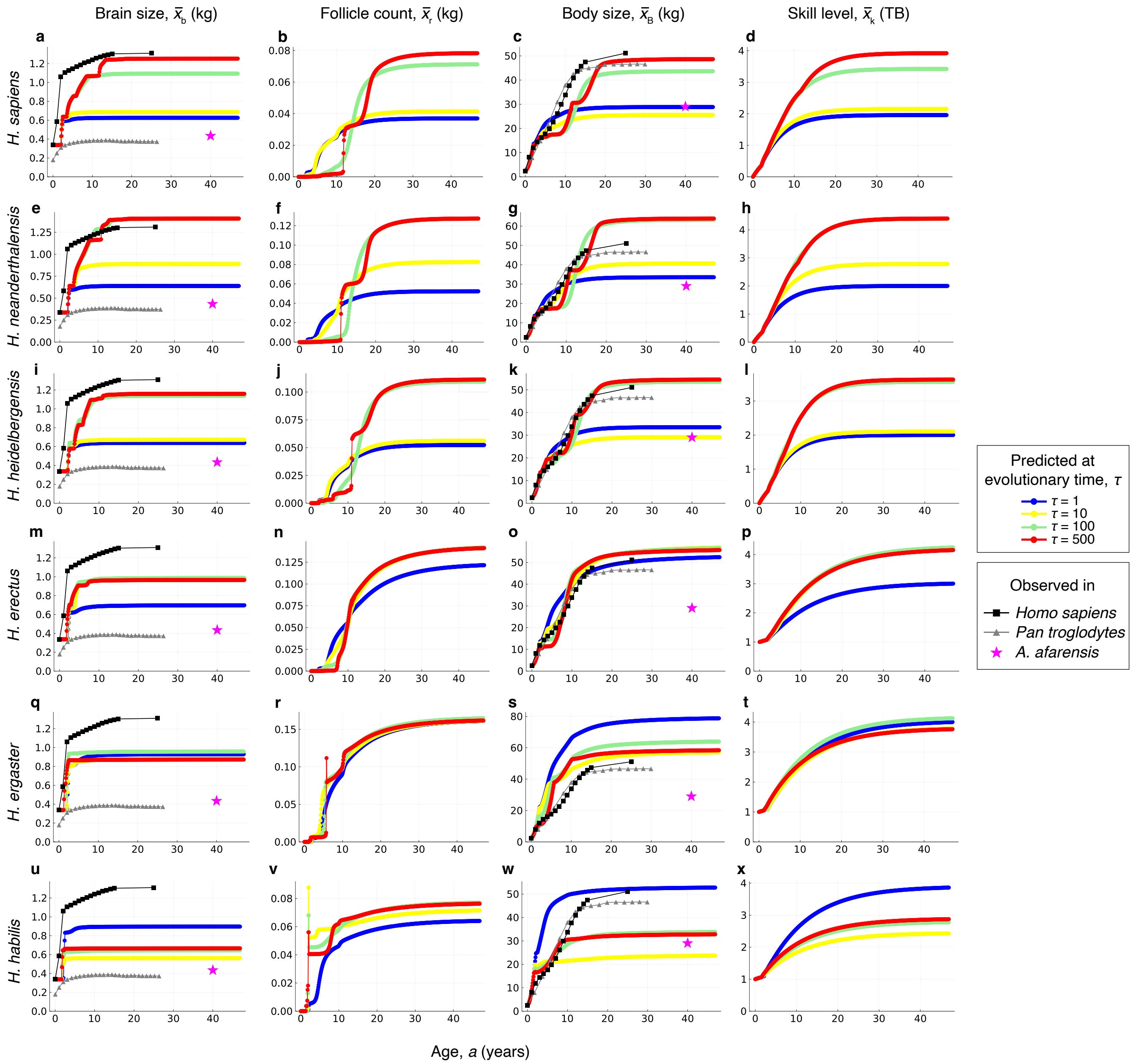

Figure 3. Predicted developmental trajectories. Panels show the developmental trajectories underlying the evolutionary trajectories shown in Fig. 1. Shown are the developmental trajectories for brain size, preovulatory ovarian follicle count, body size, and skill level. The mean observed values in a cross-sectional modern human female sample are shown in black squares (data from Table S2 of ref. [38] who fitted data from ref. [39]). The mean observed values in cross-sectional *Pan troglodytes* female samples are shown in gray triangles (body size data from Fig. 2 of ref. [79]; brain size data from Fig. 6 of ref. [68]). The mean observed values in *A. afarensis* female samples are shown in pink stars (data from Table. 1 of ref. [44]). For now, the model has used human neonatal brain and body sizes across all trajectories, as shown, but future work may incorporate available estimates for other hominin species [80,81]. Panels **a-d** are taken with modification from [33].

