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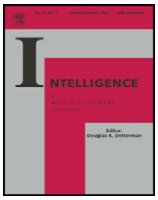

Orbital dynamics, environmental heterogeneity, and the evolution of the human brain

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ABSTRACT

Many explanations have been proposed for the evolution of our anomalously large brains, including social, ecological, and epiphenomenal hypotheses. Recently, an additional hypothesis has emerged, suggesting that advanced cognition and, by inference, increases in brain size, have been driven over evolutionary time by the need to deal with environmental complexity. The essential logic is that orbital variables have affected the quantity of solar energy reaching the earth, thus creating climatic changes that posed adaptive challenges to ancestral humans. Larger-brained humans were better equipped to deal with such changes, and proliferated accordingly, leading to the observed trajectory of increasing brain size. Though cross-citation remains rare, researchers from areas as apparently disparate as philosophy and botany are ultimately reaching similar conclusions. In order to test the validity of hypotheses linking encephalisation to climatic variability in the human lineage, the endocranial volumes of 180 fossil human skulls spanning the last 3.2 million years were collated from the literature and regressed upon a series of palaeoclimatic variables, including the amplitudes of the orbitally induced eccentricity, obliquity, and precession cycles. Multiple regression analyses demonstrate that the minimum amplitude of the eccentricity cycle explains 43% of the variance in endocranial capacity, with two further climatic variables accounting for a further 16%. These results are discussed in relation to the increasing weight of evidence that suggests that climatic instability may have played a significant part in the evolution of advanced cognition in both humans and other animals.

1. Introduction

Many explanations have been proposed for the evolution of our anomalously large brains and the advanced cognition that they support. Dunbar (1998) has classified these various hypotheses as being ecological, social, developmental, or epiphenomenal in their basic approaches, though we might also add those explanations dependent upon sexual selection. Epiphenomenal and developmental hypotheses draw attention to constraints on encephalisation rather than proposing stimuli, with the former explaining links between brain size and body size (Gould, 1975) or various brain components (Finlay & Darlington, 1995), and the latter highlighting the restrictions placed on brain development by the energetic requirements of mother and infant (Armstrong, 1985; Martin, 1981). Whether the specifics involve the complexities of the subsistence strategy (Parker & Gibson, 1977), the need to maintain detailed knowledge of a large home range to satisfy energetic requirements (Clutton-Brock & Harvey, 1980), or the demands of tracking a transient and ephemeral food source (Milton, 1981), ecological hypotheses have focused on difficulties associated with the subsistence base. In contrast, social hypotheses have concentrated on the demands of interactions with other individuals. Such hypotheses admit varying levels of deception as part of the process of dealing with other individuals (see e.g. Dunbar, 1992; Jolly, 1966; Whiten & Byrne, 1988), but all essentially agree on an evolutionary scenario in which "any heritable trait which increases the ability of an

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individual to outwit his fellows will soon spread through the gene pool" (Humphrey, 1976:21). The most developed of the social theories has come to be known as the Social Brain Hypothesis (SBH; Dunbar, 1998), and has been studied extensively in primates and other mammals.

As the foundation for the SBH, Dunbar (1992, 1993) initially quantified the relationship between brain size and social complexity via a regression of group size on neocortex ratio in extant primates. This was extended to extinct hominins (Aiello & Dunbar, 1993; Grove, 2010a) via measurement of internal capacities of fossil crania, putting the theory on a genuinely archaeological footing. The SBH has since been expanded to examine more subtle indices of social complexity, with results suggesting that both fission–fusion social systems, in which group members forage in subgroups for a large percentage of the day, and monogamous pair bonds, are more cognitively demanding than other socio-sexual configurations (Barrett, Henzi, & Dunbar, 2003; Dunbar & Shultz, 2007, 2010; Grove, 2010b, 2011a; Grove, Pearce, & Dunbar, 2012; Shultz & Dunbar, 2007, 2010a). Fission–fusion is a likely ancestral social grouping pattern for humans, found in all modern hunter–gatherers; recent work on the evolutionary anthropology of hunter–gatherer subsistence and its cognitive challenges has suggested that this pattern of social organisation is both cognitively demanding and ecologically efficient in terms of resources assimilated per unit time (Grove, 2010b, 2011a, 2012; Grove et al., 2012). Research into the cognitive demands of the pair bond extends an earlier line of reasoning into the possibility that brain size is a sexually selected trait (e.g. Greengross & Miller, 2011; Miller, 2001), with additional research suggesting that mate-guarding (or 'mate vigilance') is also cognitively demanding (e.g. Komers & Brotherton, 1997; van Schaik & van Hooff, 1983). Shultz and Dunbar (2007) have recently argued that social relationships in anthropoid primates differ from those in other animals in that relationships equivalent in strength to the pair bond have been extended to all social partners. Thus the intimacy of relationships may be as crucial a predictor of brain size as is the number of relationships.

Recently, an additional hypothesis has emerged, and is gathering support from a growing number of studies in a diverse range of disciplines. This latter hypothesis is of many forms, and has adopted myriad labels, but is referred to here as the environmental complexity thesis (henceforth ECT) after Godfrey-Smith (1996, 2002). This thesis is really a banner term for a class of ecological models, and states in general form that "the function of cognition is to enable the agent to deal with environmental complexity" (Godfrey-Smith, 1996:3). The ECT is intended to explain cognition in a very general sense, by linking neural complexity to environmental complexity, and suggesting that complexity in the environment might be best dealt with via flexibility or plasticity on the part of the animal (Godfrey-Smith, 1996). Though cross-citation is currently rare, researchers from areas as apparently disparate as philosophy (e.g. Bergstrom & Godfrey-Smith, 1998; Sober, 1994) and botany (e.g. Bradshaw, 1965; Trewavas, 2005) are ultimately reaching similar conclusions. In combination with an increasing body of empirical research founded on the zoological study of neophilia and innovation (e.g. Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; Reader & Laland, 2002; Sol, Bacher, Reader, & Lefebvre, 2008), these conclusions are now sufficiently recurrent to be considered important to the reconstruction of human brain evolution.

The current paper briefly surveys some of the relevant literature on the ECT and related issues and analyses an extensive dataset of human brain sizes derived from the fossil record (Grove et al., 2012) to determine the effects of environmental complexity on human brain evolution. The environmental proxies most commonly used to empirically test versions of the ECT involve defining levels of environmental heterogeneity (whether occurring through time or across space) that different taxa experience (Ash & Gallup, 2007; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005a, 2008, 2010; Sol & Lefebvre, 2000, Sol et al., 2008, 2010). The volumes of various brain components are then regressed on these heterogeneity levels in between-species analyses, with heterogeneity and brain volume variables often found to covary positively (Ash & Gallup, 2007; Sol & Lefebvre, 2000; Sol, Lefebvre, & Rodriguez-Teijeiro, 2005b, 2008, 2010; Sol et al., 2008, 2010). Though the comparative method is the biologist's primary tool in such cases, and can certainly lead to accurate and valuable evolutionary inferences, the analyses undertaken below allow for the correlation of values which themselves stretch back into prehistory, providing a direct picture of the links between environmental change and encephalisation. The environmental heterogeneity proxies used in the current analyses are provided by detailed palaeoclimatic records that track the shifts in our planet's climate over the past 3 million years (henceforth 3 Ma), providing a long-term picture of the response of human brain size to the complex environments that numerous researchers have suggested are the drivers of encephalisation.

