Review

Hominin cognitive evolution: identifying patterns and processes in the fossil and archaeological record

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As only limited insight into behaviour is available from the archaeological record, much of our understanding of historical changes in human cognition is restricted to identifying changes in brain size and architecture. Using both absolute and residual brain size estimates, we show that hominin brain evolution was likely to be the result of a mix of processes; punctuated changes at approximately 100 kya, 1 Mya and 1.8 Mya are supplemented by gradual within-lineage changes in *Homo erectus* and *Homo sapiens sensu lato*. While brain size increase in *Homo* in Africa is a gradual process, migration of hominins into Eurasia is associated with step changes at approximately 400 kya and approximately 100 kya. We then demonstrate that periods of rapid change in hominin brain size are not temporally associated with changes in environmental unpredictability or with long-term palaeoclimate trends. Thus, we argue that commonly used global sea level or Indian Ocean dust palaeoclimate records provide little evidence for either the variability selection or aridity hypotheses explaining changes in hominin brain size. Brain size change at approximately 100 kya is coincident with demographic change and the appearance of fully modern language. However, gaps remain in our understanding of the external pressures driving encephalization, which will only be filled by novel applications of the fossil, palaeoclimatic and archaeological records.

Keywords: hominin encephalization; variability selection; punctuated evolution; aeolian deposition; palaeoclimate

1. INTRODUCTION

One of the most distinct features of recent human evolution is the trend towards increasingly large brains over the Plio-Pleistocene. Early hominin australopithecines had a cranial capacity (CC) slightly larger than that of extant apes [1]; over the subsequent three million years, average brain size trebled. Brains are extremely expensive to both grow and maintain; the increase in early *Homo* brains imposed an estimated 20 per cent increase in metabolic costs [2]. This cost is even higher in later hominin species; resting metabolic rate of female *Homo ergaster* was an estimated 1.53 times higher than that of *Australopithecus afarensis* and is 1.64 times higher for female *Homo sapiens* [3]. An even more striking estimate is that the daily energy expenditure in female *Homo erectus* may have been more than 80 per cent higher than female australopithecines [4]. Evolutionary reasoning demands that individuals can afford to pay hefty costs only if they are outweighed by commensurate benefits. There is little doubt that the large human brain provides the machinery to execute complex cognitive tasks, including forward planning, language use, innovation and social perception. However, the search for the mechanisms driving the marked increase in human brain size over the past two million years has been the subject of much debate. This paper will (i) review the arguments for the pressures driving hominin brain expansion, (ii) quantitatively evaluate tempo changes in hominin brain size, and (iii) test environmentally based hypotheses for brain size change. Finally, we will contextualize encephalization patterns within the archaeological evidence for cognitive evolution.

(a) *Potential drivers of hominin encephalization*

Explanations for encephalization in hominins are mainly based on the evolution of behavioural flexibility and adaptability to changing or unpredictable environmental conditions. In addition to responses to climatic conditions, other suggestions focus on changes in diet, indirect effects of habitat use, social environment and technology. Here, we briefly review these hypotheses.

(i) *Climate*

Three different climatic processes have been implicated in driving hominin encephalization. The first process is the consequence of cooling, drying and the expansion of the savannah forcing individuals to move into novel

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habitats and alter their use of resources [5]; such a change is suggested in the Late Pliocene archaeological record [6]. The second process is the consequence of an increasingly unpredictable climate, which has been labelled as the *variability selection hypothesis* [7,8], whereby extreme fluctuations in the environment created dynamic and inconsistent habitats over time. The third is the impact of climatic pulses causing abrupt habitat and environmental shifts [6,9]. For all processes, flexibility and innovation in habitat, resource or space use could be adaptive behavioural responses to a changing environment. For example, a broad and a flexible diet allows the exploitation of unpredictable resources across a mosaic habitat [10,11], whereas the development and capacity to use tools opens up novel adaptive zones [12]. The correlation between environmental variance and hominin brain size over time has been argued to be the result of environmental unpredictability driving hominin brain evolution [13,14]. This assumes a causal relationship wherein brain size has evolved as a direct response to environmental variability. Rather than a simple bivariate correlation, a better test of this hypothesis would be to relate specific periods of rapid change in brain size to periods of increased environmental change or variability, which has yet to be done.

