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

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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 identify 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 (Ts) 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 Ts 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 Ts – 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."
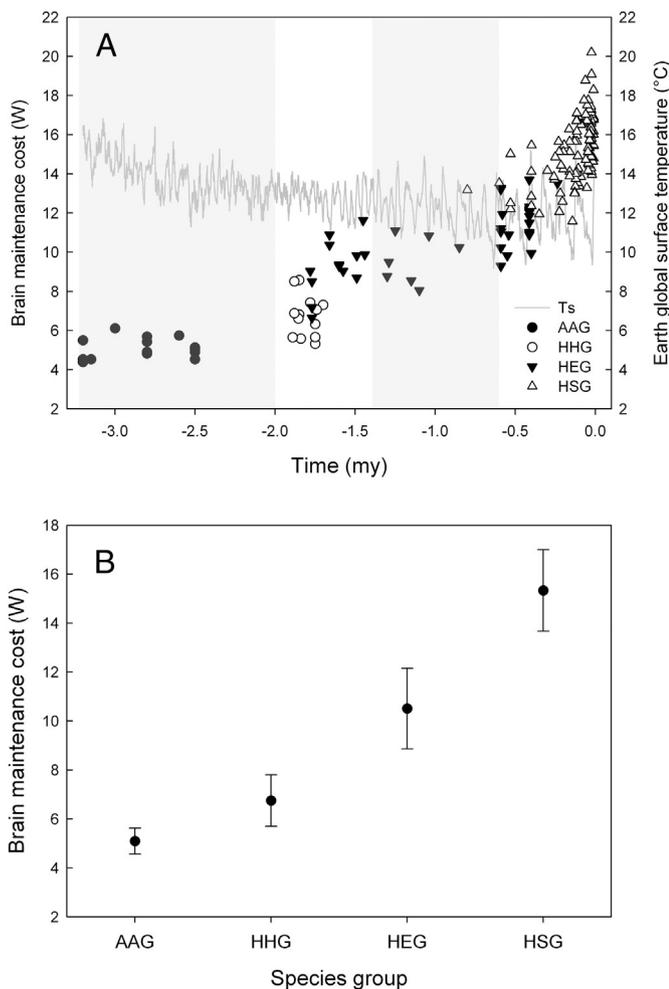
Fig. 1. *(A)* Temporal change in the energetic cost of the brain estimated for different hominid fossils (different signs) and in Earth's global surface temperature (grey line), and *(B)* brain's maintenance cost estimated for different hominids species groups (bars ± 1SD). AAG = *Australopithecus* species 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.

1.4. Energetic characteristics of the brain

The brain of modern humans represents a very active organ in terms of energy metabolism (it is the second most costly organ in absolute terms after the liver) and, in contrast to most of the other organs, its energy needs cannot be temporarily reduced (Aiello and Wheeler, 1995; Isler and van Schaik, 2009). In line with this, a study of 313 mammalian species indicates that there is a positive correlation between brain mass and basal metabolic rates, after removing the effect of body mass on both variables (Isler and van Schaik, 2006b). Noticeably, this correlation is much stronger for primates than for three other mammalian orders that were also evaluated (Isler and van Schaik, 2006b). Thus, current evidence suggests that variation in the size of the brain could have important thermoregulatory consequences, at least in primates. Moreover, at least for one other order of mammals, the cetaceans, the punctuated increase in brain size that occurred around 32 mya has been suggested as an adaptation for heat generation during the colonization of an energetically demanding environment (i.e., cold sea waters; Manger, 2006).