The first formulations of what could be considered a proto-ECT were due to the theoretical biologists of the 1950s and 1960s. Though concerned with long-term evolutionary responses rather than with the cognitively-mediated responses of individuals, researchers such as Levene (1953), Dempster (1955), and Levins (1962, 1968; see also Cohen, 1966; Lewontin & Cohen, 1969) formulated models of the maintenance of polymorphisms in fluctuating environments that provided the foundations of subsequent investigations into the evolution of flexible behaviours more generally. Empirical analyses of the palaeontological record have suggested, again on an evolutionary timescale, that organisms encountering and surviving fluctuating environments will, in the course of doing so, develop greater levels of plasticity in their behavioural repertoires, and will be better able to deal with subsequent, more pronounced fluctuations (Coope, 2004; Sheldon, 1996). Coope's (2004) analyses in particular point to the 'frequent genetic mixing' caused by the numerous and intensive climatic oscillations of the Quaternary as a key driver in the evolutionary development of more flexible strategies. Such genetic mixing could also lead to the faster spread of potentially beneficial new mutations affecting brain size and intelligence (Cochran & Harpending, 2007).

Recent ecological research has more explicitly examined the cognitive response to novel environments encountered due to both spatial and temporal heterogeneity. Work initiated by Lefebvre et al. (1997, 1998) demonstrated that the propensity to innovate—an assumed proxy for behavioural flexibility more generally—correlates with forebrain size in birds, whilst Reader and Laland (2002) found a similar result in primates. Sol et al. (2005a) demonstrated that larger brained, more innovative bird species are less likely to be migratory, the logic being that resident species must deal with seasonal changes in habitat, producing more novel behaviours in times when food is scarce. By contrast, migration ensures that the animal is exposed to only a relatively restricted range of habitats, and can therefore subsist successfully with a limited range of feeding behaviours (Sol et al., 2010). Larger-brained bird species are also more successful in surviving and establishing themselves in novel habitats; larger-brained animals showed higher innovation rates in their regions of origin and were more successful in novel habitats because of this propensity (Sol & Lefebvre, 2000; Sol, Timmermans, & Lefebvre, 2002; Sol et al., 2005b). This finding has recently been replicated in an extensive sample of mammals introduced to new environments under conservation initiatives (Sol et al., 2008), demonstrating that enlarged brains "function, and hence may have evolved, to deal with changes in the environment" (Sol et al., 2005b).

Previous research into human intelligence, particularly regarding the relationship between intelligence scores and measures of creativity, has also revealed links of direct relevance to the literature on innovation in other animals. Following from Spearman's (1904) recognition of a general intelligence factor, *g*, Cattell (1963a, 1971; Horn & Cattell, 1966) posited a distinction between crystallised (*gc*) and fluid (*gf*) intelligence, with the former being essentially a repertoire of knowledge and the latter an ability to manipulate that knowledge in the production of solutions to novel problems. Scores on modern tests of divergent thinking (DT) that "require individuals to produce several responses to a specific prompt" (Plucker & Renzulli, 1999:38) show significant positive relationships with *gf*, implying that fluid intelligence is intimately linked to creativity (Nusbaum & Silvia, 2011). DT also shows a significant positive relationship with the Openness to Experience factor of the five factor model of personality (Batey & Furnham, 2006; Costa & McCrae, 1992), a notion similar to the 'neophilia' reported by Sol and colleagues in birds and primates (Sol & Lefebvre, 2000; Sol et al., 2010). Miller and Tal's (2007) study found that openness also predicted observer ratings of performance on verbal and drawing creativity tasks.

As *gf* and *gc* correlate positively with one another, the most plausible model of creativity would seem to be one related to Mednick's (1962; see also Koestler, 1964) concept of associative processes in which a substantial store of knowledge, indexed by *gc*, is required to generate a suitable number of novel associations using the reasoning ability provided by *gf* (Batey, Chamorro-Premuzic, & Furnham, 2009). Regardless of the particular model adopted, however, there is a clear indication that intelligence is closely related to DT abilities, which are shown in a longitudinal study by Plucker (1999) to be an important factor in real-world achievement. Given the clear positive relationships between intelligence and brain size (e.g. Rushton & Ankney, 2007, 2009), it would seem likely that increases in brain size through time have led to tangible increases in precisely the creative abilities required to deal with novel environments.

The increased research effort directed towards the methodological refinement of proxies for palaeoclimatic change has also acted as a spur to a new wave of analyses within archaeology and palaeoanthropology that explicitly relate human evolution to the unstable environments experienced by our ancestors (e.g. Grove, 2011b,c; Kingston, 2007; Potts, 1996, 1998; Trauth, Larrasoana, & Mudelsee, 2009, Trauth et al., 2007, 2009). Such instability has emerged as a potential explanation for the extremely broad environmental tolerance of humans, and in particular for human omnivory (e.g. Grove, 2011c; Potts, 1996). Of particular relevance to the current study is the work of Potts (1996, 1998) on 'variability selection'. Potts examines numerous lines of evidence that combine to demonstrate a record of increasing environmental variability during the past five million years, arguing that human evolution has been a pattern of adapting to the spread of variation rather than the mean, with climatic variability favouring "any available genes and related phenotypes that helped to build adaptive versatility" (Potts, 1998:86). A substantial part of Potts' theory relates to human encephalisation, with a major contention being that a large brain that is "effective in processing external data and generating complex cognitive responses" (Potts, 1998:85) would have been our principal weapon in dealing with climatic instability.

The palaeoclimatic data of the sort employed by palaeontologists such as Sheldon (1996), Coope (2004) and Potts (1998, 2007) are becoming ever more abundant, and reveal a series of regularities in the earth's climate long theorised by astronomers and solar physicists (e.g. Croll, 1875; Hays et al., 1976; Milankovitch, 1941; see Berger, 1988). Of particular importance are the three orbital cycles formalised by Milankovitch (1941). These three cycles, each of which may play a role in evolutionary responses to climate change, are the precession cycle, the obliquity cycle, and the eccentricity cycle. The precession cycle has a length of 21 ka (thousand years), and is caused by the fact that the earth does not rotate uniformly on its axis; instead, it rotates like a spinning top, with a relatively fixed axis towards the south pole but a moveable axis to the north. The precession cycle dominated climate changes at the earth's surface from before 5 million years ago until approximately 3 million years ago, when it became subsidiary to the obliquity cycle. The obliquity cycle has a length of 41 ka, and is caused by the fact that the earth's overall axial tilt with respect to the sun is not constant, but changes by over 2° during this cycle. Finally, at about 1 million years ago, an extended climatic event known as the Mid-Pleistocene Revolution led to the longest of the three cycles, the eccentricity cycle, becoming dominant. The eccentricity cycle has a period of 100 ka, and is caused by the fact that the earth's orbit is neither perfectly circular nor perfectly centred on the sun. The eccentricity cycle has dominated the earth's climate, particularly at higher latitudes, for the last million years. These three cycles are illustrated in schematic form in Fig. 1.