(ii) Predation
In addition to changing the resource base, moving into open habitats increases predation risk as refuges are less common [15]. For this reason, terrestrial primates live in much larger groups than arboreal species; this is especially true of species that are typically found in open habitats [16]. Shifting into open, high-risk habitats would have substantially increased the risk of predation for early hominins. Predation clearly impacted on australopithecines; damage caused by both carnivores and raptors has been found on fossilized remains [17,18]. However, we do not know how much of an issue predation pressure was for early *Homo*. The shifts in *H. erectus/ergaster* towards more open habitats [19,20] would have made them potentially more vulnerable to large carnivores. Across mammals, large brain size in prey reduces predation risk, with predators showing biases towards, or preference for, small-brained prey [21,22]. The mechanism driving this association is unknown, but prey species with larger cognitive capacity could be expected to employ more diverse escape or defence strategies [22]. Thus, the predation and resource pressure resulting from using more open environments constitutes a potential factor in brain size change in early *Homo*.

(iii) Sociality
Both the preceding hypotheses (environmental variability and predation) may also impact on cognitive evolution indirectly via changes they impose on hominin social environments. Predation is the principal driver of primate sociality [23], and primate species living on the ground and in smaller groups suffer higher predation rates than those in large groups [24]. Moving from closed into riskier open habitats is associated with larger foraging groups in birds,

primates and other mammals. Maintaining bonded social groups imposes cognitive demands itself as a result of the need to solve (ecological) problems within a coordinated social environment, rather than in a demographic vacuum [25]. In fact, the complex social environment in which anthropoid primates live is one of the primary explanations for why they have exceptionally large brains for their body size [26,27]. The more disparate the needs of group members, the more difficult the task of coordination and cooperation becomes. When conflict arises, individuals in stable groups must be able to negotiate to achieve outcomes that are suitable for all group members. Of crucial importance in this respect is an individual's ability to factor in others' interests, that may be dependent on cognitive mechanisms such as empathy, perspective taking and theory of mind [28,29].

Within anthropoid primates, there is a strong correlation between group size and brain size [30,31]; Aiello & Dunbar [32] extrapolated this relationship to predict social group size in hominin species (for revised estimates, see Dunbar [33]). To date, this method remains the only model available to estimate hominin group sizes. As this approach relies on the assumption that brain size and group size in hominins are intimately coupled, it is not appropriate if we wish to verify that changes in brain size/architecture are temporally linked with changes in hominin social group structure. Alternative avenues for estimating social group size, such as artefact deposition rates, hominin assemblage numbers [14], hearth/site sizes, are fraught with potential biases, which makes their use hard to justify especially when comparing over wide time periods. Thus, at the present time, there are no independent methods which can explicitly estimate changes in social group size or population density in hominins over time.

(iv) Language evolution
While language evolution is undoubtedly tethered to sociality, its importance as a defining characteristic in human cognitive evolution cannot be overstated. Language increases an individual's understanding of the world because the individual is no longer limited to holding only information that it directly perceives [34]. Apart from the ability to share intentional thoughts, language also allows the exchange of information, ultimately leading to distributed cognition, and provides the neural substrate for symbolic thought [35]. As with other aspects of hominin sociality, language does not fossilize; instead we have to infer the evolutionary changes in the complexity of language ability from archaeological and fossil evidence. Language involves the integration of hierarchically organized subsystems [34], and understanding how cognitive ability changed in order to accommodate this is undoubtedly of major importance to understanding later hominin evolution. Thus, one argument may be that it was the cognitive demands of language *per se* that drove hominin brain evolution. In this respect, intentionality (or mentalizing) competences seem to be crucial, because these determine how complex language can become (e.g. the number of embedded clauses that can be unpacked)

[28]. If intentional competences are a function of brain (region) volume, as they seem to be in humans [36,37], then language complexity may reflect changes in brain size. Thus, rather than language being a macro-mutation-like all-or-none affair, it might have arisen as a graded process of increasing complexity over time. This allows for a feedback process in which language itself became a selection pressure for increases in brain size.

