

Paleoclimatic Variation and Brain Expansion during Human Evolution

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Abstract One of the major adaptations during the evolution of *Homo sapiens* was an increase in brain size. Here we present evidence that a significant and substantial proportion of variation in brain size may be related to changes in temperature. Based on a sample of 109 fossilized hominid skulls, we found that cranial capacities were highly correlated with paleoclimatic changes in temperature, as indexed by oxygen isotope data and sea-surface temperature. Indeed, as much as 52% of the variance in the cranial capacity of these skulls could be accounted for by temperature variation at 100 ka intervals. As an index of more short-term seasonal fluctuations in temperature, we examined the latitude of the sites from which the crania originated. More than 22% of the variance in cranial capacity of these skulls could be accounted for by variation in equatorial distance.

Keywords Cranial capacity · *Homo* · Paleoclimatic variability · Seasonal variability · Sea-surface temperature · Variability selection

The human brain has undergone a dramatic increase in size within the past several million years, but the mechanisms that prompted such an increase remain unclear. Investigation into these mechanisms is important to the understanding of the evolution of human intelligence, particularly since brain size is positively correlated with scores on standardized intelligence tests (for a review, see Wickett et al. 2000).

Scenarios that consider the environmental challenges are one means of exploring the evolution of bigger brains. Two environmental scenarios attempt to explain how adaptive complexity evolved: environmental consistency and environmental variability. The purpose of this paper is to evaluate the predictions derived from these two scenarios as they apply to brain expansion in hominids. Here we provide an

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analysis of the role climate may have played in the expansion of the human brain, as one measure of enhanced cognitive functioning within the genus *Homo*.

Environmental Hypotheses of Human Evolution

Environmental Consistency Hypothesis

Most environmental hypotheses of human evolution maintain that a particular habitat, such as the savanna, or the long-term change toward cooler and more arid environments provided the selective context for the evolution of features such as larger brains in hominids. From this view, adaptations arose in response to the consistent challenges that a specific habitat or particular trend posed. Paleo-environmental records have partially supported this argument by indicating marked global cooling and drying in a consistent manner over time. Thus, the origin of increased brain size and other features in *Homo* have been linked to the predictable effects of the trend toward cooling, drying, and the expansion of the savanna (Potts 1998b).

As of yet, however, there have been no quantitative studies to test this association. Establishing the factors that cause changes in brain size change is difficult. However, the hypothesis that an overall trend in the environment influenced brain size has testable implications. One prediction from the environmental consistency model is that global and regional environmental records should show a discernible trend across time concordant with increases in cranial capacity in hominids.

Environmental Variability Hypothesis

An alternative view, the variability selection hypothesis, maintains that trends are composed of many oscillations that have increased or decreased in amplitude (Potts 1998a,b). Thus, environmental variability may have played a significant role in promoting evolutionary change in *Homo*.

According to the variability selection hypothesis, extreme fluctuations in the environment created dynamic and inconsistent habitats over time. “Variability continued to rise to the point that, by the middle Pleistocene, the variation in single isotopic oscillations (covering 100 kyr intervals) usually equaled or exceeded the average change in (oxygen isotope records) over the past 6 million years” (Potts 1998b, p. 81).

Inconsistency in environmental settings is theorized to have favored adaptations that brought about behavioral plasticity as a means of promoting survival and reproduction throughout a multitude of habitats, rather than a single habitat or trend in climate. Specifically, a combination of alleles associated with increases in hominid brain size could have been selected because of the advantage they conferred in advanced cognitive mechanisms and the production of novel behavior important for survival in a wide range of environmental conditions. According to this account, the human brain evolved in part to solve the problems posed by a changing and unpredictable environment, in addition to those derived from uniform and recurring challenges. In general, the fitness of alleles linked with flexible adaptations that are

dissociated from specific habitats may have ultimately superseded the fitness of alleles that were selected in a narrow array of settings.

For the variability selection hypothesis to be supported, increases in cranial capacity in *Homo* should be positively correlated with widely fluctuating environmental extremes over time. Potts (1998a) argues that long-term variation created the greatest change in habitat remodeling, in turn having the greatest impact on environmental change. However, it is also possible that with displacement from the equator, short-term seasonal variation played a role as well (Calvin 1996). Therefore, a combination of long- and short-term environmental variation may account for a significant proportion of variance in hominid endocranial capacity if environmental variability contributed to the shaping of hominid adaptations.

The objective of this study was to investigate the relationship between specific environmental characteristics (i.e., consistency, variability) as it relates to global temperature and changes in absolute and relative hominid brain size.

Paleoenvironmental Data Sources

Sea-surface temperature variation and oxygen isotope analyses are two of the more common approaches to studying paleoclimates (Bradley 1999). These methods provide a means of inferring oscillations in the environment for regional as well as global climates. For this study, we examined environmental measures based on sea-surface temperature data derived from research conducted by Marlow et al. (2000), and oxygen isotope records from Shackelton (1995).