how hominins used their time. The brain model predicts that *H. sapiens* brain and body sizes evolved under a combination of ecological (60%), cooperative (30%) and between-group competitive challenges (10%), and that Neanderthal brain and body sizes evolved under a combination of ecological (80%) and cooperative challenges (20%). The differences in the predicted time budgets between Neanderthals and modern humans might reflect behavioural differences between both species [87,88]. That between-group competitive challenges are predicted in the *H. sapiens* time budget, but not in the *H. neanderthalensis* one, might arise if modern humans engaged more in building complex social networks [88,89].

Unexpectedly, the brain model predicts that the life of earlier hominin species was dominated by cooperative interactions to obtain food, and in later hominin species life became dominated by individual energy acquisition [32]. This seems to contrast observation, for instance, as cooperative feeding is variable in chimpanzees, with cooperative male hunting being more prevalent in Taï than in Gombe [90], and female cooperative foraging involving smaller groups than in males [91]. Yet, it has been suggested that cooperative breeding was required for the genus *Homo* to evolve a large brain size [92]. This suggestion may be consistent with the brain model in that substantive maternal or allomaternal care is needed for human-size brain evolution in the model and that cooperative foraging is predicted in early hominins. However, peer-cooperation is predicted by the model to cause the evolution of smaller brains because individuals can rely on others' skills [32], in accordance with previous suggestions [93] (but see [94]).

Interestingly, the two Eurasian hominin species, Asian *H. erectus* and *H. neanderthalensis*, are the two species where ecological challenges are predicted to be more prevalent, involving 80% of their energy extraction time budgets. It seems feasible that non-African environments, with strong temperature fluctuations, involved more prevalent ecological challenges, which the model predicts to cause brain expansion, in accordance with previous suggestions [11,95,96].

Second, we assess the other key factor causing human brain expansion as identified by the model, namely, the returns of learning, or the deceleration of energy extraction efficiency as skill level increases. All the model conditions reported above involve diminishing returns of learning: when an individual has low skill level, energy extraction efficiency increases substantially when she increases her skill level, but when an individual has high skill level, energy extraction efficiency does not increase so strongly when she increases her skill level. Now, some conditions allow learning returns to be either strongly or weakly diminishing: with the latter, the rate at which an individual's energy extraction efficiency increases when she increases her skill can be sustained as she learns, rather than decaying as with the former. In principle, weakly diminishing returns of learning could arise from culture if individuals can keep learning from accumulated knowledge in the population [32,33]. The brain model predicts a shift from strongly to weakly diminishing returns of learning, that is, to what could be cumulative culture, after the evolution of *H. erectus*, and before the evolution of *H. heidelbergensis*, meaning that *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens* are the only species considered that would be predicted to have, seemingly, cumulative culture. Interestingly, it has been suggested based on stone tool complexity that cumulative culture arose in Middle Pleistocene hominins [97], which would make cumulative culture part of the behavioural repertoire of *H. heidelbergensis, H. neanderthalensis*, and *H. sapiens*, consistently with the brain model. Similarly, other complex behaviours that would be indicative of cumulative culture, such as fire control and woodworking, are also thought to have evolved or consolidated during the Middle Pleistocene [98,99]. Yet, the treatment of culture remains implicit in the model, and a more explicit consideration of culture is needed before the model can make more decisive predictions on this regard.

5. Why does the human brain size evolve in the model? Human brain size as a spandrel

Given that the brain model recovers many, but not all, patterns of human brain evolution and development, we can use it to address our question of why the human brain size evolved, at least in this imperfect *in silico* replica. Sensitivity analyses, which are *in silico* interventions, show that, in the model, two key factors causing brain expansion from australopith to *H. sapiens* sizes are experiencing a challenging ecology and cumulative culture, specifically, facing more ecological challenges in the energy extraction time budget and transitioning from strongly to weakly diminishing returns of learning; in contrast, neither cooperation nor competition cause the predicted human brain expansion [32]. One would be inclined to interpret this as ecology and culture increasing selection for brain size, but this is not correct.