(v) *Metabolic demands and life-history changes*
The adaptive benefits associated with larger cognitive capacities are not the only consideration when understanding processes driving brain evolution: mitigating constraints is also necessary to permit the development of larger brains. Large brain size is associated with a prolonged life history such as extended juvenile periods and delayed reproduction [38,39]. If long dependency periods are crucial for developing large brains, then social changes involving increased parental care and provisioning are likely to coincide with brain size increases [40,41]. Metabolic demands also exert strong constraints on brain size [39,42]; unless individuals can meet the increased metabolic demands of a large brain, they cannot develop or maintain them. High-energy diets such as meat could release metabolic constraints on brain size [43,44]. Apart from dietary changes, an intriguing possibility is that the use of fire for cooking made food more digestible [45], which became increasingly important as hominins expanded their range into more temperate zones [46].

A key issue remains as to whether environmental pressures are ultimately the cause of changes in the other selection pressures that influence brain size. If so, then periods of rapid brain size change should be associated with corresponding periods of changes in climate or in climate envelopes.

2. TEMPO AND BRAIN EVOLUTION
In order to identify the causal forces driving the increase in hominin brain size over the past three million years, we must first understand the tempo and process of brain size change. Large-scale evolutionary changes in continuous characters can result from two processes, punctuated equilibrium (a series of steps (saltations) followed by stasis) or gradualism (whereby there is an accumulation of small incremental changes) [47]. If the tempo of evolution is short rapid changes followed by long periods of stasis, then it is likely that there are pulses of selective pressures associated with either external drivers or the appearance of novel phenotypes. Conversely, if evolutionary change is underpinned by a gradual and continuous process, then the selective pressures are likely to be either a ratchet process or driven by long-term low-level directional selection. A number of proponents support gradualism [48,49], whereas others argue that there have been long periods of stasis in brain size followed by bursts of change [50], or that rates of change vary over time [51,52] and space [53,54]. One likely reason for the different inferences made about the process of hominin brain size changes is that different methodologies have been used. These vary from qualitative [46] to least-squares regression of brain size against time [55–58], to examining differences in brain size (or CC) between adjacent time periods [49]. One conclusion that all methods agree upon is that brain size has increased, but the tempo of those changes remains unresolved.

We suggest that one reason for the disagreement is that there may be a combination of processes occurring across hominin evolution, leading to different temporal signatures in brain size change. The methods used to date have been appropriate for identifying the signatures of a gradual process, but may not identify punctuational ones. For example, a least-squares regression will identify whether there are long-term trends in brain size over time [40]. However, a regression will not necessarily detect deviations from an underlying (or superimposed) linear relationship [54]. Additionally, treating hominins as a single population is potentially problematic: multiple hominin species have coexisted at different points in time [59], often at geographically distinct locations [60]. The appearance of a later lineage often precedes the extinction of pre-existing ones: for example, archaic humans (*Homo heidelbergensis*) appear nearly 700 ky before the last evidence of *H. erectus* in the fossil record. If we evaluate all lineages together, we are likely to increase the error in our estimates for any given time period. To characterize patterns of brain evolution in hominins, analyses should ideally be done both comprehensively over all hominins and within specific lineages.

If encephalization is the result of a single gradual process, there should be an increasing trend (i.e. positive slope for the regression of brain size against time), but there should be no systematic difference in mean residual CC between time periods. Conversely, if brain size has changed as a result of a series of punctuated events, there should be periods of fast growth (associated with large step changes and positive residuals) followed by periods with no size change. The latter can be detected by evaluating whether there is evidence of change in brain size or residuals between some adjacent time steps but not between others. If encephalization is solely the result of step changes associated with speciation events, then there should be little evidence of within lineage changes (i.e. a flat line in between speciation events). Finally, if encephalization is caused by a mixture of processes, we would expect to see large steps *in conjunction* with within-lineage trends.

(a) *Methods*
Data on hominin CC from 0.01 to 1.9 Mya were taken primarily from Bailey & Geary [14] and Ash & Gallup [13] (electronic supplementary material, table S1). Data were cross-checked with additional sources, and additional data were added from the literature to include hominins up to 3.2 million years ago (see the electronic supplementary material). As there is considerable disagreement about the phylogenetic relationships between hominin groups [61], we execute the analyses at several levels. Firstly, we evaluate the temporal change over all hominins; we then divide the groups

into four super-species (*Australopithecus* spp., *Homo habilis*, *H. erectus* (including both *H. erectus* and *H. ergaster*) and *H. sapiens* (*H. sapiens*, *H. heidelbergensis* and *Homo neanderthalensis*); finally, we break down the *H. sapiens* group into anatomically modern humans (AMHs), Neanderthals and *H. heidelbergensis*. The reasons for this are twofold. Firstly, if multiple species with different brain sizes coexist, an evaluation of all hominins together will overestimate the variance at any point in time. Secondly, we want to evaluate whether there is stasis or evidence for directional change within lineages.