Sea-surface temperature (SST) data were obtained using a well-developed technique called the ketone unsaturation index, which is based on chains of unsaturated ketones (alkenones) found in marine sediments throughout the world. SST reconstructions were derived from site 1084 off the coast of southwest Africa, where a well-preserved and continuous sedimentary record from 4.6 to 0.093 Ma is found (Marlow et al. 2000). Although the temporal resolution of the SST record from site 1084 is low, with average measurements of <50 ka, the strengths of this methodology and the similarity of the oxygen isotope record from site 1084 to that of the global ice volume record are the two main reasons for using these data. As Marlow et al. (2000) point out, data from this site are not restricted to changes in the local oceanography of the South Atlantic, but instead represent accurate accounts of global climatic variation. This is important since our analyses investigate multiple hominid fossil locations across the globe.

Oxygen isotope ($\delta^{18}\text{O}$) records from site 677 (Shackelton et al. 1990) and site 846 (Shackelton et al. 1995), both located in the East Pacific, were employed as an alternative index of past climate because these locations provide the best available high-resolution data for the Pliocene and Lower Pleistocene time periods, respectively (Shackelton 1995). The oxygen isotope record from site 677 is available for the interval 0.34–1.811 Ma, and that from site 846 is available for the interval 1.811–8.35 Ma, with 3,000-year sampling intervals at both sites. Use of these records contributes to an understanding of climate evolution because oxygen isotope records provide a proxy of both global glacial ice volume and temperature

change (Potts 1998a). In conjunction, these paleoclimatic sources provide a means of tracking glacial and interglacial periods to determine both millennial climatic variations and climatic trends. For a more detailed discussion of the methodology underlying these paleoclimatic data sources see Ash and Gallup (2007).

Materials and Methods

Materials

A total of 109 crania from the *Homo* genus, including *H. habilis*, *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis*, and archaic *H. sapiens*, in which endocranial capacity could be reasonably measured and originating from a site or stratigraphic context that could be dated with relative accuracy, were selected. These crania are individually identified and listed in the [Appendix](#). We chose these populations within the *Homo* lineage for two reasons. First, we were interested in examining the pattern of brain evolution that led to modern human brains. Second, during the stage of human evolution represented by these crania, populations were exposed to even more diverse and varying natural environments than those that existed before 2.8 Ma, as evidenced from Plio-Pleistocene records which reveal dramatic shifts in the amplitude and periodicity of variation beginning around 2.8 Ma (deMenocal and Bloemendal 1995). Thus, the Plio-Pleistocene climate is ideal for our investigation of the relationship between environmental factors and brain size.

The age and cranial capacity of each cranium was obtained either from data compiled by De Miguel and Henneberg (2001), who created a comprehensive file with all estimates of cranial capacity for fossil hominids in the Pliocene and Pleistocene found in the literature up to April 2000, or from more recent estimates found in the literature (see the [Appendix](#) for references). If multiple estimates for the age and cranial capacity of a particular specimen were listed in the De Miguel and Henneberg (2001) database, the age that was most often given in the literature was used and the average of the cranial capacity estimates was calculated for each specimen. If the cranial capacity or date for any particular cranium had been revised/updated in more recent literature, recent estimates were assumed to be more accurate and were used in our study.

Gross cranial capacity measurements are often used as a basis for inferring the evolution of general cognitive abilities in hominids. However, because interpreting the significance of absolute brain volume has been contentious, we also used an encephalization quotient for hominids, which provides an index of brain size relative to body size. This method is not fail-safe, however, because it relies on postcranial remains to estimate body size, which are often poorly preserved in the prehistoric record and difficult to associate directly with the crania. To overcome these problems, we relied on Rightmire's (2004) data, which estimate body size on the basis of the orbital height of the cranium, a reliable predictor of body mass (Aiello and Wood 1994). We used Rightmire's (2004) encephalization quotient (EQ) data for 15 crania from *Homo erectus* and Middle Pleistocene hominids, all of which were included in the sample described above.

Procedure

To address the idea that environmental variation might be related to brain evolution in the genus *Homo*, climatic variation was operationally defined as the standard deviation of the climatic parameter (either SST or $\delta^{18}\text{O}$ measurements) for the 200,000 years prior to the age of each cranium. For example, a cranium dated 1.7 Ma was viewed as a product of 200,000 years of environmental variation *prior* to that date. So, for this cranium, the standard deviation of SSTs or $\delta^{18}\text{O}$ measurements would be calculated from 1.9 to 1.7 Ma. A 200 ka time frame was used because the variability selection hypothesis predicts that large episodic shifts in adaptive settings occurred at a scale of approximately 100–200 ka, exceeding the scale of seasonal or lifetime fluctuations and, as a result, affecting a lineage of organisms (Potts 1998a). However, to avoid a possible statistical artifact of 200 ka periods, we also examined the standard deviation and mean of $\delta^{18}\text{O}$ measurements over 100 ka periods for each cranium.

To evaluate whether the consistent effects of the environment impacted brain evolution, climatic consistency was operationally defined as the mean of the climatic parameter for 200 ka and 100 ka periods prior to the age of each cranium.

Correlation coefficients were used to analyze the relationship between these climatic characteristics and hominid endocranial capacity. Evaluation of these data revealed non-normality and heteroscedasticity of the residuals; therefore, Spearman's rank-order correlations were used because this coefficient (being a nonparametric statistic) is not sensitive to asymmetrical distributions or to the presence of outliers (Cohen et al. 2003).