The ecological consequences of these orbital cycles are manifold, and relate to changes in the strength of insolation (the amount of solar energy reaching the surface of the earth). Changes in obliquity amplify or suppress the strength of the seasons, with these effects felt most strongly at higher latitudes. At lower and middle latitudes, seasonal cycles are driven primarily by precession; however, whilst precession is an oscillation of relatively regular amplitude, it is heavily

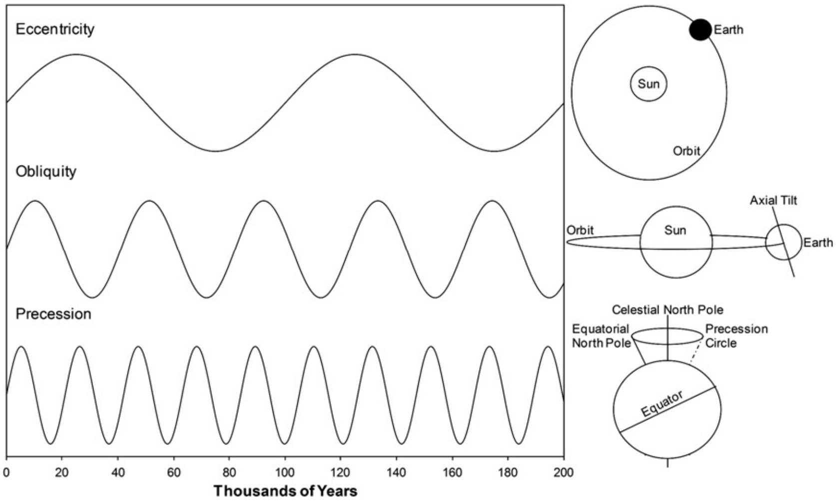

Fig. 1. The schematic shows the approximate periods of the eccentricity, obliquity, and precession components of the earth's climate. To the right, the diagrams show the aspects of earth's orbit that cause each cycle: the eccentricity cycle is caused by the elliptical shape of the earth's orbit around the sun, the obliquity cycle by the varied axial tilt of the earth, and the precession cycle by the 'wobble' of the equatorial north pole spinning through the precession circle.

modulated by the eccentricity cycle, which is of highly irregular amplitude. The net effect at low latitudes is of a complex combination of out-of-phase 21 ka and 100 ka oscillations that leads to constant remodelling of environments. The strong fluctuations in seasonality driven by this combination have knock-on effects over longer temporal spans; for example, strong seasonality often brings about high inter-annual variation, with a harsh winter one year following the previous year's milder temperatures. As Foley (1987) has pointed out, the woodland–savannah margin, thought to be so important an environment for our ancestors, is defined by its marked seasonality relative to other biomes.

In a classic synthesis, Whittaker (1975; see also Holdridge, 1947, 1967; Pianka, 1974) demonstrates that climatic change is the major determinant of vegetation change; as such, it is also the principal influence on the structure and composition of the faunal community. This latter relationship has both direct and indirect elements: to be habitable for a given animal, a region must provide both a temperature and precipitation range that the animal can tolerate and a suitable suite of flora and/or fauna to enable subsistence. Fig. 2 shows the relationships formalised by Whittaker between temperature, precipitation, and vegetation formation. Although the boundaries between types of vegetation are approximate, with one type actually grading into another, the basic structure of this graph has proven to be exceptionally robust (see e.g. Leriche et al., 2003; O'Connor et al., 2011; Rommerskirchen et al., 2006; Zheng et al., 2003). It demonstrates that simple changes in temperature, especially at the boundaries between habitat types, could dramatically affect the nature of primary productivity, with equivalent—though potentially more pronounced—changes in the faunal guilds.

Studies of extant hunter–gatherers have repeatedly shown that temperature and precipitation, and their links to environmental productivity, are vital in determining subsistence patterns. The variable most often computed in such studies is Effective Temperature (ET; Bailey, 1960), a simultaneous measure of the intensity of solar radiation and its distribution throughout the year. Low ET values are characteristic of cold environments and high seasonal variance in temperature, whilst high-ET values are associated with warm environments with lower differences between the warmest and coldest months of the year. Cold, high-variance environments have a markedly shorter growing season, and therefore lower plant productivity. Kelly (1995) demonstrates that hunter–gatherers in low-ET environments have to relocate their foraging bases more frequently than those in high-ET environments to compensate for the fact that primary resource density is lower (see also Binford, 1980; Grove, 2010c).

There is, then, a clear link between changes in insolation determined by the orbital cycles, the flora and fauna in

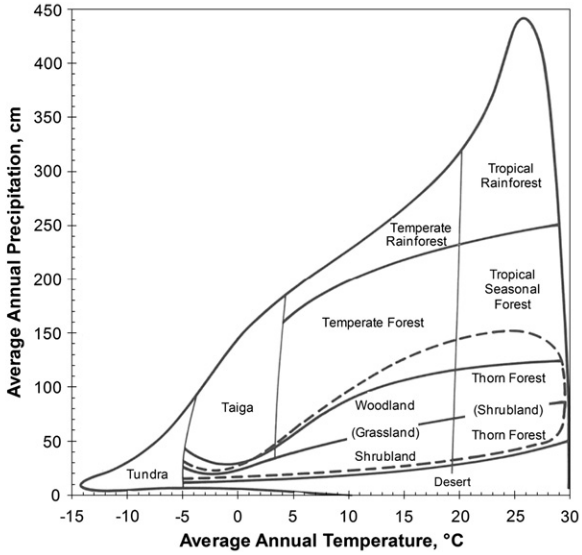

Fig. 2. Whittaker's (1975) attempt to relate floral communities to levels of temperature and precipitation. Though approximate, the figure shows that changes in temperature can have marked effects on vegetation composition and habitat quality.
Redrawn after Whittaker (1975:167).

ecological communities, and the ways in which humans (and, by extension, hominins) structure their subsistence patterns. Higher insolation levels (greater amounts of solar energy reaching the earth) increase temperatures and also melt the ice caps, leading to higher levels of 'free water' circulating as precipitation. Broadly speaking, warmer and wetter periods are periods of greater productivity.

The link between the experience of novel environments, subsistence stress, and encephalisation is made explicit above in the discussion of innovation rates and tendencies towards social learning, both of which correlate with brain size measures. Of particular relevance here are Reader and Laland's (2002) results regarding innovation rates in primates. Not only were larger-brained primates more innovative, but many of those innovations related to the manufacture and use of novel tools; the vast majority of these, in turn, were used to aid in the acquisition of food or water (Reader & Laland, 2002). A recent re-analysis by Overington et al. (2009) demonstrates that technical innovations drive the relationship between innovative propensity and brain size, whilst the diversity of innovations is a better predictor of brain size than the number. In sum, the frequent experience of novel environments is likely to lead to increases in brain size via selection for fitness-conferring innovative abilities, particularly when these abilities relate directly to the subsistence challenges faced in such environments.

Previous palaeoanthropological analyses of evolving brain size in relation to climatic fluctuations have employed crude measures of overall variability (e.g. Ash & Gallup, 2007; Bailey & Geary, 2009), but signal processing techniques allow for a more detailed examination of the individual effects of the precession, obliquity, and eccentricity cycles on human encephalisation. In order to provide such an examination, the analyses below filter a generic climate signal to extract the amplitudes of the oscillations corresponding to the frequencies of these three cycles, employing them as separate variables in multiple regression analyses to determine the potential influence of each on patterns of encephalisation.