1.5. A new climatic hypothesis for brain size evolution

The aim of the present study is to propose a complementary climatic hypothesis, which is based on the mechanistic connection between ambient temperature, thermoregulatory costs, and internal organs size that exists in homeothermic–endothermic species (see Naya et al, 2013). Specifically, we hypothesized that the increases in thermoregulatory costs associated with the decrease in Earth temperature could represent an evolutionary driver for the evolution of an expanded, heat-generating brain – i.e., the fall in Earth temperature represented a "prime mover" for brain enlargement – or, at the very least, it could imply the relaxation of a negative selection pressure acting on brain size, due to its high cost of maintenance – i.e., the fall in temperature facilitated the action of other(s) "prime mover(s)" for brain enlargement. To test this idea, we estimated – and compared between them – the change in the energetic costs of thermoregulation and brain maintenance for different hominid species that inhabited our planet during the last 3.2 my. In addition, we analyzed the relationship between Earth global surface temperature and brain maintenance cost for the same period of time, taking into account the effect of body mass and fossil age. Note that in the two scenarios depicted above, it should be expected that (i) changes in thermoregulatory costs should be commensurable with changes in the maintenance cost of the brain and (ii) there should be a negative correlation between Earth temperature and brain maintenance cost during hominid evolution. However, while in the first scenario, we predict a strong correlation between Earth temperature and brain cost (because in this case, temperature is the cause behind brain enlargement), in the second scenario, we predict a much loose correlation between both variables (because in this case temperature only facilitates the action of other "prime mover(s)").

2. Material and methods

2.1. Estimation of brain maintenance cost and thermoregulatory costs during hominid evolution

Data from modern humans on mean cranial capacity (1350 cm^3) and energetic cost of the brain (14.6 W) were taken from Aiello and Wheeler (1995) and used to estimate the volume-specific cost of brain maintenance (0.0108 W/cm^3). Then, we combine this information with data on cranial capacity for hominid fossils, taken from Shultz et al. (2012), in order to estimate the energetic cost of brain maintenance for the latter (Online Table 1). Given the scarcity of data on brain mass-specific cost for primates, we assumed that no changes in this variable occurred through hominid evolution. In this sense, data for rhesus monkeys (Macaca mulatta) and modern humans indicate that mass-specific cost of brain maintenance is fairly similar in both species (0.037 and 0.033 ml O$_2$ g^{-1} min^{-1}, respectively; Parker, 1990).

Changes in the costs of thermoregulation during hominid evolution were estimated as the difference in the Earth temperature at two different times multiplied by the minimum thermal conductance recorded for modern humans. For this propose, we downloaded data on Earth global surface temperature (Ts) for the last 3.2 my (from Hansen et al., 2013), and data on minimum thermal conductance for modern humans (compiled by Haman, 2006). These last studies indicate that the rate at which the metabolic rate (at rest) increases with a decrease in air ambient temperature below the lower critical temperature (T$_{LC}$) is about 4.0 W °C^{-1} (95% range for 8 independent estimations: 2.2–5.7 W °C^{-1}). Note that T$_{LC}$ values in naked modern humans range between 28 °C and 22 °C, depending on subcutaneous fat thickness (from 0 to 40 mm) (Scholander, 1955; Kingma, 2011), whereas T$_{LC}$ in the seven primates species analyzed to date ranges between 22.5 °C and 36.6 °C (Takemoto, 2004). Thus, the fall in Earth global surface temperature that occurred during the last 3.2 my (from about 15 °C to 12 °C) probably dropped far below the T$_{LC}$ of all the hominid species included in our analysis. Finally, it is important to note that in primates, hypometabolic responses to lower ambient temperatures (e.g., torpor) – which could also affect the validity of our argument – have been reported for some small-sized Strepsirrhini, but not for Haplorrhini (Nowack et al., 2010).

Table 1
Partial correlation coefficient (r) and associated probability (P) for each independent variable, together with sample size (N), proportion of variance explained (r^2), and Bayesian Information Criterion value (BIC) for each regression model correlating brain maintenance cost (in W) with Earth global surface temperature (Ts) and/or body mass (m$_b$) and/or fossil age (FA). p = number of model parameters; ΔBIC = BIC model−lowest BIC.