Results

Figure 1 displays the SST record and the cranial capacity data. Analysis of this record reveals the following generalizations. First, the entirety of this SST record is characterized by prolonged gradual cooling. From 2.0 to 1.4 Ma a pause in the cooling trend is apparent, and this hiatus highlights increasing variability that may reflect an increase in amplitude in the ice volume record at 41 ka obliquity frequencies (Marlow et al. 2000). A rapid decline in SST is noticeable beginning at 1.4 Ma, followed by a transition at 0.6 Ma to fluctuating SSTs similar to the 100 ka glacial–interglacial cycles (Marlow et al. 2000). Endocranial capacity shows a marked increase beginning with heightened SST variability between 2.0 and 1.4 Ma, followed by what appears to be a stasis in the cranial capacity trend from 1.4 to ca. 0.6 Ma. Then, as SST variability peaks in amplitude, endocranial capacity reaches its highest values with marked variation in cranial capacity scores.

A similar pattern is revealed in Fig. 2, which displays the $\delta^{18}\text{O}$ records and the cranial capacity data. This figure also suggests a trend toward cooler climates in more recent time periods. However, deviations in this trend are more apparent in these records because of the greater resolution of the sampling interval of $\delta^{18}\text{O}$ measurements. The range of $\delta^{18}\text{O}$ extremes increases over time, with concomitant increases in endocranial capacity beginning at time intervals similar to those in the SST record.

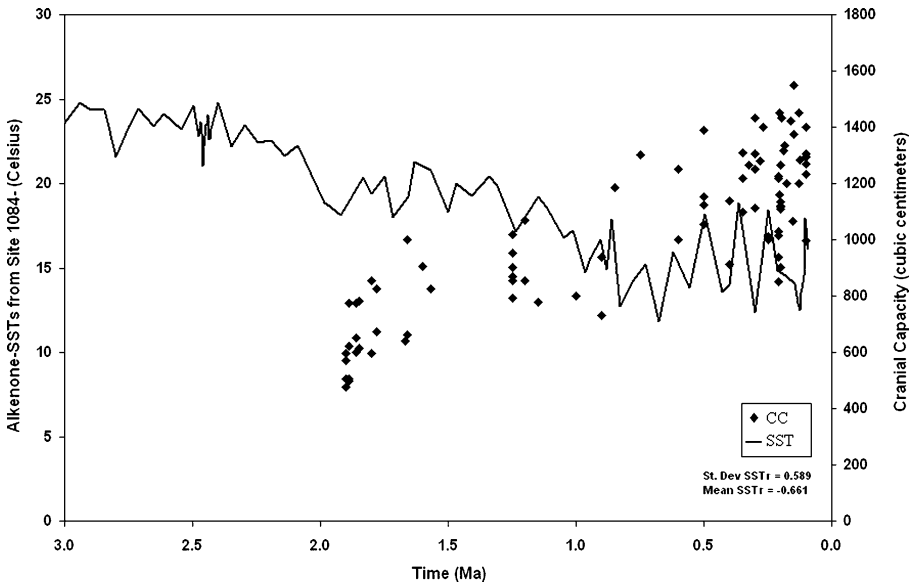


Fig. 1 Sea-surface temperature record from site 1084 compared with hominid cranial capacity across time

The first analyses compared the correlations between climatic consistency and cranial capacity, and climatic variation based on $\delta^{18}\text{O}$ measurements and cranial capacity. The correlation between cranial capacity and the standard deviations of the corresponding $\delta^{18}\text{O}$ measurements at 200 ka intervals was significant ($n=109$, $r=0.535$, $df=108$, $p < 0.01$), accounting for 28.6% of the variance in cranial

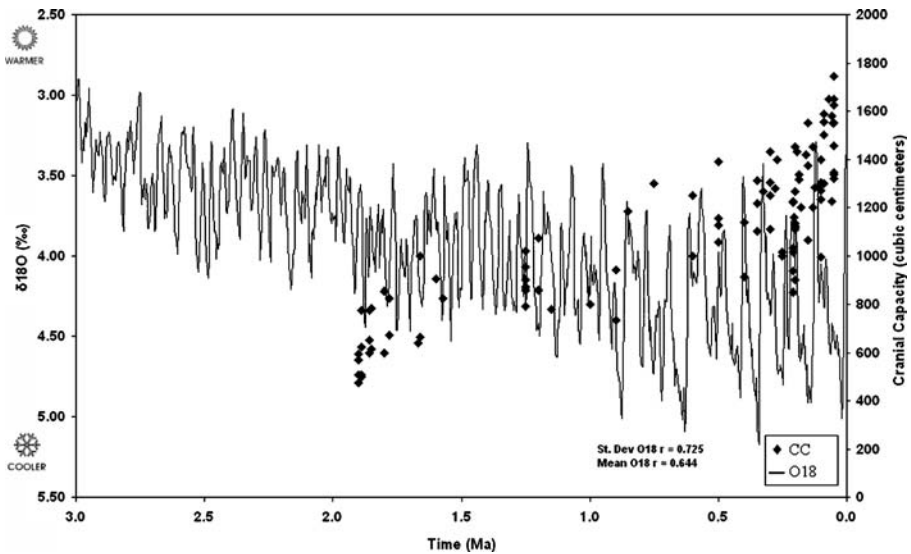


Fig. 2 Marine oxygen isotope records from sites 677 and 846 compared with hominid cranial capacity across time

capacity. In addition, the correlation between cranial capacity and the means of the corresponding $\delta^{18}\text{O}$ measurements at 200 ka intervals was also significant ($n=109$, $r=0.599$, $df=108$, $p < 0.01$), accounting for 35.8% of the variance in cranial capacity. Although this correlation is positive, it provides evidence for a decrease in average temperatures through time because larger $\delta^{18}\text{O}$ percentages reflect cooler temperatures. Thus, as cranial capacity increases, there was a trend toward cooler climates.