The recognition of a tight positive allometric relationship between brain and body size has led to the widespread use of residuals for interspecific comparisons. However, recent evidence suggests that for closely related species (and individuals within a species), absolute brain size is arguably a better predictor of cognitive ability than relative brain size, as the latter introduces errors [62,63]. Additionally, the difficulty in estimating body sizes for hominins and the potential for introducing additional errors justifies the use of absolute brain size [50,54,64,65]. However, we do acknowledge that changes in body size and shape have occurred throughout hominin evolution [1,65] and that these will be associated with brain size changes. To avoid confounds introduced by large errors in body size for the individual fossils, we have used absolute brain size within and between hominin lineages through time.

We use several analytical approaches to evaluate changes in brain size:

— *Changes in mean CC*. We classified fossil specimens into discrete time periods (see electronic supplementary material). We then estimated the mean $\log_{10}$CC for each time block and evaluated the change in mean $\log_{10}$CC across adjacent time blocks.
— *Residual brain size*. To evaluate the underlying temporal trend in brain size, we used model II major axis regression to evaluate change in $\log_{10}$CC against time. We then compared the mean residuals across adjacent time blocks.
— *Changes over time*. To test whether there is also evidence for gradual change within lineages, we replicated the regression against time within taxa to determine whether there is evidence for stasis or continuous change.
— *Regional analyses*. From about 1.6 Mya, hominins occupied both Africa and Eurasia. As the environments were very different, it is possible that there are differences in tempo changes between the two continents.

(b) Results

We explored multiple line-fitting options; linear regression of $\log_{10}$CC against time ($\beta = -0.189$, $t = 35.43$, $p < 0.001$, $r^2 = 0.87$) provided as good a fit as nonlinear models. There was evidence for significant changes between 0–100 kya and 200–400 kya, 1–1.2 Mya and 1.6–1.8 Mya and 1.8–2.6 Mya (figure 1a). The significant differences in the residuals mirror the differences in $\log_{10}$CC (i.e. 0–100 kya; 1–1.2 Mya; 1.6–1.8 Mya, figure 1a,b; electronic supplementary material, table S2). The consistent signal for step

changes suggests that hominin brain expansion is not a single, gradual process but is rather characterized by step changes. The first two step changes coincide with the appearance of early *Homo* (*H. habilis* approximately 1.9 Mya and *H. erectus sensu lato* approximately 1.8 Mya); the final two steps occur at 200–400 kya and at less than 100 kya. Of the latter pair, the first coincides with the appearance of the AMHs approximately 195 kya, but the second does not coincide with a species appearance. Although there is no evidence for temporal trends in encephalization within the australopithecines and *H. habilis*, there is evidence for continued increase across the other species groups (table 1). Early *H. erectus sensu lato* is characterized by a large step increase in brain size, which may be associated with changes in body size [1,3], but there is also evidence for a gradual and continuous change within the lineage over time (figure 2 and table 1). This temporal trend within *H. erectus* has been previously suggested [52,64]. *Homo sapiens* brain size increases over time within the *sapiens* super-species clade (figure 2 and table 1). As *H. sapiens sensu lato* is arguably a number of distinct species, we subdivided the group into *H. heidelbergensis*, *H. neanderthalensis* and *Homo sapiens sapiens* (AMH) to determine whether changes within or between these species were driving the overall temporal trend. *Homo heidelbergensis* shows long-term stasis in brain size; in contrast, within lineage encephalization is suggested for both AMH and Neanderthals (table 1).