|	Ts (°C)		m$_b$ (kg)		FA (my)		r^2	p	BIC	ΔBIC	N
	r	P	R	P	R	P					
All hominid species	–	–	0.17	0.003	−0.76	<0.00001	0.83	3	664.43	–	171
	−0.08	0.037	0.17	0.002	−0.71	<0.00001	0.83	4	665.04	0.61	171
	–	–	–	–	−0.91	<0.00001	0.83	2	681.19	16.76	175
	−0.08	0.048	–	–	−0.86	<0.00001	0.83	3	682.31	17.88	175
	−0.26	<0.00001	0.68	<0.00001	–	–	0.69	3	762.14	97.71	171
	–	–	0.80	<0.00001	–	–	0.64	2	783.87	119.44	171
	−0.58	<0.00001	–	–	–	–	0.33	2	915.52	251.09	175
Species belonging to Homo	−0.12	0.005	0.11	0.043	−0.75	<0.00001	0.78	4	602.12	–	158
	–	–	0.12	0.039	−0.79	<0.00001	0.77	3	605.08	2.96	158
	−0.08	0.048	–	–	−0.86	<0.00001	0.79	3	613.04	10.92	161
	–	–	–	–	−0.88	<0.00001	0.78	2	616.39	14.27	161
	−0.26	<0.00001	0.62	<0.00001	–	–	0.55	3	711.73	109.61	158
	–	–	0.70	<0.00001	–	–	0.49	2	726.76	124.64	158
	−0.47	<0.00001	–	–	–	–	0.21	2	815.90	213.78	161

2.2. Relationship between brain maintenance costs and ambient temperature for the last 3.2 my

To analyze the relationship between ambient temperature and brain maintenance cost, we used the data on Earth global surface temperature (Ts) for the last 3.2 my and the data on brain maintenance cost, estimated as explained above (Online Table 1). For each fossil, we estimated Ts for their specific date by interpolation. We prefer to work with point temperature estimations – instead of pooled data for 0.1 or 0.2 my intervals, as usually done – because artificial selection experiments show that some internal organs can noticeably increase their size after a few generations of intense selection (Konarzewski and Ksiazek, 2012). We evaluated the relationship between brain maintenance cost and Ts through standard least-squares regression techniques, using body mass (m_b) and fossil age (FA) as covariates (Online Table 1). Then, we estimated the goodness of fit (r^2) of the seven the possible models (i.e., combinations of Ts, m_b, and FA as independent variables), and used the Bayesian Information Criterion (BIC) to compare among them. Specifically, a model was selected as a "good model" if its BIC value did not differ from the overall best model BIC value – which represents, by definition, the lowest BIC value – in more than 2.3 units (Raftery et al., 1997). All these conventional analyses were conducted in R, using functions in "base" and "stats" packages (R Development Core Team, 2008).

In addition, we evaluated the effect of phylogeny on the relationship between the dependent variable (brain maintenance cost), the independent variable (Ts), and the covariates (m_b and FA), using a Bayesian Phylogenetic Mixed Model (Bayesian PMM; Naya et al., 2006; Hadfield, 2010), in addition to Bayesian Model Averaging (BMA; Raftery et al., 1997). We started with a recently published phylogenetic tree for great apes and hominids species (Fig. 2B in Organ et al., 2011) and then incorporated phylogenetic uncertainty (using BMA), since there are several polytomies in *Homo erectus* and *H. sapiens* species groups. In particular, phylogenetic uncertainty was included generating 100 trees in which polytomies were randomly resolved (by transforming all polytomies into a series of dichotomies with one or several branches of length zero), and branch lengths were randomly sampled from a uniform distribution (ranging between 0.01 and the maximum branch length). For each comparative model, the effect of Ts, m_b, and FA on brain maintenance cost was estimated from the proportion of posterior estimates larger than zero (gt0). In short, gt0 can be viewed as the probability of observing a positive (if gt0 > 0.5) or negative (if gt0 < 0.5) association between the dependent variable and each independent variable. Note that when the dependent variable (i.e., brain maintenance cost) is not affected by an independent variable (e.g., Ts), this probability is equal to 0.5 (i.e., the distribution of the regression coefficients is centered on zero). Finally, to select among phylogenetic comparative models, we used the deviance information criteria (DIC; Spiegelhalter et al., 2002). Specifically, a model was considered as a "good model" if its DIC distributions across different trees overlap the distribution of DIC values corresponding to the best model. In other words, a model was selected as a "good model" when its minimum DIC value (DIC_{min}) was less than the maximum DIC value (DIC_{max}) of the best model. All comparative analyses were performed using the software R, through packages "APE" (Paradis et al., 2004) and "bmaMCMCanalysis" (L. Spangenberg, R. Romero, and H. Naya; available upon request).

