



# Brain size and thermoregulation during the evolution of the genus *Homo*



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## ARTICLE INFO

### Article history:

Received 14 April 2015

Received in revised form 18 August 2015

Accepted 24 September 2015

Available online 3 October 2015

### Keywords:

Brain evolution  
Encephalization  
Energetics  
Hominids  
Plesitocene

## ABSTRACT

Several hypotheses have been proposed to explain the evolution of an energetically costly brain in the genus *Homo*. Some of these hypotheses are based on the correlation between climatic factors and brain size recorded for this genus during the last millions of years. In this study, we propose a complementary climatic hypothesis that is based on the mechanistic connection between temperature, thermoregulation, and size of internal organs in endothermic species. We hypothesized that global cooling during the last 3.2 my may have imposed an increased energy expenditure for thermoregulation, which in the case of hominids could represent a driver for the evolution of an expanded brain, or at least, it could imply the relaxation of a negative selection pressure acting upon this costly organ. To test this idea, here we (1) assess variation in the energetic costs of thermoregulation and brain maintenance for the last 3.2 my, and (2) evaluate the relationship between Earth temperature and brain maintenance cost for the same period, taking into account the effects of body mass and fossil age. We found that: (1) the energetic cost associated with brain enlargement represents an important fraction (between 47.5% and 82.5%) of the increase in energy needed for thermoregulation; (2) fossil age is a better predictor of brain maintenance cost than Earth temperature, suggesting that (at least) another factor correlated with time was more relevant than ambient temperature in brain size evolution; and (3) there is a significant negative correlation between the energetic cost of brain and Earth temperature, even after accounting for the effect of body mass and fossil age. Thus, our results expand the current energetic framework for the study of brain size evolution in our lineage by suggesting that a fall in Earth temperature during the last millions of years may have facilitated brain enlargement.

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## 1. Introduction

### 1.1. General framework

The large brain size of modern humans is widely recognized as energetically costly, and hence, explaining its evolution implies understanding two different issues. First, we need to know how different hominid species afforded the elevated cost of maintenance of this organ through the evolution of our lineage; that is, to understand the proximal causes that allowed brain enlargement from an energetic point of view (“prime releasers” *sensu Aiello, 1997*). Second, we need to know which were the adaptive advantages associated with larger brains through our history; that is, to understand the final causes that promoted brain enlargement (or “prime movers” *sensu Aiello, 1997*). Regarding the first issue, several specific hypotheses, which can be placed into a general framework, have been proposed in recent years (e.g., *Isler and van Schaik, 2006a,*

*2009; Navarrete et al., 2011*). According to this framework, a series of complementary pathways, which increased overall energy inputs (e.g., improved diet quality) or reduced energy allocated to some process (e.g., reduction in locomotion costs), allowed for the increase in brain size. In regard to the second issue, there are also several not-mutually-exclusive hypotheses which recall different advantages of larger brains at different moments and under different environmental contexts (see Discussion section). Some of these hypotheses identify the change in Earth climate that started about three million years ago (mya) as the main cause for the beginning of brain enlargement. For instance, the “proportional growth prolongation” hypothesis states that the long-term fall in Earth temperature may have caused a general increase in body size, which mainly occurred by prolonged fetal and early postnatal growth, and thus, resulted in an even greater increase in brain size due to allometric relationships (*Vrba, 1994, 1998*). Similarly, the “climatic variability” hypothesis points out that the long-term rise in Earth climatic variability may have favored an increase in brain size, since larger brains allow for novel behaviors that are important for survival in a wide range of environmental conditions (*Potts, 1998; Ash and Gallup, 2007*). Finally, the “pulsed climate variability” hypothesis identifies the extreme wet-dry climate short-term cycles, specifically

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recorded for East Africa, as the most important factor to explain – among other things – the largest change in brain size that occurred at 1.8 mya (Shultz and Maslin, 2013). Thus, climatic hypotheses for the evolution of brain size have been related with the progressive expansion of the savannas during a cooler and more arid period (Vrba, 1994; Reed, 1997), and also with long- and short-term periods of landscape variability characterized by fluctuating regimes in moisture, resource availability, and spatial heterogeneity (Shultz and Maslin, 2013; Anton et al., 2014).

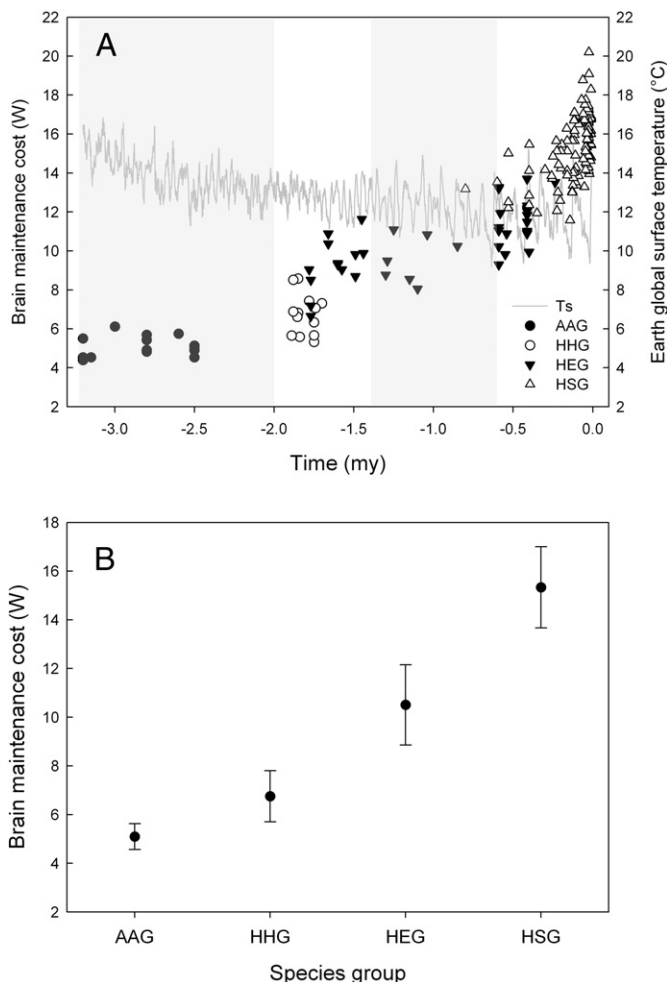
### 1.2. Changes in Earth temperature during the last 5 my