2. Methods

2.1. Palaeoclimatic data

To provide suitable independent variables, global climate data were drawn from the LR04 stack (Lisiecki & Raymo, 2005; see Fig. 3A), an aligned and averaged composite of 57 globally distributed benthic δ^{18}O‰ records reflecting changes in palaeoclimate extending back beyond the 3.2 Ma for which there are reliable estimates of endocranial capacity. Benthic δ^{18}O‰ records measure the ratio of two isotopes of oxygen—^{18}O and ^{16}O—in the carbonate skeletons of micro-organisms, such as foraminifera, dwelling on the sea floor; during warmer periods, these micro-organisms take up greater quantities of ^{18}O. Cores drilled from the ocean floor contain foraminiferan skeletons dating back over multi-million year sequences, enabling the reconstruction of Palaeolithic temperature variation. As the LR04 Stack is an unevenly spaced time series, it was interpolated to 2.5 ka intervals using linear interpolation. To reconstruct the amplitudes of periodicities associated with the eccentricity, obliquity, and precession cycles over the past 3.2 Ma, three Butterworth bandpass filters of order 5 were constructed

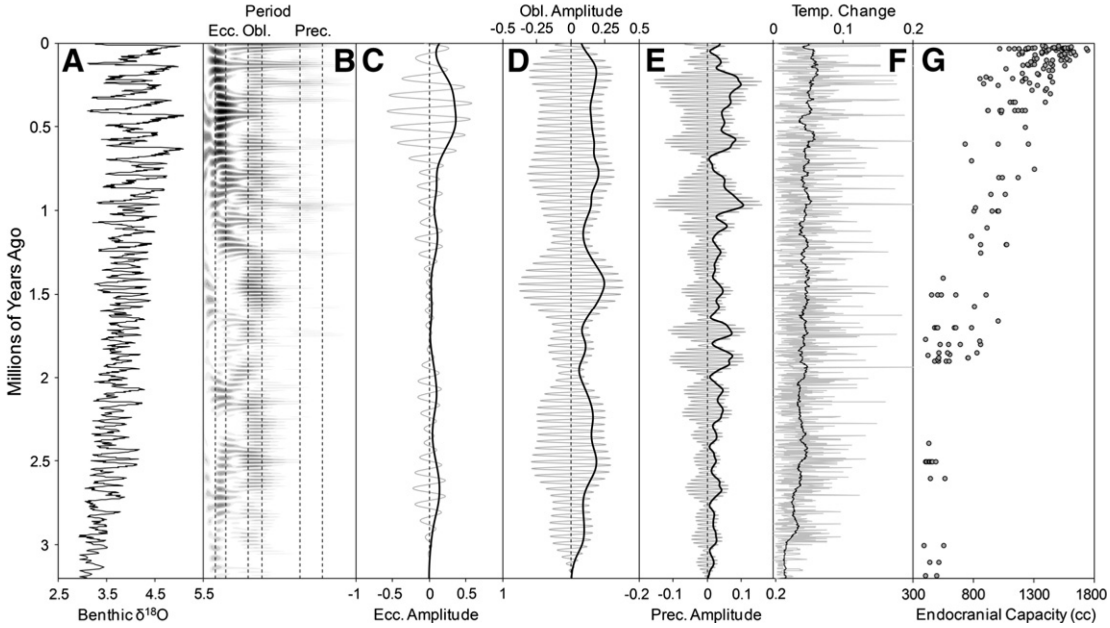

Fig. 3. A composite picture of palaeoclimatic change and human brain evolution over the last 3.2 million years. A) shows the raw data of the LR04 stack, an aligned stack of 57 globally distributed palaeotemperature records (after Lisiecki & Raymo, 2005). B) shows a wavelet analysis of the LR04 stack, with frequencies corresponding to the eccentricity, obliquity, and precession cycles highlighted. Darker areas indicate higher levels of activity at a given frequency. C), D), and E) present outputs of the bandpass filters designed to isolate and extract activity within the eccentricity, obliquity, and precession frequencies. Raw filter output is shown in grey, demodulated amplitudes (the variables to be correlated with endocranial volume) are shown in black. F) Shows temperature change. Data at 2.5 ka intervals are shown in grey, with the 100 ka mean (as used in analyses) shown in black. G) demonstrates the pattern of human brain evolution over the period, with each point representing a distinct fossil endocranial measurement.

using Matlab's `butter` function. Bandpass filters extract a certain frequency band from a complex signal (in this case the LR04 Stack) in order to facilitate examination of that frequency band in isolation. Filters were therefore constructed to examine bands of periodicities 19–23 ka, 36–46 ka, and 80–120 ka, where the boundaries around the 'ideal' values of 21 ka, 41 ka, and 100 ka are consistent with the standard deviations recovered from empirical samples by Berger and Pestiaux (1987). The LR04 Stack was then passed through each of these filters independently, with phase shifts avoided using Matlab's symmetrical `filtfilt` function (Trauth, 2010). The outputs of these filters are sinusoidal waves, shown as thin grey lines in Fig. 3C–E. The amplitudes of these waves are extracted using amplitude demodulation, which removes the 'wiggles' of the sine waves to leave the base amplitudes, shown as thick black lines in Fig. 3C–E.

In additional to the three 'Milankovitch variables' of eccentricity, obliquity, and precession amplitudes, a more basic general index of the rate of climatic change was also developed. This rate of change, R, is effectively the first derivative of the LR04 Stack, though the sign of the derivative is unimportant, hence $R=|\Delta c/\Delta t|$. Here c is the value of the Stack with Δt after interpolation being a constant 2.5 ka. As a lag will necessarily occur between a change in the palaeoclimatic regime and the evolutionary response to that change, the 100 ka interval preceding the estimated date of any particular endocranial capacity was considered to be associated with that measurement. Thus, each endocranial capacity is regressed upon an average of the value of each palaeoclimatic variable over the preceding 40 2.5 ka intervals. This lag time reduces the potential bias introduced by any errors or uncertainties in the dating of the fossil specimens, allows sufficient time for selection pressure to alter morphology, and is commensurate with lag times employed in earlier analyses of human evolutionary dynamics in relation to climatic change (Ash & Gallup, 2007; Bailey & Geary, 2009; Foley, 1994; Kimbel, 1995; Vrba, 1985, 1995). Analyses carried out with alternative lags of 50 ka and 200 ka confirm the results of previous analyses (Ash & Gallup, 2007; Bailey & Geary, 2009; Foley, 1994) that the precise lag employed does not significantly affect results. As the four primary independent variables (precession amplitude, obliquity amplitude, eccentricity amplitude, and absolute change in temperature) each represent an aggregate of values over the previous 100 ka interval, minimum, mean, and maximum values of each variable over that interval are entered into the analyses separately, yielding 12 independent variables in total. These 12 variables can still be considered to represent four primary predictors, but dividing them in this way allows for a more refined interpretation of the results in terms of the evolutionary drivers of encephalisation.

2.2. Endocranial capacities

Measurements of endocranial capacity, the dependent variable in the analyses reported below, were gathered from the extensive literature on changes in hominin fossil brain size (e.g. Aiello & Dunbar, 1993; Ash & Gallup, 2007; Bailey & Geary, 2009; de Miguel & Henneberg, 2001; Falk, 2007; Grove et al., 2012; Holloway et al., 2004). A total of 180 endocranial measurements were assembled for fossils dating to the period from 3.2 mya to the present. This dataset is the largest current compendium of endocranial measurements available for the hominins; importantly, it represents a number of hominin lineages, including some that are not directly ancestral to modern humans.

Due to biases in the preservation of skeletal material, more recent periods are better represented, yet the data provide a relatively complete picture of changes in brain size over the period (see Fig. 3G). So as to avoid multiple data points at any given age, endocranial capacities of the same age were averaged to provide single data points. This reduced the dataset to 78 averaged and age-matched endocranial capacities; each of these 78 data points was then assigned values of the 12 independent variables via the use of lookup tables matching those variables to age.

The relationship between endocranial capacity and brain size itself was examined in detail by Aiello and Dunbar (1993). Using data on endocranial capacities from Martin (1989) and on brain sizes from Stephan et al. (1981) for a wide range of primate species, Aiello and Dunbar (1993) found a predictably close relationship between the two ($R^2=0.995$, $N=36$, $p<0.001$). As endocranial capacity explains such a large proportion of the variance in brain size, rather than adding an additional layer of complexity to the analyses below, endocranial capacity is simply taken to be a direct proxy for brain size.