3. Results

Data on brain maintenance cost for modern humans indicate that (1) brain energetic cost in Australopithecine species that lived between 3.2 and 2.5 mya averaged 5.1 W (95% range: 4.6–5.6 W); (2) there are no fossils for the period between 2.5 and 2.0 mya, but when fossils reappear, the energetic cost of the brain was higher: 6.8 W (95% range: 6.2–7.3 W) for the species in the *H. habilis* group, and 8.9 W
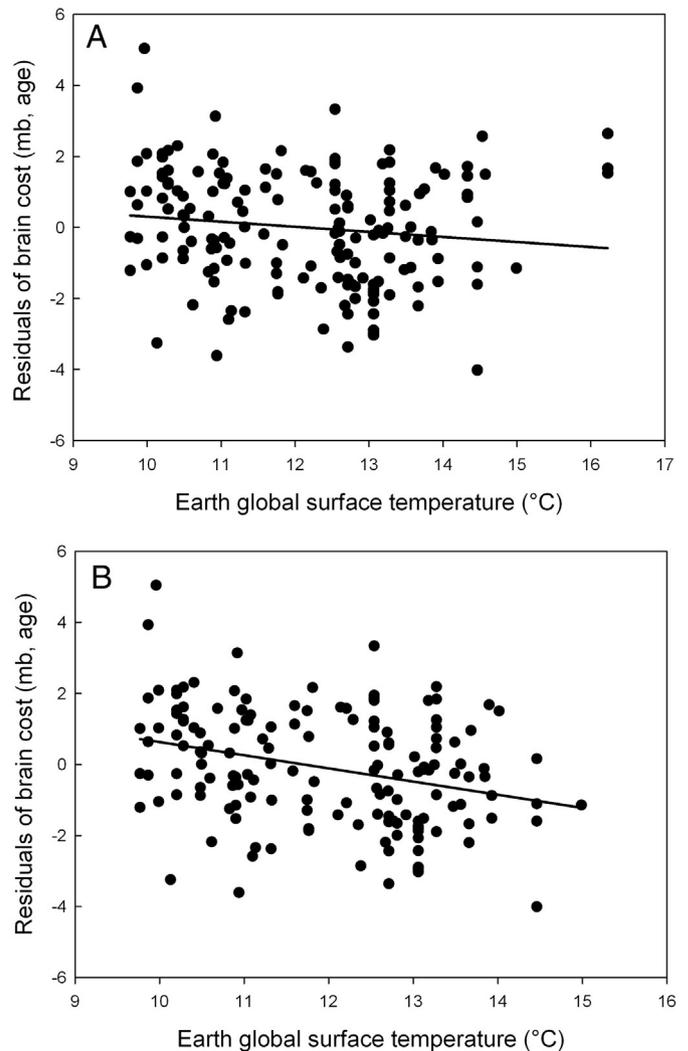
Fig. 2. Correlation between residuals of brain maintenance cost – with regard to body mass (mb) and fossil age (age) – and Earth global surface temperature for *(A)* all hominid species, and *(B)* species belonging to the genus *Homo*.

(95% range: 8.3–9.6 W) for the species in the *H. erectus* group that lived between 2.0 and 1.5 mya; (3) a fairly continuous increase in the energetic cost of the brain occurred during the last million years, ending 0.01 mya when the cost is set around 15.0 W (Fig. 1b). Based on data on thermal conductance for modern humans, we estimated that the increase in metabolic rate (at rest) associated with a fall in Earth temperature from 15 °C to 13 °C (i.e., from 3.2 to 1.8 mya) was 8.0 W, while the increase in metabolic rate (at rest) associated with a fall from 15 °C to 12 °C (i.e., from 3.2 mya to the present) was 12.0 W. Both values are above the energetic difference due to brain enlargement from Australopithecines to *H. erectus* (3.8 W) and from Australopithecines to *H. sapiens* (9.9 W), and at the same time, the energetic cost associated with brain enlargement represents an important fraction (i.e., between 47.5% and 82.5%) of the increase in energy needed for thermoregulation during hominid evolution.