A mathematical framework integrating development and evolution [100] provides tools to analyse why human brain sizes evolve in the brain model, including to establish what is under selection. These tools show that the effects of ecology and culture in the model are not to change direct selection but genetic covariation. There is no direct selection for brain size in the model but only for preovulatory ovarian follicle count. Thus, in contrast with standard thinking, all the patterns described above including brain size expansion from *H. habilis* to *H. sapiens* are in a specific sense byproducts of selection for follicle count in the model: brain size evolves because it is genetically correlated with follicle count [33]. This positive genetic correlation means that mutations in the genotype that increase brain size also tend to increase follicle count, or mutations that decrease one also tend to decrease the other. Such genetic correlation is not necessarily present in the model but arises under certain conditions that affect development, that is, how brain size and follicle count are built according to the derived equations using energy conservation. These conditions include facing a challenging ecology and cumulative culture, which affect the individual's energy budget and so her development, in turn affecting the genetic covariation between brain size and follicle count. Thus, in the model, the human brain size evolves because a challenging ecology and cumulative culture affect development making preovulatory ovarian follicles and the brain genetically correlated. Indeed, by doing an *in silico* intervention where individuals both face more ecological challenges and switch from strongly to weakly diminishing returns of learning, an intervention that is mathematically proven in the model not to change direct selection but the genetic covariation between brain size and preovulatory ovarian follicles, the model finds that brain and body sizes evolve from those of australopiths to those of *H. sapiens* [33]. Thus, ecology and culture cause hominin brain expansion in the model, not by affecting selection, but by affecting development and so genetic covariation.

These findings mean that the human brain size in the model matches Gould and Lewontin's notion of a spandrel [30]: in the model, a higher follicle count is the "arch", which in our evolutionary context refers to what is under direct selection; instead, a larger brain is a byproduct of direct selection for ovarian follicles. Gould and Lewontin noted that spandrels need not be maladaptive; similarly, larger brains are not necessarily maladaptive in the model although they become slightly so: total selection for them is typically positive during early evolutionary times, and becomes typically slightly negative during late evolutionary times (Extended Data Fig. 3a of ref. [33]). Larger brains in the model are not under direct selection, which contrasts with the longstanding view that human brain expansion was caused by direct selection for increased cognitive ability or behavioural complexity increasing survival, as this is not the case in the model, with similar conclusions to those of [101]. Empirically, an aspect of human brain variation that has been linked to human-specific cognitive abilities, namely neurocranial globularity [102–104], has been suggested to be genetically associated with female reproductive tissues [105]. Indeed, Moltz and colleagues find that genes associated with endocranial globularity are also more highly expressed in the cardiovascular and female reproductive systems, which makes them suggest that changes affecting pregnancy and fertility can also affect brain structure as an indirect byproduct [105]. These empirical results align well with the results of the brain model.

It can also be said that brain expansion in the model is, counter-intuitively, caused by developmental constraints defined as the developmental rules imposed by the derived equations describing development. The developmental constraints that occur when individuals experience a challenging ecology and seemingly cumulative culture make brain and follicles genetically correlated in the model, triggering the evolution from *Australopithecus* to *H. sapiens* brain and body sizes. Without such developmental constraints, brain expansion is not directly favoured and human brain sizes do not evolve in the model, at least for the conditions evaluated so far; instead, with such constraints, brain expansion is still not directly favoured but evolves due to the genetic correlations generated. Thus, unexpectedly to us but as anticipated by Gould and Lewontin, and in agreement with proponents of an extended evolutionary synthesis [106,107], "constraints themselves become more interesting and more important in delimiting pathways of change than the selective force that may mediate change when it occurs" [30].

6. Conclusion

We have outlined a strategy to advance our understanding of why the human brain evolved. The strategy involves formulating mechanistic models that predict evolutionary and developmental trajectories, and model comparison to determine which model best explains the data. The strategy rests on the assumption that, while all models are wrong, some are less wrong. Difficulties may arise when deciding which models best explain the data, particularly if the least wrong models are equally wrong. These difficulties might be mitigated by models making wide-ranging predictions as the brain model does, which may diminish the possibility that the least wrong models are equally wrong, by "mak[ing] theories elaborate" as recommended by Fisher [27,108]. We have begun the illustration of this strategy by qualitatively testing a model's predicted evolutionary and developmental trajectories with available data, but quantitative testing is possible and there are rapidly advancing tools for this task [109]. Being a single model so far, the brain model has only answered why the human brain size could have evolved, in particular, as a byproduct of selection for ovarian follicles, which is consistent with recent empirical research [105]. To advance toward answering why the human brain size actually evolved, more models or model variations must be studied. While the proposed strategy has long been exploited in many scientific domains but has remained largely unexploited to establish why the human brain evolved, recent mathematical tools suggest this strategy may now be feasible.

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Data Accessibility. The computer code used to generate all the figures is available online as Supplementary Information. This code is that of [33] modified slightly to generate figures reported here.

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