Using 200 ky blocks, we finally evaluated whether there were differences in tempo between hominins in Africa and those in Eurasia, owing to limited sample sizes for dates older than 200 kya. Although there was evidence of a temporal trend towards encephalization on both continents, there were some marked differences between the two. Firstly, in Africa, the only significant differences between adjacent time periods were between 1.6 and 1.8 Mya and 1.8 Mya and earlier periods (figure 2). In Eurasia, in contrast, there were significant differences between the most recent time period and 100 kya, between 200 and 400 kya, and between 1.6 and 1.8 Mya. Therefore, the step changes between the two continents show some similarity, but several differences. The step changes in Eurasia are contemporary with migration events (i.e. AMH, *H. heidelbergensis* and *H. erectus*). However, within Eurasia, there was further evidence of encephalization within *H. erectus* ($\beta = -0.08$, $t = -4.57$, $p < 0.001$) and *H. neanderthalensis* ($\beta = -0.46$, $t = -2.67$, $p = 0.01$), but not within *H. heidelbergensis* nor within *H. sapiens*. Conversely, in Africa, there was no evidence of encephalization within any species; the changes were primarily due to the appearance of new chronospecies (GLM with species as main effect: $F_{7,37} = 86.83$, $p < 0.001$; figure 2). The lack of trend in African populations is likely to be a consequence of short-lived species with fewer specimens per species; the chronospecies designation effectively divides up a long-term trend of encephalization. This is further supported by continental differences in mean CC within the *H. erectus* super-species ($F_{1,37} = 3.95$, $p = 0.05$) and *H. sapiens* ($F_{1,57} = 4.3$, $p = 0.04$) but not within *H. heidelbergensis*, with larger brains in Eurasian populations. However, if Neanderthals are viewed as a continuum from
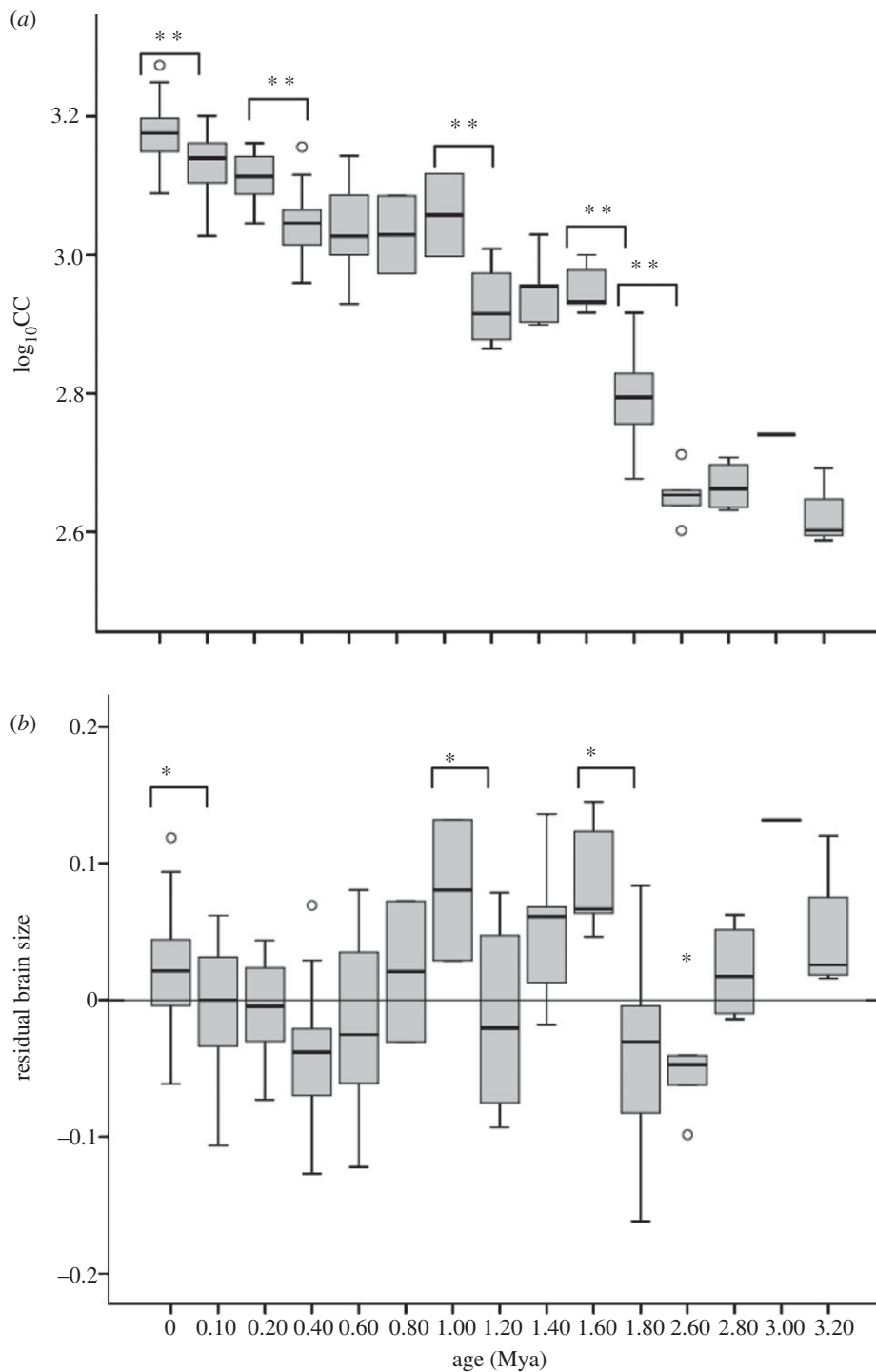
Figure 1. (*a*) Absolute hominin brain size across 100 ky blocks (significant differences between adjacent time blocks: ***$p <$ 0.01, **$p <$ 0.05, *$p <$ 0.10). (*b*) The distribution of residuals from a regression of cranial capacity against time (***$p <$ 0.01, **$p <$ 0.05, *$p <$ 0.10).