Finally, we found that for all hominid species and also for species belonging to the genus *Homo*, fossil age (FA) is the best predictor (i.e., higher partial correlation coefficient) of brain maintenance cost (Table 1). This indicates that, at least, one other factor correlated with time was more relevant than Earth temperature (Ts) for the increase in brain size. However, we also found that there is a significant negative correlation between brain cost and Ts, even after accounting for the effect of both m_b and FA (Table 1; Fig. 2). In addition, the model that includes all the three independent variables (i.e., Ts, m_b and FA) is one

of the two models selected as "good models" for the case of all hominids species, and the only model selected as a "good model" for the case of species belonging to the genus *Homo* (Table 1). In line with this, DIC values indicate that the model including all the three independent variables (i.e., Ts, m_b and FA) also represents one of the two models selected as "good models" in the phylogenetically informed analysis (Table 2). Thus, available data suggest that changes in Earth temperature have been related with brain enlargement, in particular for those species belonging to the genus *Homo*.

4. Discussion

4.1. A brief overview of current explanations for enlarged brains in Homo

Brain evolution in *Homo* represents a paradigmatic case in which there is much more interest than data, resulting in numerous relevant hypotheses that are hard to test (Gibbons, 2013). Most of these hypotheses identify the evolution of bipedalism as a central factor leading to several interconnected phenotypic changes, which then had acted as "prime releasers" or "prime movers" for brain size evolution (Fig. 3). Here, for the sake of simplicity, we divide these factors into three categories:

(1) Energetic factors: since bipedalism represents a more economic way of locomotion, a greater amount of energy can be allocated to other energetically costly process, such as brain enlargement (Isler and van Schaik, 2009). At the same time, bipedalism allows for the liberation of the hands permitting tool production and use. These two changes are thought to increase the efficiency of hominids as active hunters, leading to a rise in food availability and diet quality (i.e., animal meat). In this sense, it is noteworthy that among living primates, the relative proportion of energy allocated to the maintenance of the brain is positively correlated with dietary quality (Leonard et al., 2003). In addition, the control of fire allowed hominids to cook food, increasing its digestibility (Wrangham and Conklin-Brittain, 2003). High-quality diets probably caused a reduction in feeding time (Organ et al., 2011) and maybe also in the size of the digestive tract, which is one of the most expensive systems in terms of energy and proteins; thus, additional energy could be allocated to brain enlargement (the "expensive tissue" hypothesis; Aiello and Wheeler, 1995; but see Navarrete et al., 2011). Finally, both the increase in energy inputs (due to the increase in food quantity and quality), and the reduction in energy allocated to locomotion and maintenance costs (due to bipedalism and gut size reduction, respectively), may result in the ability to support a larger number

of descendents, and consequently, in larger group size. Thus, energetic factors are interconnected with social factors (see below), since the use and control of fire has been related with sexual division of labor and novel implications for the regulation of social behavior (Wrangham et al., 1999), and also with thermoregulatory factors (see below), since larger group size is expected to increase ectoparasitic load, which may favor the loss of body hair (Rantala, 2007).

(2) Thermoregulatory factors: Heat dissipation is considered a central issue in brain evolution in *Homo*, because the human brain is extremely sensitive to changes in body temperature. Thus, it is possible that large brains could suffer important damages from heat stroke events, mainly during active hunting in hot environments (Carrier, 1984). In line with this, several adaptations for efficient heat dissipation appear to have co-evolved with brain enlargement in the lineage leading to and including *Homo*. Some of these adaptations include (i) the replacing of a body hair covering by a layer of fat that permits an efficient heat loss by sweating, and that can be "by-passed" during heat stress through vasodilatation of the capillaries in the skin (Wheeler, 1984); (ii) the retention of hair on the head, which protects the surface of the body most exposed to solar radiation at midday and reduces the amount of heat reaching the brain by conductivity from the cranium (Wheeler, 1984), and (iii) the presence of complex anatomical modifications in blood circulation pattern that permit rapid heat dissipation from the brain to the rest of the body (i.e., the "radiator" hypothesis; Falk, 1990). Again, bipedalism is at the base of several of these changes, since it is considered a pre-requisite for the adaptive loss of body hair. The reason for this is that bipedalism allowed a noticeable reduction in the area of the body that is exposed to the incoming rays of the sun, and also because it increases the height of the body over the floor level, increasing the amount of heat that can be dissipated by convective process (Wheeler, 1984). Finally, as thermoregulatory factors are fundamental "prime releasers" for both active hunting and brain enlargement, they are tightly linked with many energetic and behavioral factors.