2.3. Statistical analyses

Following tests of conformity to the normal distribution, the nine independent variables composed of minima, means, and maxima of the eccentricity, obliquity, and precession amplitudes were natural log transformed to account for positive skew. Endocranial capacities and absolute changes in temperature did not deviate significantly from normal in their raw states. To provide an overview of the relationships between all variables and to give an indication of potential collinearities, Pearson correlations were first calculated on the entire dataset. Following this procedure, a series of multiple regressions were carried out using SPSS (PASW Statistics v.18) to determine which variables are best able to explain changes in endocranial capacity. Regressions were carried out using the SPSS Stepwise procedure, with an associated probability of F for entry at 0.05 and for removal at 0.1. Initially, only the nine variables derived from the amplitudes of the three major climatic cycles were entered into the analyses, allowing for an assessment of which of the minima, mean, and maxima variables would be of most importance. In the final model, the analyses were re-run with all twelve independent variables as potential predictors of endocranial capacity. This model provides not only an indication of which of the three climatic cycles are important in determining brain size, but also shows the extent of relevant climatic variation that exists outside of these cycles.

3. Results

3.1. Correlations

The Pearson correlation coefficients relating each of the thirteen variables are shown in Table 1. As expected, there

Table 1
Pearson correlation matrix of endocranial capacity and the twelve palaeoclimatic variables.

	Mean precession amp	Mean obliquity amp	Mean eccentricity amp	Max precession amp	Min precession amp	Max obliquity amp	Min obliquity amp	Max eccentricity amp	Min eccentricity amp	Change in temperature	Max temp change	Min temp change
Endocranial volume	0.053	0.435**	0.618**	0.097	−0.047	0.508**	0.265*	0.589**	0.655**	0.583**	0.351**	0.157
Mean precession amp		0.132	0.372**	0.935**	0.872**	−0.014	0.323**	0.443**	0.256*	0.392**	0.102	−0.024
Mean obliquity amp			0.512**	0.121	0.234*	0.961**	0.937**	0.516**	0.537**	0.648**	0.127	−0.049
Mean eccentricity amp				0.327**	0.383**	0.493**	0.494**	0.988**	0.984**	0.571**	0.185	0.248*
Max precession amp					0.725**	−0.040	0.320**	0.415**	0.209	0.414**	0.156	−0.017
Min precession amp						0.095	0.418**	0.435**	0.291**	0.279*	0.003	0.007
Max obliquity amp							0.811**	0.468**	0.545**	0.593**	0.108	0.001
Min obliquity amp								0.528**	0.483**	0.619**	0.103	−0.084
Max eccentricity amp									0.952**	0.609**	0.211	0.199
Min eccentricity amp										0.546**	0.177	0.286*
Change in temperature											0.561**	−0.166
Max temp change												−0.407**

Note: $^{*}p<0.05$, $^{**}p<0.01$ (2-tailed), $n=78$.
Amp = amplitude.

are a number of highly significant correlations throughout. Of potential importance are the results that, in isolation, the eccentricity variables all correlate strongly with endocranial capacity. The obliquity variables are all significant but of lesser impact, whilst none of the precession variables correlate with endocranial capacity. Mean absolute change in temperature is highly correlated with endocranial capacity, as well as with the amplitude variables, particularly the set derived from the amplitude of the obliquity cycle.

3.2. Multiple regressions

The initial multiple regression model, in which only the nine amplitude variables were entered, provides a highly complex picture of the potential involvement of the 'Milankovitch variables' in human brain evolution. Though the variable of greatest explanatory importance is the minimum amplitude of the eccentricity cycle, explaining as it does 43% of the variance in endocranial capacity, a further five variables contribute to the final model, explaining between 3.6% and 7.6% of the remaining variance. Though it is unwise to over-interpret this result, particularly given the fact that these nine variables essentially measure only three major axes of change, it is suggestive of the high concordance between environmental variability in general and evolutionary changes in human brain size. A more conservative result is obtained by altering the stepwise probability of F for entry to 0.01 and for removal to 0.05; in this instance, only minimum eccentricity amplitude and minimum precession amplitude remain in the model. Furthermore, a regression of endocranial capacity on only the first-entered variable representing each climatic cycle (minimum eccentricity amplitude, minimum precession amplitude, and maximum obliquity amplitude) drops the latter from the model. In summary, the results of this initial analysis can be conservatively interpreted as suggesting that the minimum amplitude of the eccentricity cycle is key in explaining the variance in endocranial capacity, with the minimum amplitude of the precession cycle also showing a significant (though negative) association (Table 2).

Results of the final model, in which all twelve independent variables were entered, are shown in Table 3. The final output includes only minimum eccentricity amplitude, change in temperature, and minimum precession amplitude as predictor variables. Each of these variables is a highly significant predictor ($p<0.001$ in all cases), though a considerable majority of the variance explained by the regression is accounted for by the relationship between minimum eccentricity amplitude and endocranial capacity. Results suggest, as per the correlations of Table 1, that change in temperature is a better predictor of endocranial capacity than all the amplitude variables except minimum eccentricity amplitude. Furthermore, it shows collinearity with the majority of those variables, displacing them from the final regression equation. It should also be noted that the beta coefficient relating minimum precession to endocranial capacity is negative, contrary to the initial expectation that any variable indexing climatic variability would relate positively to endocranial capacity. The implications of the final model results are discussed in detail below. Partial plots of endocranial capacity regressed upon minimum eccentricity amplitude, absolute

Table 2
Stepwise multiple regression model of endocranial capacity regressed on the nine 'Milankovitch variables'.

		B	SE B	β
Model 1	Constant	1729.935	85.988	
	Min eccentricity amp	272.785	36.129	0.655 ****
Model 2	Constant	1350.901	150.515	
	Min eccentricity amp	304.085	35.915	0.730 ****
	Min precession amp	− 116.066	38.691	− 0.259 ***
Model 3	Constant	1662.380	195.791	
	Min eccentricity amp	304.265	34.839	0.730 ****
	Min precession amp	− 206.267	53.251	− 0.460 ****
	Max precession amp	242.997	101.764	0.277 *
Model 4	Constant	2247.389	293.958	
	Min eccentricity amp	246.899	40.191	0.593 ****
	Min precession amp	− 216.732	51.459	− 0.483 ****
	Max precession amp	291.526	99.806	0.333 **
	Max obliquity amp	350.068	134.916	0.244 *
Model 5	Constant	2711.307	294.048	
	Min eccentricity amp	225.261	37.185	0.541 ****
	Min precession amp	− 162.418	49.093	− 0.362 ***
	Max precession amp	415.275	96.661	0.474 ****
	Max obliquity amp	1100.847	228.627	0.766 ****
	Min obliquity amp	− 637.122	163.313	− 0.617 ****
Model 6	Constant	2456.559	286.366	
	Min eccentricity amp	228.974	34.889	.550 ****
	Min precession Amp	− 118.950	47.888	− 0.265 *
	Max precession amp	377.520	91.366	0.431 ****
	Max obliquity amp	− 1752.280	891.404	− 1.220
	Min obliquity amp	− 2323.487	533.845	− 2.250 ****
	LN obliquity amplitude	4307.015	1306.142	3.429 ***

Note: $n = 78$, $R^2 = 0.429$ for Model 1, $\Delta R^2 = 0.061$ for Model 2, $\Delta R^2 = 0.036$ for Model 3, $\Delta R^2 = 0.040$ for Model 4, $\Delta R^2 = 0.076$ for Model 5, $\Delta R^2 = 0.048$ for Model 6.
All R^2 changes are significant at at least the $p < 0.05$ level.
$^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.005$, $^{****}p < 0.001$.

change in temperature, and minimum precession amplitude are shown in Fig. 4.