H. heidelbergensis [66,67], there is evidence for encephalization within this lineage, but not for a considerable period after colonizing Eurasia. These differences suggest that fundamentally different processes may have been acting on hominins in Eurasia and Africa. Speciation appears to be the key to change in Africa, whereas step changes associated with migration followed by within lineage encephalization are more characteristic of the Eurasian lineages.

These analyses strongly suggest that there is a combination of processes driving hominin brain evolution. When evaluated as a whole, there are apparent step

changes coincident with the appearance of early *Homo*, followed by steps at 1 Mya and 100 kya. The first step occurs at a period of high rates of hominin speciation and species turnover. However, the step at approximately 1 Mya is not obviously contemporary with species turnover. The steps in brain size at 100 kya and at 200–400 kya are clearly driven by the migration of African hominin species into Eurasia. These step changes are not mirrored within Africa, where there are no significant step changes following the appearance of *Homo*. The appearance of *H. erectus* and *H. sapiens* in Eurasia is associated with
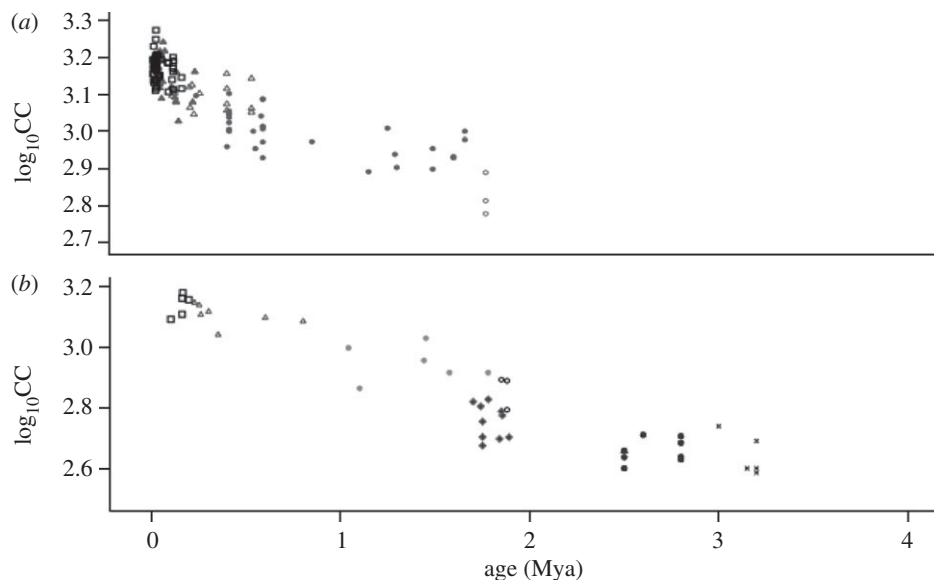
Table 2. Correlations between absolute brain size and residual brain size (size controlled for time) and environmental variables, both over all hominins and within lineages. Positive correlations between mean isotope and CC residual indicate larger brains are associated with periods of cooling; positive correlations between isotope standard deviation and brain residuals indicate that periods of increased environmental variability are associated with periods of increase in brain size ($*p < 0.05$, $**p < 0.01$). Bold type highlights results consistent with environmental hypotheses.