The same analyses conducted at 100 ka intervals revealed even more striking results. The correlations between cranial capacity and the standard deviations of the corresponding $\delta^{18}\text{O}$ measurements ($n=109$, $r=0.725$, $df=108$, $p < 0.01$), and the correlation between cranial capacity and mean of the corresponding $\delta^{18}\text{O}$ measurements ($n=109$, $r=0.644$, $df=108$, $p < 0.01$), were both significant and larger than what we found at 200 ka intervals. At 100 ka intervals, climatic variation accounts for more of the variance in cranial capacity (52.5%) than climatic consistency (41.4%). Figures 3 and 4 depict the scatterplots for these correlations. Likewise, the correlation between cranial capacity and the standard deviations for the corresponding SSTs at 100 ka intervals was also significant ($n=89$, $r=0.589$, $df=88$, $p < 0.01$), and the same was true for the correlation between cranial capacity and the corresponding means of the SST measurements ($n=89$, $r=-0.661$, $df=108$, $p < 0.01$).

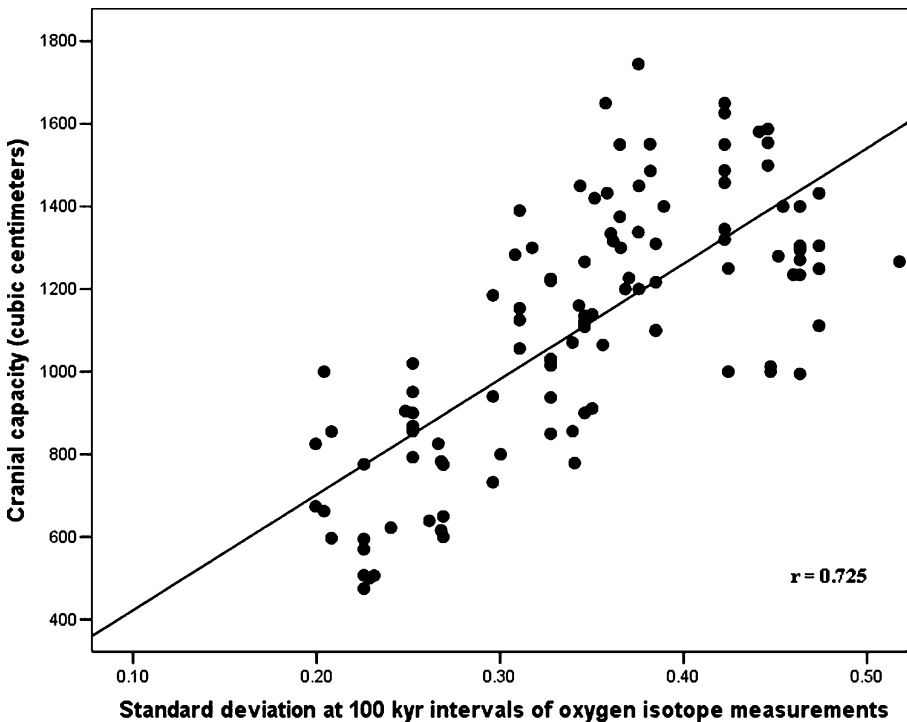


Fig. 3 Cranial capacity as a function of standard deviations of oxygen isotope measurements at 100,000-year intervals