The Earth global surface temperature ( $T_s$ ) was fairly stable at ca. 16 °C from 5.0 to 3.2 mya, and then began a cooling phase that finished near the present at ca. 12 °C (Hansen et al., 2013). In turn, this cooling process can be divided into two periods during which  $T_s$  clearly fell – one from 3.2 to 2.0 mya and another from 1.4 to 0.6 mya (grey background in Fig. 1a) – and two periods of relative stasis in  $T_s$  – one from 2.0 to 1.4 mya and another from 0.6 to 0.01 (white background in

Fig. 1a) – (Marlow et al., 2000). In addition, the general cooling trend was not monotonic: temperature records from 5.0 to 0.8 mya were dominated by the response to the 41-ky period tilt forcing (with an increasing amplitude toward the present) and a low-amplitude 21-ky precession response, while temperature records from 0.8 mya to the present were dominated by 100-ky cycles (Miller et al., 2005).

### 1.3. Phenotypic adjustments to cope with a drop in ambient temperature

Homeothermic–endothermic animals exposed to a fall in ambient temperature below their critical lower temperature ( $T_{LC}$ , i.e., the temperature that defines the lower limit of the thermoneutral zone) can modify different phenotypic traits in order to cope with the concomitant increase in thermoregulatory costs (see McNab, 2002, 2012; Steegmann et al., 2002). First, they can increase the internal heat production through the use of active heat generation mechanisms, such as the futile cycle or shivering thermogenesis. Second, they can adjust other energetic variables, such as the basal rate at which internal heat is produced (e.g., by modifying the size of different organs) and/or lost to the environment (e.g., by modifying skin properties or subcutaneous fat thickness). In addition, some species can rely on hypometabolic responses (e.g., use of torpor) or on a circulatory separation between core and shell body temperature. Third, animals can modify morphological variables affecting their surface-to-volume ratio, such as body shape or body size. Finally, they can modify their behavior, changing, for example, the level of activity sustained in nature or the pattern of activity in time. Most of these phenotypic adjustments, however, do not provide any additional benefits to solving the thermoregulatory problem itself (e.g., increases in active heat generation, changes in thermal conductance or body shape, circulatory separation between core and shell temperature), or, even worse, they could entail important fitness costs by increasing, for example, predation risk (e.g., rise in activity levels). Thus, leaving aside some behavioral adjustments – like the use of shelters or, in our species, the use of fire and wearing clothes – an increase in body size has been classically visualized as the best evolutionary solution for the thermoregulatory problem imposed by a fall in ambient temperature (Bergmann, 1847; Hone and Benton, 2005). However, in recent years, it has been proposed that an increase in the size of visceral organs, which usually are composed of metabolically expensive tissues, could represent another “good” solution to this thermoregulatory problem (Naya et al., 2012, 2013). According to the “obligatory heat” model (Naya et al., 2013), during the colonization of a colder environment by a homeothermic–endothermic species, those individuals with larger visceral organs (and thus with greater basal rates of internal heat production) within a given population are no longer penalized for their “luxurious way of life.” This is simply because all the members of the population have to increase the generation of internal heat (in order to maintain a constant body temperature) in the new, colder, environment. Then, if greater masses of visceral organs are linked to greater physiological capacities (Diamond, 1998), those animals with larger organs will be now in an advantageous condition in relation to the other members of the population. This way, natural selection should result in a negative correlation between ambient temperature and mass-specific basal metabolic rates, and also between the former variable and the size of (at least some) metabolically expensive organs. It is important to mention that the “obligatory heat” model states that the specific physiological function that is enhanced as a by-product of selection for higher heat production rates could change depending on the attributes of each taxon and the selection pressures acting on them at a given evolutionary moment. For instance, according to Naya et al. (2013), “[p]erhaps adjustments in gut size affecting basal metabolic rates were selected in rodents, but changes in muscle metabolic intensity were selected in species of the order Carnivora; adjustments in the size of the heart, kidneys, and pectoral muscles could have been relevant for birds, but changes in the brain size occurred in primates.”



**Fig. 1.** (A) Temporal change in the energetic cost of the brain estimated for different hominid fossils (different signs) and in Earth's global surface temperature (grey line), and (B) brain's maintenance cost estimated for different hominids species groups (bars  $\pm$  1SD). AAG = *Australopithecus* species group (includes *A. afarensis*, *A. africanus* and *A. garhi*). HHG = *Homo habilis* species group (includes *H. habilis* and *H. rudolfensis*). HEG = *Homo erectus* species group (includes *H. ergaster*., *H. georgicus*, and *H. erectus*). HSG = *Homo sapiens* species group (includes *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*). Grey backgrounds in panel (A) indicate those periods during which Earth temperature clearly fell.

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