taxon	sea-level mean		sea-level s.d.		dust mean		dust s.d.	
	$\log_{10}$CC	CC residual	$\log_{10}$CC	CC residual	$\log_{10}$CC	CC residual	$\log_{10}$CC	CC residual
all hominins	−0.77**	−0.08	0.57**	−0.18*	0.28**	0.09	0.16	0.06
australopithecines	−0.08	0.34	0.18	−**0.64***	0.27	−0.34	0.20	−0.22
H. habilis	0.05	0.24	−0.18	0.01	0.25	0.06	0.99	0.625
H. erectus	−0.65**	**0.56****	0.65**	−**0.57****	−0.25	**0.62****	−0.25	**0.50****
H. sapiens	−0.13	−0.04	−0.17	−0.04	0.33**	0.03	0.06	−0.11

consistent evidence at the super-species level to support either the variability selection or the aridity hypotheses using sea-level indicators (table 2). Furthermore, when we use aeolian dust records, which provide a continental indicator for both aridity and variability, we do not find consistent evidence to support either hypothesis (table 2). There were no significant models incorporating more than one climate record for any of the taxonomic levels. The main weakness with the palaeoclimate records used in these analyses is that they are unable to explain the large step changes in brain size that have periodically occurred throughout hominin evolution. The most marked and unexplained increase is contemporary with the appearance of *H. erectus* (or *H. ergaster*) in Africa. The global sea-level palaeoclimate records have some predictive power for within species change over all hominins and within *H. erectus*. As we have better resolution in the data from Eurasia, this suggests that sea-level changes are likely to reflect environmental processes at higher latitudes, but they are unable to explain the environmental processes operating within Africa.

4. DISCUSSION

We revaluated patterns of hominin brain size change and demonstrate that, rather than being a monotonic increase, hominin brain size increase is dominated by step changes with limited evidence for long-term gradual increases. Over time, both brain size and environmental stochasticity have increasing trends, which has led to the conclusion that it was environmental unpredictability that drove hominin brain evolution [7,13]. However, we have shown that brain size changes do not track patterns of increase in environmental variability or unpredictability. Nor do the data support the suggestion that continent-wide patterns of cooling or unpredictability fully explain patterns of encephalization. Neither of the palaeoclimate records that we use explain the step-wise changes in brain size at approximately 1.8 Mya or 100 kya. Moreover, our analyses suggest that the processes that have acted on encephalization in Eurasia differed from those in Africa. Long-term trends in Eurasia map onto global sea-level records, but the changes within African hominins map onto neither Arabian Sea dust records nor global sea-level records. The geological history and climate processes operating in East Africa have been shown to be distinct from

those outside this area [71]. Thus, we suggest that any future analyses that attempt to tie encephalization to environmental processes consider carefully the impact of local conditions and the relevance of global climate records for understanding selection pressures operating across a wide environmental gradient.

Finally, we turn to consider evidence from the archaeological record and ask how it might allow us to evaluate the arguments for encephalization presented earlier in the paper.

(a) *Early* Homo

The appearance of the genus *Homo*, and subsequently of *H. erectus* (or *ergaster*), was historically associated with the expansion of the savannah [72]. However, recent reinterpretations of the palaeoclimate record have questioned this hypothesis [9,71,73]. Recent re-evaluations of the African palaeoclimate data suggest that pulsed changes may be more important than long-term trends [71,73]. Moreover, these analyses suggest that the periods associated with this step-change in encephalization may have occurred during a wet rather than a dry period. Although there is evidence for cultural and technological innovation contemporary with *H. ergaster*, including the appearance of the Acheulian stone tool industry, the material culture during the remainder of *H. erectus sensu lato* existence is broadly characterized by stasis [12]. This means that the gradual encephalization in *H. erectus* was not associated with increasingly sophisticated technologies.