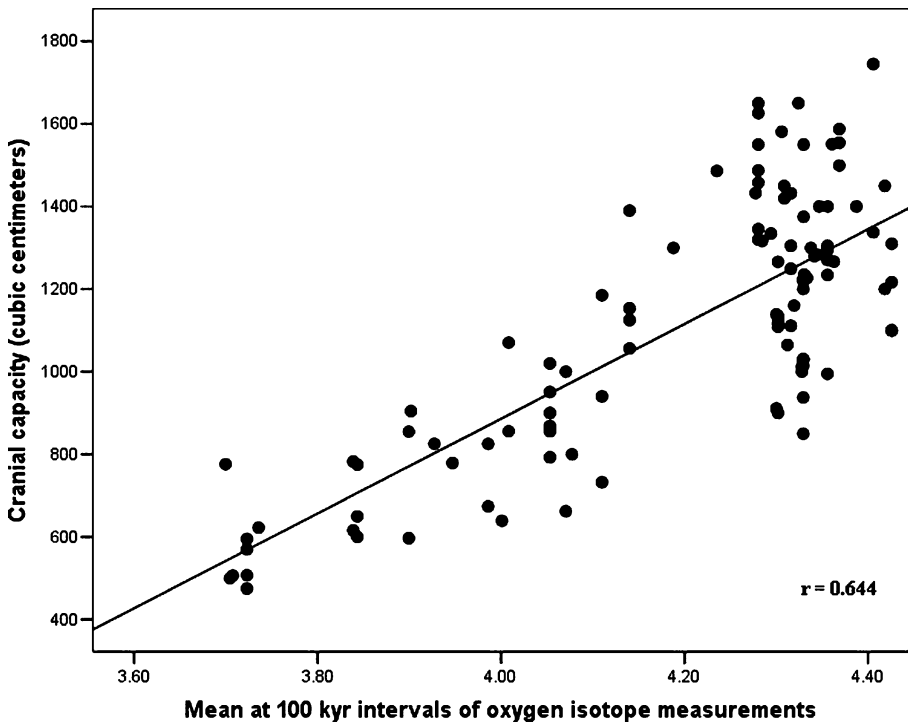


Fig. 4 Cranial capacity as a function of mean values of oxygen isotope measurements at 100,000-year intervals

As another way to examine the apparent impact of paleoclimatic variation on brain size, we analyzed the distance from the equator of the sites at which each of the crania was found. Seasonal variation is especially marked in mid to high latitudes, where temperature is the dominant climatic variable (deMenocal and Bloemendal 1995). Moreover, short-term variation may account for the widest range of environmental change to which hominids had to adapt (Calvin 1996). In other words, if temperature variation was a factor in promoting the development of bigger brains, hominids located farther north or south from the equator should show correspondingly larger cranial capacities. To test this idea, a Spearman's correlation coefficient was calculated between cranial capacity and the absolute decimal degrees of latitude of the geographical site for each fossilized cranium. Results of this analysis clearly indicated that with increasing distance from the equator of the sites where the crania were found there was a concomitant increase in cranial capacity ($n=109$, $r=0.478$, $df=108$, $p < 0.01$).

Finally, a Spearman's correlation coefficient was performed to evaluate the encephalization quotient (EQ) of the *Homo* specimens in our sample that were included in Rightmire's (2004) data. The correlation between EQ and the associated standard deviations of $\delta^{18}\text{O}$ measurements was significant ($n=14$, $r=0.731$, $df=13$, $p < 0.05$), but although the correlation based on the means of the $\delta^{18}\text{O}$ measurements was in the predicted direction, because the sample size was small the correlation was not significant ($n=14$, $r=0.493$, $df=13$, $p=0.073$). The $\delta^{18}\text{O}$ measurements were

the only parameters used in this analysis owing to the detailed resolution of these records.

Discussion

Although the data are of necessity only correlational, our results have implications for the debate over climatic consistency versus climatic variation as a selective force behind the evolution of bigger hominid brains. First, the pattern of results at 200 ka intervals suggests that the evolution of the human brain may have been influenced (directly or indirectly) by both erratic climatic conditions as well as an overall trend toward climate cooling and greater ice volume. Comparable analyses conducted at 100 ka intervals suggest that climatic variability may have been even more influential than the trend toward cooler climates. Based on means and standard deviations, climate changes at 100,000-year periods appear more sensitive to climate extremes, providing better resolution of the variables that may have impacted the evolution of crania size. Climatic variation oscillating at 100 ka intervals is still consistent with the predictions from Potts's environmental variability hypothesis. In addition, the results from the EQ data stand as further testament to the possibility that environmental complexity created changes in brain size, independent of body size, that led to adaptive benefits such as enhanced memory and spatial processing of information about surroundings. Uncertainty about the environment, for example, may have increased reciprocity and food sharing, thereby enhancing more complex social skills. Therefore, it would appear on the basis of these data that both the hypothesis regarding gradual decreases in average temperature and Potts's (2001) environmental variability hypothesis have merit.

Consistent with the position taken by Rushton and Jensen (2005), it seems reasonable to suppose that increases in cranial capacity were associated with more sophisticated cognitive functioning and skills, and as such led to the increase in behavioral flexibility needed for survival and reproductive success under various environmental conditions. This conclusion is supported by the consistent finding that scores on standardized IQ tests and brain volume correlate at the 0.40 level (Andreasen et al. 1993; Egan et al. 1994, 1995; Gignac et al. 2003; Harvey et al. 1994; Kareken et al. 1995; Posthuma et al. 2002; Raz et al. 1993; Reiss et al. 1996; Wickett and Vernon 1994; Wickett et al. 2000; Willerman et al. 1991). Furthermore, after correcting for restriction of range and attenuation in these studies, the population value of the brain volume–IQ correlation is closer to 0.50 (Wickett et al. 2000). After conducting a vector analysis on factor scores, Wickett et al. (2000) found that the more highly *g*-loaded a test, the more it correlated with brain volume ($r=0.59$, $p < 0.01$). Individual lobe volume and aggregate gray and white matter volumes have been found to correlate with IQ as well (Andreasen et al. 1993; Posthuma et al. 2002).