(3) Behavioral and social factors: as we mentioned above, bipedalism allowed for a greater efficiency of active hunting. In turn, active hunting may determine a greater level of cooperation between individuals (the "Man the Hunter" hypothesis; Washburn and Lancaster, 1968), increasing social interactions and the need for more efficient ways of communication (i.e., allowing the evolution of cognition, language, and symbolic culture). All these changes may have favored other cooperative behaviors (e.g., cooperative breeding) as well as site stability, leading to

Table 2
Parameter estimation (B), standard deviation (SD), and proportion of posterior estimates larger than zero (gt0) for each independent variable, together with the deviance information criteria (DIC) for each model, according to phylogenetically informed analysis. Ts: Earth global surface temperature, m_b: body mass, FA: fossil age.

	Ts (°C)			m_b (kg)			FA (my)			DIC_{min}	DIC_{max}
	B	SD	gt0	B	SD	gt0	B	SD	gt0		
All hominid species	–	–	–	7.6	2.6	>0.99	−206.4	37.2	<0.001	2129	2132
	−6.2	8.3	0.23	7.4	2.6	>0.99	−205.4	37.1	<0.001	2130	2135
	–	–	–	10.4	2.9	>0.99	–	–	–	2143	2144
	−6.1	8.8	0.24	10.2	2.9	>0.99	–	–	–	2145	2146
	–	–	–	–	–	–	233.5	38.9	<0.001	2181	2184
	−8.5	8.3	0.15	–	–	–	−230.2	38.1	<0.001	2182	2185
	−10.5	8.8	0.11	–	–	–	–	–	–	2201	2201
Species belonging to *Homo*	–	–	–	7.3	2.7	>0.99	−207.8	43.2	<0.001	1975	1978
	−8.3	8.9	0.18	7.0	2.7	>0.99	−210.8	43.3	<0.001	1977	1979
	–	–	–	10.3	3.0	>0.99	–	–	–	1988	1989
	−5.9	9.2	0.26	10.0	3.0	>0.99	–	–	–	1990	1991
	–	–	–	–	–	–	−232.3	43.5	<0.001	2015	2016
	−11.1	8.8	0.10	–	–	–	−233.6	43.6	<0.001	2016	2018
	−10.6	9.3	0.13	–	–	–	–	–	–	2032	2033
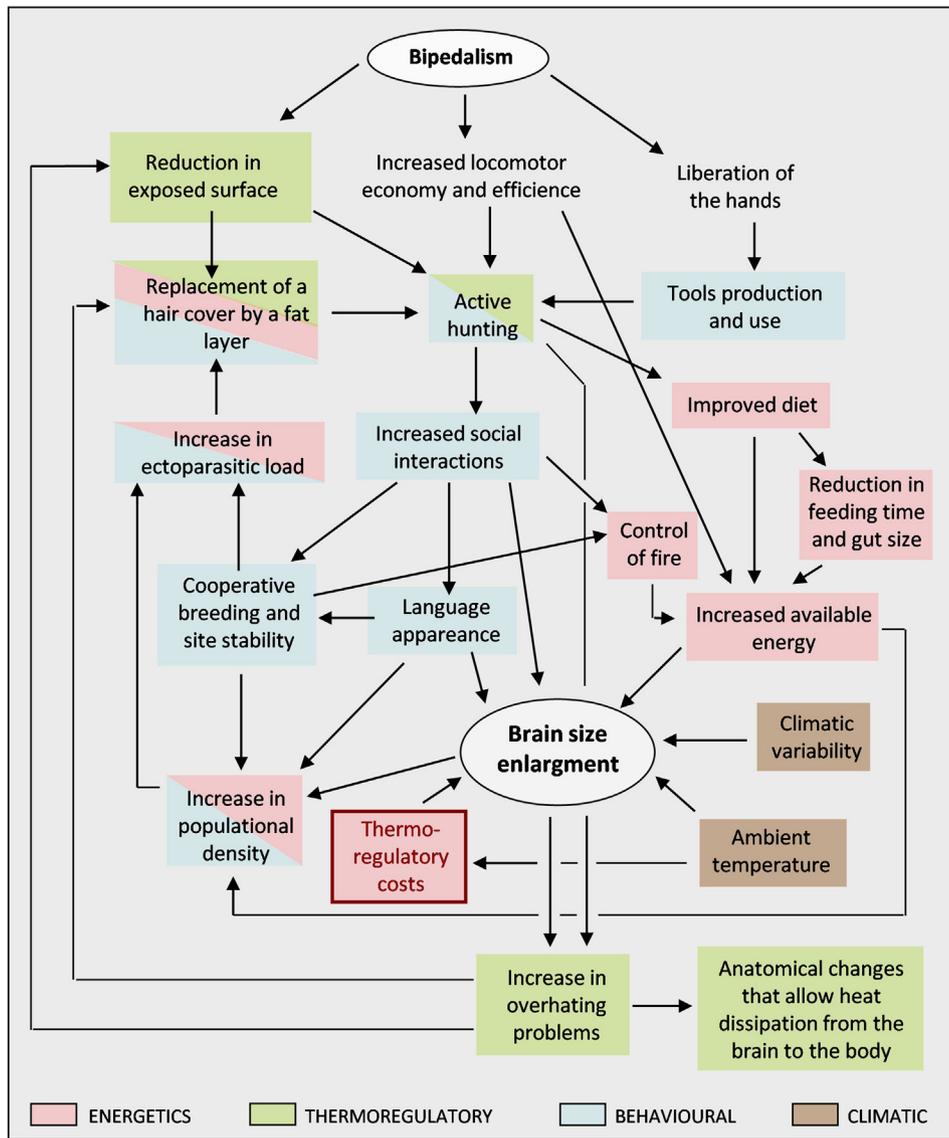
Fig. 3. Diagram depicting some potential factors that have been proposed as "prime movers" and/or "prime releasers" of brain enlargement in hominids (*sensu* Aiello., 1997), and their putative causal relationships. For the sake of simplicity, feedback loops between different factors (e.g., social interaction and language) and between factors and brain size (e.g., energy availability and brain size) are not represented.