4. Discussion

First and foremost, the results presented above demonstrate that environmental heterogeneity, indexed via palaeoclimatic variables, explains a substantial component of the variation in human brain size evolution. A great strength of the model is the fact that climatic variables explain both increases and decreases in average hominin brain sizes over the period examined. Though average hominin brain size increases over the period as a whole, short-term decreases in average brain size correlate with decreases in environmental heterogeneity. In particular, the amplitude of the eccentricity cycle explains 43% of the variance in endocranial capacity over the past 3.2 million years, a result consistent with the environmental complexity thesis. However, the results are

Table 3
Stepwise multiple regression model of endocranial capacity regressed on all twelve independent palaeoclimatic variables.

		B	SE B	β
Model 1	Constant	1729.935	85.988	
	Minimum eccentricity amplitude	272.785	36.129	0.655 *
Model 2	Constant	767.185	302.305	
	Minimum eccentricity amplitude	199.551	40.565	0.479 *
	Absolute change in temperature	6271.521	1897.499	0.322 *
Model 3	Constant	158.987	318.332	
	Minimum eccentricity amplitude	224.820	37.772	0.540 *
	Absolute change in temperature	7296.161	1760.364	0.374 *
	Minimum precession amplitude	-138.074	35.490	− 0.308 *

Note: $n = 78$, $R^2 = 0.429$ for Model 1, $\Delta R^2 = 0.073$ for Model 2, $\Delta R^2 = 0.085$ for Model 3.
$^*p < 0.001$.

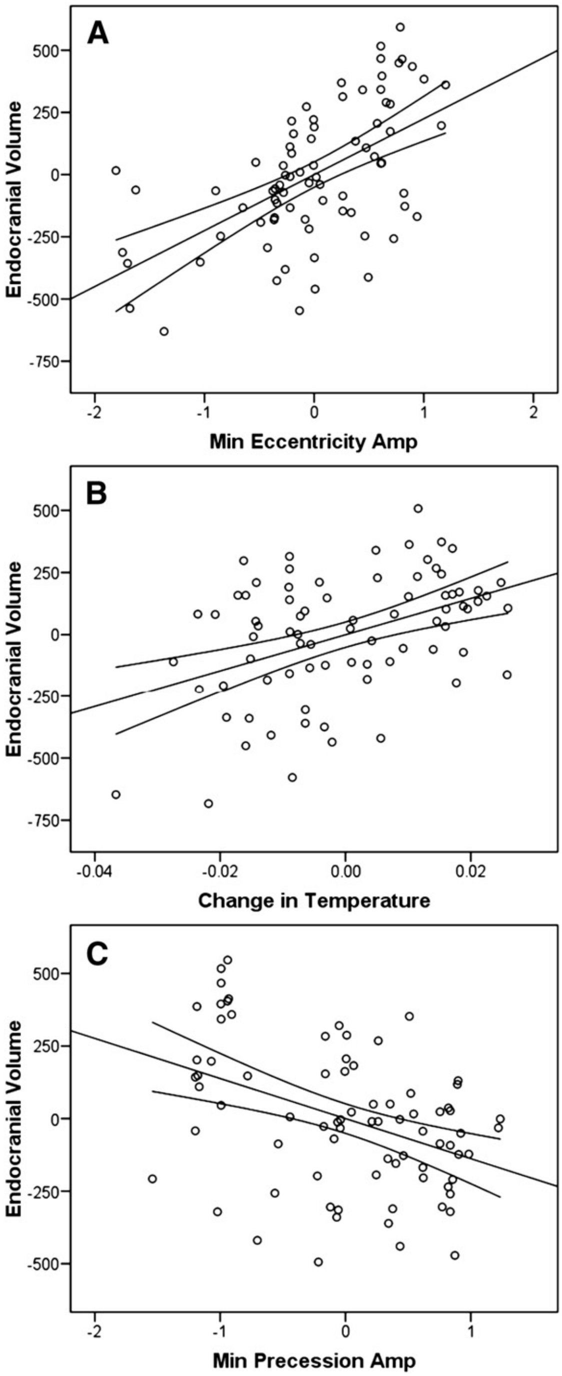

Fig. 4. Plots of the final stepwise multiple regression model. The figure shows partial plots of endocranial capacity regressed on the three significant variables in the final model: a), minimum amplitude of the eccentricity cycle, b), absolute change in temperature, and c), minimum amplitude of the precession cycle (for statistical details see Table 3).

complex, and raise a number of issues regarding evolutionary causation, as well as about the scales at which climate variability interacts with brain evolution. Below, these issues are untangled with reference to known patterns of human brain evolution and major events in the climatic history of the earth.

That the eccentricity cycle accounts for a substantial proportion of the final model's power is consistent with recent analyses of evolutionary speciation-extinction dynamics in the hominin lineage (Grove, 2011b). As the cycle with the longest period, the eccentricity of the Earth's orbit naturally modulates the effects of the shorter cycles, particularly the relatively short-period precession cycle (Milankovitch, 1941; Ruddiman, 2008). Traditionally, the eccentricity cycle is considered to dominate climatic patterns only after approximately 1 mya (e.g. deMenocal, 1995, 2004), but the results of Fig. 3 together with the multiple regression analyses reported above suggest that it had far-reaching effects on hominin adaptations over a substantially longer period. The interpretation suggested by the above results accords with certain elements of the traditional picture of orbitally-driven climatic change, but adds key insights about the *longue durée* of human brain expansion.

In particular, two major climatic 'revolutions' occurred over the past three million years, both of which had major effects on human populations. The first occurred shortly after 3 mya, and the second around 1 mya. Sometime after 4.6 mya the closure of the Isthmus of Panama isolated the Atlantic basin (Haug et al., 2001; Raymo, 1994), leading ultimately to the onset of high-latitude glacial cycles between 3.2 and 2.6 mya (deMenocal, 2004). High-latitude glaciation after 3 mya is generally associated with the increasing dominance of the obliquity cycle over the previously dominant precession cycle; though Fig. 3 supports this notion in generic terms, the full picture is rather more complex. As humans did not leave Africa until after 2 mya (million years ago), human brain evolution during these early phases is necessarily linked to low-latitude climate. Following the onset of northern hemisphere glaciation, African aridity cycles were inextricably linked to high-latitude glacial cycles that periodically removed large quantities of water from global circulation, causing increased aridity at low latitudes (Clemens et al., 1996; deMenocal, 1995; deMenocal & Bloemendal, 1995; Tiedemann et al., 1994). In addition to a gradual increase in aridity, patterns of palaeoclimatic variability at 10 ka to 100 ka scales in Africa over the past 2.8 mya have been driven primarily by the eccentricity cycle (deMenocal, 1995; Tiedemann et al., 1994).

Prior to the onset of northern hemisphere glaciations, the hominin lineage is represented in the fossil record primarily by various species of *Australopithecus*, a genus that first emerged around 4 mya. The data suggest that within the Australopithecine genus brain size persisted at or around the 400 cm^3 level—equivalent to that of the modern common chimpanzee—for at least 1.5 million years. This uneventful period of brain evolution ended at approximately 2.75 mya with the appearance of a new genus, *Paranthropus* (Suwa et al., 1996), and proceeded towards dramatic increases with the evolution of our own genus, *Homo*, at approximately 2.3–2.4 mya (Bromage et al., 1995; Hill et al., 1992; Schrenk et al., 2007). Though dated and measurable *Homo* crania do not appear in the fossil record until approximately 400 ka after the likely first appearance of our genus, it is likely that increasing brain size was a trait that marked *Homo* as distinct from the australopithecines from the very base of the radiation. That both *Paranthropus* and *Homo* appear soon after the onset of northern hemisphere glaciation, and that *Homo* in particular begins to display signs of increasing brain size during the first significant burst of activity in the eccentricity spectrum (see Fig. 3B, C) provides the first temporally localised instance of increases in the amplitude of the eccentricity cycle correlating with increases in human brain size.