The geographical location of the fossil crania as expressed in decimal degrees latitude accounted for more than 22% of the variance in absolute cranial capacity, providing convergent evidence for a relationship between brain evolution and variation in temperature on much shorter (seasonal) time scales. The fact that brain size in hominid fossils increases with distance from the equator is consistent with the

relationship between latitude, coldness of climate, and brain size among contemporary human populations (Beals et al. 1984). To evaluate the effect of seasonal variation, Beals et al. (1984) conducted a linear regression using degrees of latitude as the predictor of brain size for 122 contemporary ethnic populations and found a 2.5 cm³ increase in cranial capacity for every degree of latitude displacement from the equator. Following their precedent, we conducted a comparable analysis and found an even more substantial 8.27 cm³ increase in brain volume among the fossilized crania in our sample for every degree of equatorial distance ($t=5.306$, $n=109$, $df=108$, $p < 0.01$). Inhabiting colder climates with greater seasonal change may have put added pressure on inventing novel ways to cope with greater environmental extremes, such as controlling fire and eating meat. Although correlational data do not necessarily constitute evidence that migration away from the equator prompted increases in brain size, the fossil record clearly shows that dramatic increases in cranial capacity did not predate and therefore promote northern migrations.

Some might argue that the relationship between cranial capacity and distance from the equator is not due to colder climates or greater seasonal variation but instead may be a consequence of Bergmann's rule, which states that large-bodied animal species tend to live further north than their small-bodied relatives. However, there are important limitations, exceptions, and objections to this rule (see Blackburn et al. 1999). First, the validity of this rule remains controversial, because the "rule" does not consistently account for intra- and interspecific gradients in body size at various latitudes. Blackburn et al. (1999) cite studies showing numerous exceptions to this rule among warm-blooded species. Moreover, Bergmann's rule was meant to be applied between, rather than within, species. Second, there is little or no consensus as to the mechanism(s) responsible for this pattern when it does obtain. Third, there is no compelling evidence that this rule applies to the *Homo* genus. Finally, and perhaps most importantly, our analysis of Rightmire's (2004) encephalization quotient (EQ) data for the skulls in our sample takes into account any inherent differences in body size, and the EQ results are comparable to those obtained for the entire sample of 109 crania.

In addition to the question of *why* larger brains evolved, an equally important question relates to *how* larger brains were maintained since they are costly in energetic terms. One intriguing answer to the latter question is provided by the radiator hypothesis, which assumes that an immense system of tiny emissary veins evolved to selectively cool hominid brains under hyperthermic conditions (Falk and Gage 1997). This network has been shown to become increasingly extensive with brain expansion from gracile australopithecines to *Homo sapiens* (Falk 1990). In modern humans the diploic veins in the cranium are thought to provide an anatomical means of brain cooling, and larger skulls tend to have a well-developed and more extensive diploic system than smaller skulls (Hershkovitz et al. 1999). In addition, diploic vein patterns appear to be more intricate in humans compared with nonhuman primates, suggesting a phylogenetic connection (Hershkovitz et al. 1999).

The importance of effective brain cooling/thermoregulation may be related to the correlation between distance from the equator and cranial capacity, since seasonal variation is thought to have had the greatest impact on changes in mean annual

temperature during the Pleistocene (Crowley and North 1991). Seasonal oscillations between hyper- and hypothermic conditions may have been an important part of the selective pressure for thermoregulation of the brain that led to a diploic vein system. This system could have evolved to maintain constant brain temperature in the face of thermal conditions that are subject to substantial daily and seasonal variation.

Implications and Conclusions

A common idea about brain evolution in mammals is that natural selection did not operate on brain volume per se, but instead there was pressure on particular behavioral/cognitive capabilities that in turn led to changes in brain areas mediating those features (Barton and Harvey 2000). Examination of this question using the fossil record has been limited. However, research in nonhuman primates has shown that as social groups increase in size there is a concomitant increase in neocortex size (Dunbar 1998). This finding has implications for humans as well because the neocortex is an area linked with high-order cognitive processing. It would be interesting to compare the proportion of the neocortex to the rest of the brain in modern mammalian species that occupy a variety of climatic niches to determine if climate characteristics, in addition to social group size, have impacted the expansion of particular brain areas.

But the question remains, what was it about colder climates and more variable temperatures that might have led to selection for bigger brains? For most species, problems posed by climate cooling and increased variation in temperature have been solved by physical and physiological adaptations (e.g., metabolic and thermoregulatory mechanisms, fat deposits, fur, hibernation, migration). Perhaps a major point of departure for human evolution was the fact that solutions to these problems instead featured detailed and progressively more refined cognitive/intellectual strategies. For example, living under conditions that are appreciably displaced from the equator means having to cope not only with seasonal fluctuations in temperature, but corresponding fluctuations in food availability as well. During the winter, living at higher latitudes would necessitate an increased reliance on hunting and meat eating. For primitive humans this may have put a premium on the kinds of cognitive and intellectual skills needed for more effective patterns of cooperative hunting and social intelligence, along with the development and refinement of more sophisticated weapons. Similar pressures related to the need for improved clothing and shelter, along with mastering the use of fire as a means to keep warm, may have further accelerated the development of other intricate cognitive/intellectual skills needed to compete for scarce resources and survive in colder climates (for more detail see Ash and Gallup 2007)

Although some individuals (e.g., Klein 1999) question whether a quantitative approach to the study of evolution is reasonable, our results suggest the application of correlational statistics may offer a valuable tool for understanding key issues related to brain evolution. This is not to say that all studies in human evolution can be evaluated from an entirely statistical approach. Instead, future approaches may

focus on the combination and interaction of traditional ideas and quantitative verification. While our understanding of brain evolution is less than complete, this study provides preliminary evidence for a putative role of climate as a possible selective force in promoting brain expansion and ultimately human intelligence.