larger group size. In addition, more social interactions among member of larger groups may have resulted in the development of greater social intelligence, which is mainly related with the increase of the neocortex area of the brain (the "Machiavellian intelligence" hypothesis, Byrne, 1996; and the "social brain" hypothesis, Dunbar, 2003). Note that cooperative behaviors resulting in larger group size link behavioral factors with energetic factors, while a greater ectoparasitic load (due to larger group size and/or site stability) connects behavioral factors with thermoregulatory ones.

Finally, as we mentioned in the introduction, changes in climatic factors have been also ascribed as "prime movers" in the evolution of the brain in hominids. First, the fall in Earth temperature during the last millions years may have caused a general increase in body size by prolonged growth, resulting in even greater increases in brain size due to the strong positive allometry of brain size with body size during fetal and early postnatal growth (the "proportional growth prolongation" hypothesis; Vrba, 1994, 1998). Second, the increase in climatic

variability that occurred during the same period may have favored an increase in brain size, since larger brains allow for behavioral plasticity and cognitive mechanisms that produce novel behaviors, which are important for survival in a wide range of environmental conditions (the "variability selection" hypothesis; Potts, 1998; Ash and Gallup, 2007). Finally, the extreme wet-dry climate short-term cycles in East Africa – and the concomitant changes in general environmental conditions – has been proposed as the factor that could explain the noticeably change in brain size that occurred with the appearance of *H. erectus* (sensu lato) at 1.8 mya (the "pulsed climate variability" hypothesis; Shultz and Maslin, 2013).