The second localised coincidence of rapid increases in both eccentricity amplitude and brain size occurs after the second major climatic event of the past three million years, the so-called 'Mid-Pleistocene Revolution' (henceforth MPR) at approximately 1 mya. Though the exact structure of the MPR is still debated (e.g. Maslin & Ridgwell, 2005; Mudelsee & Stattegger, 1997), it is clear from the majority of climate records that by 1 mya at the latest the eccentricity cycle has markedly increased in amplitude, coming to dominate the overall climate system at a global scale (see Grove, 2011b, and Fig. 3B, C). Fig. 3C shows a possible lead-in to the post-1 mya dominance of the eccentricity cycle as far removed as 1.5 mya, and demonstrates that the highest amplitude of the eccentricity cycle occurs at approximately 0.5 mya. This date coincides with a second major burst of hominin encephalisation identified by Ruff et al. (1997), and marked in the fossil record by the large-brained *Homo heidelbergensis*, the ancestor of both our own species and the Neanderthals (Endicott et al., 2010; Green et al., 2010). The post-1 mya co-occurrence of the highest amplitude eccentricity signal in prehistory and the greatest increase in brain size yet documented in the entire hominin lineage provides the most profound example of a persistent link between climatic change and human encephalisation.

Whilst the close link between endocranial capacity and the amplitude of the eccentricity cycle seems indisputable, the fact that it is the *minimum* amplitude of the eccentricity cycle per 100 ka that brain size is apparently attuned to requires further explanation. There are three potential explanations for this relationship, and they could reasonably be expected to work in concert. Firstly, and of most importance, it has long been noted that the brain is an exceptionally expensive organ in metabolic terms (e.g. Aiello & Wheeler, 1995; Isler & van Schaik, 2009a), with this expense forming a severe constraint on evolutionary increases in the mass of neural tissue. Given the frugality of evolution in this (and any) process, we can propose that a brain sufficient to deal with eccentricity minima is one that will 'satisfice' in conditions when to optimise would be a great deal more expensive (Simon, 1956:136). Secondly, if we regard a larger brain as being constructed to deal with environmental heterogeneity brought about by orbital effects on climate, it seems probable that our ancestors would also have been able to deal with elements of that heterogeneity via relocation. The majority of animals geographically track their native habitats when environmental conditions change, and we must expect that early hominins would also have done so (see Lahr & Foley, 1998). Sol's research (Sol et al., 2005a, 2010), cited in the introduction, demonstrates the two poles of mobility—residency and migration—and how brain sizes are affected by them. With a brain sufficient to deal with the general shape of eccentricity-driven fluctuations and a mobility strategy sufficient to deal with the finer details, early humans would have had a comprehensive solution to changing environments. Finally, given that the period of the eccentricity cycle is 100 ka, the minimum and maximum amplitudes during any 100 ka period will be relatively close to one another, making the habitat tracking solution an entirely viable one.

If the correlation of minimum eccentricity amplitude and endocranial capacity explains the effect of very long-term oscillations on brain evolution, the second independent variable retained in the final model deals, by contrast, with the very short-term component. Mean temperature change explains only 7% of the variance in endocranial volume, but it is a highly significant addition to the model. The relatively small effect of this variable relative to minimum eccentricity amplitude is likely due to the fact that short-period fluctuations are modulated by longer term cycles; once the latter are partialled out, any apparent correlations between endocranial volume and the former are substantially weakened. As shown in Fig. 3F temperature change, when averaged over the 100 ka lag time employed in the analyses above, displays a consistently high variance and a relatively constant mean over the last 3 Ma. These dynamics clearly suggest that adjusting cognitive power so as to track the mean rather than the minimum or maximum would be a preferable evolutionary strategy; given the high variance, an animal tracking the maximum would be investing in expensive brain tissue that was seldom used in practice, whilst an animal tracking the minimum would more often than not be ill equipped to deal with the challenges posed by the variability of the environment. In reference to this argument, data recently published by van Woerden et al. (2009, 2010) suggest that rapid changes in habitat may restrict encephalisation in primates due to lack of available food resources, rather than promoting encephalisation as a cognitive solution to the problem of novel environments.

The final independent variable included in the final model is minimum precession amplitude, explaining an additional 9% of the variance in endocranial volume. This is an unexpected result, given that none of the precession variables correlate with endocranial capacity in Table 1, and it is well known that precession is heavily modulated by the eccentricity cycle. In addition, the six precession and eccentricity variables are all themselves significantly correlated, suggesting that the strongest predictor might cause the model to omit the weaker predictors due to collinearity effects. In fact, tracing the progress of the model via correlation coefficients, one can see that it is the partialling out of minimum eccentricity amplitude that creates a significant negative correlation between endocranial capacity and minimum precession amplitude (from Pearson's $r=-0.47$, $p=0.686$ to $r=-0.327$, $p=0.004$, $n=78$), with the subsequent partialling of mean temperature change only slightly increasing the power of this correlation (to $r=-0.412$, $p<0.001$, $n=78$). That this correlation is negative is an unexpected result, but may stem from the changing relative strength of the precession signal over the period analysed. DeMenocal's (1995, 2004) well-studied scheme of the major climatic transitions of the past 5 Ma, in which the precession signal is dominant prior to c. 3 mya, but cedes dominance to the obliquity cycle after that age, and is overshadowed further by the eccentricity signal by 1 mya, points to the gradual decrease in the influence of the precession signal on global climate. Though precession can be seen as the cycle that contributes most to shorter-term climatic fluctuations throughout the past 5 Ma (Maslin & Ridgwell, 2005), its strength relative to the obliquity and eccentricity cycles has waned during that period (Fig. 3C–E); indeed, there is very little activity in the precession band of the wavelet analyses shown in Fig. 3B. As the relative strength of the precession signal decreases, and as that of the eccentricity signal increases, so human brain size also increases. With minimum eccentricity amplitude the first predictor of endocranial volume in the final model, there remains a negative relationship between endocranial volume and minimum precession amplitude as a result of the decreasing relative importance of precession in the composite climatic record. This result is an interesting challenge to predictions of positive relationships between brain size and climatic variability at all temporal scales (e.g. Richerson & Boyd, 2000; Richerson et al., 2005), and demonstrates that there is far more work to be done in this area.

Recent inter-specific research in primatology (Reader et al., 2011; Shultz & Dunbar, 2010b) has definitively established what has always been implicitly assumed in studies of human evolution—that a larger brain predicts enhanced cognitive abilities applicable to a number of tasks. Specifically, however, there is also mounting evidence that encephalisation may have been geared particularly towards increasing the ability to innovate or think creatively (e.g. Coward & Grove, 2011; Reader & Laland, 2002), and that this ability was of particular use to animals inhabiting heterogeneous environments (e.g. Sol, 2009; Whitehead, 2007). Though a constellation of inter-related factors were involved in the evolution of human encephalisation (Coward & Grove, 2011; Grove & Coward, 2008), the parallels found in numerous other species support the results of the current paper in suggesting that environmental variability could have acted as a major driver of the three-fold increase in brain size documented over the last 3.2 million years.