Appendix

Fossil information

Number	Fossil	Taxon [†]	Capacity (cc)	Date (Ma)
1	SK 47 (adult)	Early h	595.000 ^a	1.900 ^a
2	Stw 53	Early h	570.000 ^a	1.900 ^a
3	SK 847	h, hh/he	507.000 ^a	1.900 ^a
4	SK 27	h	475.000 ^a	1.900 ^a
5	KNM-ER 1470 (Koobi Fora)	hher	776.000 ^a	1.890 ^a
6	KNM-ER 3732 (Koobi Fora)	hher	622.500 ^a	1.890 ^a
7	KNM-ER 1813 (Koobi Fora)	hh	506.333 ^a	1.890 ^a
8	Omo L894-1	h	500.000 ^a	1.890 ^a
9	Dmansi 2280	hh	775.000 ^b	1.860 ^b
10	Dmansi 2282	hh	650.000 ^b	1.860 ^b
11	Dmansi 2700	hh	600.000 ^c	1.860 ^b
12	KNM-ER 1590 (Koobi Fora)	hr	782.500 ^a	1.850 ^a
13	KNM-ER 1805 (Koobi Fora)	hh	616.000 ^a	1.850 ^a
14	Modjokerto (adult)	he	855.000 ^a	1.800 ^a
15	OH 24 (Olduvai)	hh	597.000 ^d	1.800 ^a
16	KNM-ER 3733 (Koobi Fora)	hher	825.400 ^a	1.780 ^a
17	OH 7 (adult) (Olduvai)	hh	674.000 ^a	1.780 ^a
18	OH 16 (adult) (Olduvai)	hh	639.200 ^a	1.670 ^a
19	Sangiran 4	he	856.000 ^a	1.660 ^a
20	OH 13 (adult) (Olduvai)	hh	662.286 ^a	1.660 ^a
21	Sangiran 31	he	1,000.000 ^a	1.660 ^a
22	KNM-WT 15000 (adult) (Nariokotome)	he	904.500 ^a	1.600 ^a
23	KNM-ER 3883 (Koobi Fora)	hher	825.667 ^a	1.570 ^a
24	Sangiran 12	he	951.000 ^a	1.25
25	Sangiran 3 (adult)	he	900.000 ^a	1.25
26	Sangiran 10	he	868.600 ^a	1.25
27	Sangiran 9	he	856.000 ^a	1.25
28	Sangiran 2	he	792.571 ^a	1.25
29	Sangiran 17	he	1,020.000 ^a	1.25
30	OH 9 (Olduvai)	he	1,070.500 ^a	1.200 ^a
31	Gongwangling 1	he	779.000 ^a	1.150 ^a
32	Buia	he	800.000 ^a	1.000 ^a
33	Trinil 2	he	940.000 ^a	0.900 ^a
34	Ceprano	hhei	1,185.000 ^a	0.850 ^k
35	OH 12 (Olduvai)	he	732.330 ^a	0.840 ^a
36	Ternifine	ahs	1,300.000 ^a	0.750 ^a
37	Bodo	hhei	1,250.000 ^f	0.600 ^f
38	Nanjing	he	1,000.000 ^c	0.600 ^c
39	Atapuerca 4 (AT 600)	hant	1,390.000 ^a	0.500 ^g
40	Atapuerca 6 (11- to 14-year-old)	hant	1,153.333 ^a	0.500 ^g
41	Atapuerca 5 (AT 700)	hant	1,125.000 ^a	0.500 ^g
42	Sambungmacan 1	he	1,056.333 ^a	0.500 ^a
43	Salé 1	he	911.000 ^a	0.400 ^a