4.2. Insights gained from the present analyses

There are many sources of uncertainty in most of the existing data about *Homo* evolution (e.g., Earth climate, fossil dates, cranial capacities, body mass), which preclude fine-grained evaluations of these evidences. However, using relatively rough estimations and simple analyses, we were able to show that the increase in thermoregulatory investments associated with the decrease in Earth temperature that

took place during the last 3.2 my may have been related with the evolution of larger brains in our lineage. Specifically, we found that the energetic cost associated with brain enlargement might represent an important fraction of the increase in energy needed for thermoregulation during hominids evolution. Also, we showed that there is significant negative correlation between brain cost and ambient temperature, even after controlling for changes in body mass and fossil age. Even though we do not have a formal way to know the specific role of Earth temperature on brain size evolution – that is, if it was a "prime mover" or just a facilitator for the effect of other "prime mover(s)"– the fact that brain cost was more closely related to fossil age than to ambient temperature suggests that the fall in Earth temperature facilitated, rather than caused, brain enlargement in our lineage. That is, if there was a balance between the benefits and the energetic cost of having larger brains at a given evolutionary moment, then a fall in the ambient temperature should cause a relaxation of the negative selection pressure acting on brain size. This is because all the individuals should increase their energy expenditure (for thermoregulatory purposes) in the new colder environment. This way, the falls in ambient temperature that occurred during the last millions of years may have allowed the effective realization of the effect of other(s) prime mover(s) selecting for larger brain throughout the evolution of our lineage.

To end, some caveats and ideas related with our results are worthy to be mentioned. First, our estimation of thermoregulatory costs did not take into account several factors – such as the effect of wind (increasing heat loss) or the use of shelters and wearing clothes (reducing heat loss) – that could affect thermoregulation in nature. Second, our estimation of thermoregulatory costs is based on instantaneous measures of metabolic rates, without considering existing mechanisms at larger temporal scales that can reduce the amount of energy devoted to thermoregulation. That is, our study assumed that metabolic curves of all the hominid species included in the analyses are similar among them and also similar to those recorded for modern humans. Third, our results do not exclude that changes in other variables that can affect energy budgets in nature (e.g., body size, body insulation, activity levels) might be also implicated in the adaptation of hominids to climate change. For instance, as we mentioned above, a general increase in body size in parallel to the decrease in Earth temperature has been suggested for the lineage leading to and including *Homo* during the last millions of year (Vrba, 1994, 1998). This way, our hypothesis is not mutually exclusive but complementary to other hypotheses, including other climatic hypotheses (see below), that have been proposed to explain brain size evolution in our lineage. Fourth, even though all the calculations presented here correspond to adult individuals (due to data availability), if falls in Earth temperature were a "prime mover" for brain size evolution at any moment in the history of our lineage, this probably was by acting on newborns and children. Human infants are much more thermally stressed by cold than adult individuals because, among other things, they have a much larger surface-to-volume ratio. In effect, even nowadays, mortality due to extremely low temperatures mainly affects infants (Kilbourne, 1997). Hence, an increase in the size of a metabolically expensive organ could be of paramount importance at early developmental stages. In line with this, it is noteworthy that brain maintenance cost in modern human newborns is close to a 90% – instead of *ca.* 20% in adults – of overall maintenance costs (Snodgrass et al., 2009). In addition, in contrast to adult individuals, for whom physical activity could represent an important part of the overall energy budget (Eaton and Eaton, 2003), maintenance costs in newborns are expected to be close to the total energy expenditure. In this sense, it is remarkable that the positive allometry in brain size (Vrba, 1998), as well as the amount of brown adipose tissue (Steegmann et al., 2002), starts to vanish when human babies begin to engage in physical activities by themselves. Thus, from this perspective, the energetic argument depicted in our work provides additional support for the hypothesis of "proportional growth prolongation" (Vrba,

1994, 1998). Finally, it is worth noting that our climatic hypothesis also predicted that both basal metabolic rate and brain size should increase with geographic latitude in modern humans, an idea that appears to have some empirical support (basal metabolic rate: Leonard et al., 2002; Snodgrass et al., 2005, brain size: Bharati et al., 2001; Roseman, 2004; Hubbe et al., 2009). Thus, we suspect that not only further research on hominid fossils but also on basal metabolism and brain size in modern human populations could yield more insight into the evolution of brain size in our linage.

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