At the within-species level, numerous analyses have found positive relationships between brain size and various measures of intelligence (e.g. Deary et al., 2007; McDaniel, 2005; Rushton & Ankney, 2007, 2009; Rushton & Rushton, 2004). MacLullich et al. (2002) used a latent trait approach to derive relatively error-free measures of both *g* (the general factor of intelligence) and brain volume, finding a correlation of 0.42. McDaniel (2005) performed a meta-analysis of the correlation between general cognitive ability (most studies considered measured this ability via the *Ravens Progressive Matrices*) and in vivo brain size (determined via MRI scans), estimating a population correlation for 37 samples across 1530 individuals of 0.33. Rushton and Ankney's (2007) more recent meta-analysis yields a population correlation of 0.37 for 27 samples from brain imaging studies across 1341 individuals. Finally, in the most comprehensive meta-analysis to date, Rushton and Ankney (2009) correlate general mental ability (GMA) with brain volume measures taken both from direct brain imaging studies and studies using external head size measures as proxies. Using brain imaging techniques, the correlation for 28 samples across 1389 individuals is 0.40; in 59 samples across 63,405 individuals using external head size measures this falls to 0.20. Importantly, Rushton and Ankney (2009) also report a meta-analysis of six studies using the method of correlated vectors to distil *g*; these provide a correlation with brain size measures of 0.63. These analyses collectively demonstrate that, despite the undisputed value of the modular or 'domain-specific' approaches often espoused by evolutionary psychologists, there is also considerable merit in viewing overall brain size as an index of intelligence.

Analyses of brain size and intelligence variation within our own species have also touched on the issue of environmental novelty as a stimulus (e.g. Kanazawa, 2004, 2008; Lynn, 1991, 2006; Rushton, 1995, 2012). Both Lynn (1991) and Rushton (1995) favour the idea that temperature is a key driver of intelligence in modern humans, focusing particularly on what has come to be known as the Cold Winters Theory (CWT; Kanazawa, 2012; Rushton, 2012). This theory suggests that cold climates and hard winters, particularly at higher latitudes, led to cognitive challenges relating to the scarcity of resources and the need to construct shelters and adequate clothing; against this backdrop, those individuals more able to provide successful solutions would be more likely to propagate their genes. Lynn (2006; see also Rushton & Ankney, 2009) supports this theory by way of a correlation of 0.62 between cranial capacity and distance from the equator in 20,000 crania. In a subtly but importantly different interpretation, Kanazawa (2004) suggests that it is the evolutionary novelty of the environment, rather than cold climates per se, that selects for greater innovation and intelligence. Using a comprehensive list of national IQs for all nations with populations greater than 40,000 ($n = 192$), Kanazawa (2008) correlated IQ values with national annual mean temperatures and distances of each nation from proposed ancestral environments (including central Ethiopia). Kanazawa (2008) found a significant negative relationship between annual mean temperature and national IQ, a result he interprets as supporting the CWT; he also found a significant positive relationship between distance from the ancestral environment and national IQ, a result interpreted as supporting the evolutionary novelty hypothesis. At this stage, therefore, the effects of these two hypotheses cannot be disentangled; the evolutionary novelty hypothesis, however, is more consistent with the literature surveyed here. The use of absolute distance rather than a direct measure of ecological difference is less than ideal, but the evolutionary novelty hypothesis merits further investigation.

That environmental novelty might demand behavioural versatility and, ultimately, a higher level of intelligence is an intuitively appealing thesis, and one borne out by the results presented above. However, the question arises as to the effects of climatic variability (or other drivers of environmental novelty) on species other than the hominins; if climatic variability made humans intelligent, did it have a similar effect on other animals? Over very long timescales, this may in fact be the case. Both Jerison (1973) and Russell (1983) plot brain sizes of available fossil taxa over periods extending back to the Palaeozoic (≈540 to≈250 mya), demonstrating a generic increase in brain size in living forms over this period. The exponential increase in brain sizes documented by Russell (1983) may be related to increasing climatic variability, though there are a number of equally probable alternative explanations. The second, more enlightening answer to the question involves an examination of the strategies animals use to counter changing environments. The first and most widely used strategy is relocation; most organisms simply track their favoured environments, with the net result that the climatic change that might occur in any given location is not actually experienced by any given organism. When the pace of environmental change outstrips the organism's potential for mobility, the organism faces extinction unless it can adapt to the new environmental regime. The most obvious means of adaptation is natural selection itself, but this is only likely to act as a viable response to rapidly fluctuating environments if the organism has a short generation time, and a correspondingly high intrinsic rate of increase. For organisms with longer generation times, the only way to remain viable in rapidly fluctuating environments is to achieve a measure of behavioural flexibility via either phenotypic plasticity (broadly construed), enabling within-generation responses to novelty. The well known positive correlations between generation time and brain size both within (Rushton, 1985, 2004) and between species (Isler & Van Schaik, 2009b; Joffe, 1997; Ross, 1988) can be interpreted as suggesting that there is a cognitive continuum between rapidly reproducing, small-brained animals that rely primarily on natural selection to deal with climatic change and slowly reproducing, large-brained animals that have shifted the burden at least partially towards a reliance on cognitive solutions. This would suggest that the animals most likely to have followed a similar route to *Homo sapiens* in terms of cognitive evolution would have been the long-lived, larger-brained species such as the capuchin monkey, the chimpanzee, the odontocete cetaceans (toothed whales, including the bottlenose dolphin), and the proboscids (elephants, and the extinct mammoths and mastodons). Preliminary results indicate that each of these species have formidable cognitive abilities (Bearzi & Stanford, 2010; Marino, 1997; Roth & Dicke, 2005; Whiten et al., 1999).

More generally, ecologists and philosophers of science alike have long considered that only environments varying in particular ways are conducive to the evolution of advanced cognition. Stephens (1987, 1989, 1991), in a series of papers on the evolution of learning, establishes that whilst learning is necessarily more beneficial in a changing environment than a static one, it is only of use provided that there is a certain predictability to the environment. Mirroring Colwell's (1974) classic treatment of predictability and contingency, Stephens (1991) demonstrates that there must be regular associations between aspects of the environment over time in order to provide anchor points for learning to occur. An environment must be variable in order to provide a stimulus to the evolution of learning, yet it must be predictable such that present experience is a reliable lesson regarding future events (Staddon, 1983).

With this model of evolution in mind, it is unsurprising that the results presented above find substantial correlations between the most notable periodic climate cycles of the past 3.2 Ma and the evolution of the human brain. Whilst current human adaptive behaviour is composed of a combination of genetic inheritance and learned abilities, we must infer that our genetically determined hardware has gradually ceded dominance to our increasingly sophisticated cerebral software over the course of evolutionary time. The three-fold advantage in brain size relative to that of our closest genetic relatives has provided phenomenal cognitive abilities, yet it seems increasingly likely that these are built upon simpler architectures shared by numerous other species. For example, the innovative propensity found in large-brained birds and primates (Lefebvre et al., 1997, 2004; Reader & Laland, 2002) might be seen as a parallel of the fluid component of general intelligence defined by Cattell (1963b:3) as facilitating “adaptation to new situations”.

It is not the intention here to belittle the capacities for metaphor, analogy, and creativity that define our species' higher cognitive functions, nor to deny their superiority over those possessed by other animals. Rather, the current work suggests that due consideration of the environments in which our evolutionary history was played out will be highly informative in future reconstructions of the nature and function of human intelligence. In particular, future research should focus on the specific intellectual abilities favoured by periodically fluctuating climates, and on the ways in which the cognitive demands placed on our ancestors by their environments might be evaluated in modern populations via measures such as ‘divergent thinking’ and ‘fluid intelligence’. Overall, a greater integration of the literatures on the nature of contemporary human intelligence, the progression of human cranial evolution, and the reconstruction of prehistoric climates should provide a stimulating context for future enquiry.

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