Number	Fossil	Taxon [†]	Capacity (cc)	Date (Ma)
44	Araho 21	hhei	1,138.667 ^a	0.400 ^a
45	Broken hill 1 (Kabwe)	hhei	1,310.000 ^a	0.350 ^a
46	Saldanha 1 (Elandsfontein)	hhei	1,216.667 ^a	0.350 ^a
47	Yunxian	he	1,100.000 ^a	0.350 ^a
48	Ndutu 1	ahs	1,100.000 ^a	0.350 ^a
49	Petralona 1	hhei	1,266.556 ^a	0.325 ^a
50	Reilingn	hhei	1,432.000 ^a	0.300 ^a
51	Swanscombe 1	hhei	1,305.000 ^a	0.300 ^a
52	Narmada 1	he	1,249.333 ^a	0.300 ^a
53	Steinheim 1	hhei	1,111.192 ^a	0.300 ^a
54	Florisbad 1	ahs	1,280.000 ^a	0.279 ^h
55	KNM-ER 3884	ahs	1,400.000 ^a	0.270 ^a
56	Ngawi	he	1,000.000 ^c	0.250 ^c
57	Hexian	he	1,012.500 ^a	0.250 ^a
58	Zhoukoudian (III)	he	937.500 ^a	0.210 ⁱ
59	Zhoukoudian (VI)	he	850.000 ^a	0.210 ⁱ
60	Zhoukoudian L1 (X)	he	1,225.000 ^a	0.210 ⁱ
61	Zhoukoudian h3 (V)	he	1,220.000 ^a	0.210 ⁱ
62	Zhoukoudian D1 (II)	he	1,030.000 ^a	0.210 ⁱ
63	Zhoukoudian L3 (XII)	he	1,030.000 ^a	0.210 ⁱ
64	Zhoukoudian L2 (XI)	he	1,015.000 ^a	0.210 ⁱ
65	Dali 1	ahs	1,160.000 ^a	0.205 ^a
66	Ehrinhdsdorf 9	hhei	1,450.000 ^a	0.203 ^a
67	Sambungmacan 3	he	900.000 ^a	0.200 ^a
68	Solo 5, Ngandong V	he	1,266.167 ^a	0.200 ^a
69	Solo 9, Ngandong IX	he	1,135.000 ^a	0.200 ^a
70	Solo 1, Ngandong I	he	1,121.429 ^a	0.200 ^a
71	Solo 6, Ngandong VI	he	1,115.714 ^a	0.200 ^a
72	Solo 10, Ngandong X	he	1,109.000 ^a	0.200 ^a
73	Omo 2	ahs	1,432.500 ^a	0.195 ^j
74	Jinniushan	he	1,316.667 ^a	0.187 ^a
75	Vértesszöllös 2	ahs	1,334.571 ^a	0.186 ^a
76	Biache	hhei	1,200.000 ^a	0.178 ^a
77	Fontéchevade 2	hn	1,420.000 ^a	0.160 ^a
78	La Chaise	hn	1,065.000 ^a	0.151 ^a
79	Singa 1	hn	1,550.000 ^a	0.150 ^a
80	KNM-ES-11693 (Eliye Springs)	ahs	1,375.000 ^a	0.150 ^a
81	Jebel Irhoud 2	hn	1,400.000 ^l	0.140 ^a
82	Jebel Irhoud 1	hn	1,305.000 ^l	0.140 ^a
83	Krapina-D	hn	1,450.000 ^a	0.130 ^a
84	Krapina 3	hn	1,200.000 ^a	0.130 ^a
85	Ngaloba	ahs	1,283.500 ^a	0.125 ^a
86	Daka (BOU VP-2/66)	he	995.000 ^c	0.100 ^c
87	Saccopastore 2	hn	1,295.000 ^a	0.100 ^a
88	Tabun C1	hn	1,270.500 ^a	0.100 ^a
89	Saccopastore 1	hn	1,234.333 ^a	0.100 ^a
90	Skhul 9	hn	1,587.333 ^a	0.090 ^a
91	Skhul 4	hn	1,554.500 ^a	0.090 ^a
92	Skhul 5	hn	1,499.500 ^a	0.090 ^a
93	Skhul 2	hn	1,300.000 ^a	0.090 ^a
94	La Ferrassie 1	hn	1,650.200 ^a	0.068 ^a
95	Teshik-Tash (adult)	hn	1,581.000 ^a	0.060 ^a
96	Gibraltar 1 (Forbes' Quarry)	hn	1,226.750 ^a	0.060 ^a
97	Monte Circeo I	hn	1,551.000 ^a	0.055 ^a
98	Amud 1	hn	1,745.000 ^a	0.051 ^a
99	Shanidar 1	hn	1,650.000 ^a	0.050 ^a
100	La Chapelle-aux-Saints	hn	1,626.000 ^a	0.050 ^a

Number	Fossil	Taxon [†]	Capacity (cc)	Date (Ma)
101	Shanidar 5	hn	1,550.000 ^a	0.050 ^a
102	Spy 2	hn	1,487.400 ^a	0.050 ^a
103	Spy 1	hn	1,457.500 ^a	0.050 ^a
104	La Quina 5	hn	1,345.250 ^a	0.050 ^a
105	Neandertal 1	hn	1,337.750 ^a	0.050 ^a
106	Ganovce 1	hn	1,320.000 ^a	0.050 ^a
107	Le Moustier 1	hn	1,486.200 ^a	0.040 ^a
108	Galilee	ahs	1,400.000 ^a	0.040 ^a
109	Eyasi	ahs	1,235.000 ^a	0.035 ^a

[†]Legend for taxa:

ahs: *Archaic Homo sapiens*

h: *Homo*

hant: *Homo antecessor*

he: *Homo erectus*

hher: *Homo ergaster*

hh: *Homo habilis*

hhei: *Homo heidelbergensis*

hn: *Neandertal*

References:

^aDe Miguel and Henneberg (2001)

^bLee (2005)

^cLee and Wolpoff (2003)

^dTobias (1991)

^eLarick et al. (2001)

^fConroy et al. (2000)

^gBischoff and Shamp (2003)

^hKunman et al. (1999)

ⁱShen et al. (2004)

^jMcDougall et al. (2005)

^kBruner and Manzi (2005)

^lHolloway et al. (2004)

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