The appearance of early *Homo* was also associated with profound changes in life history, as well as body size and shape. Some of these adaptations could also be linked to the step-increase in brain size between *H. habilis* and *H. erectus/ergaster* [1,3]. Tobias [74] identified a marked difference in the demography of hominin assemblages between the late australopithecines and early *Homo*. The former were characterized by a large number/proportion of physically mature individuals, whereas the latter were characterized by a large number of immature individuals. He argues that this is the result of a high mortality rate in subadults caused by environmental stress resulting from the changing environment during the Plio-Pleistocene. Increased mortality, however, could also result from increased predation pressure. Increasing immature mortality would provide a strong selective pressure to increase birth rates

and could explain the modern human life history with 'stacking' of weaned, but immature offspring [3,75]. Having multiple immature-dependent young will cause knock-on consequences for social group structure, foraging behaviour and range use, and could drive the evolution of cooperative breeding, crèches and central place foraging. An extended juvenile period allows for a protracted learning period [76,77], during which sophisticated reasoning and problem-solving capabilities have the opportunity to develop. Although the fossil record suggests an increase in reproductive rates, a fully modern life-history strategy does not appear until the arrival of AMH [78]. Unfortunately, we have little quantitative data that can be used to test hypotheses about changes in social behaviours. We can, however, evaluate what neurological changes are associated with the step changes in brain size. Early *Homo* brain morphology is characterized by increases in the frontal and temporal lobe, both of which are heavily implicated in social tasks [36,37,79,80]. Evidence that social group size changed in steps concurrently with brain size changes would more conclusively support the social brain hypothesis.

(b) *Later changes*

After the appearance of the genus *Homo*, the rate of encephalization is less straightforward. Within Africa, brain size increases at a roughly consistent rate, whereas the introduction of migrants into Eurasia creates periodic step-wise changes. Whether it was changes in environmental conditions or competence that impelled these migratory events remains unclear. Moreover, despite an increasing brain size, there is little from the archaeological record that conclusively identifies cognitive advances. For much of the period following the appearance of *H. erectus sensu lato*, Acheulian technology is largely static until approximately 300 kya when it gave way to the prepared core technology in the Middle Palaeolithic/Stone Age [46,81]. There is tantalizing evidence for the first controlled use of fire together with charred seeds and wood [82] coincident with the first appearance of *H. heidelbergensis* in Eurasia. It has been proposed that language and controlled use of fire may have co-evolved as part of an adaptive suite that helped to socially bond groups [12]. However, it is not straightforward to identify the cognitive inferences associated with fire use.

Interestingly, although AMH first appeared in Africa around 200 kya, signatures of behavioural (and cognitive) modernity in the archaeological record remain uncommon for a protracted period following their arrival. From around 80–100 kya, there is increasing evidence of symbolic behaviour and cultural variation in tool manufacture [83]; however, this evidence remains sporadic and does not become widespread until much later [84]. Additionally, technologies and innovations appear and then disappear at individual sites [83], suggesting that either cultural behaviours are lost within populations or site occupancy is ephemeral. In contrast, this period is followed by a veritable explosion of material and symbolic culture, increasingly sophisticated technologies and long transport distances. This marked increase in archaeological evidence has led

to the suggestion of a sea-change in human behaviour called the Upper Palaeolithic revolution [84]. Although contention remains about when modernity first arose or whether there was an explosion, there is no denying the exponential increase in signatures of behavioural modernity over the past 30 kya. Critically, we cannot determine from the archaeological record whether this cultural explosion is the result of a cognitive advance or a more mundane process.

For example, the sudden explosion of symbolic material, specialized tools and changes in material use that characterize the Upper Palaeolithic have been linked to a demographic tipping point whereby population density is high enough to maintain culturally transmitted information [85]. In this scenario, demography allows a scaffolding of underlying gradual accumulated changes in technology and cognitive ability [83]. Population density increases could result from either ecological or social changes (i.e. being able to live at higher densities). The ability to maintain larger population sizes could ultimately be a consequence of increased cognitive capacity. The brain size evidence suggests that the most recent period of brain size increase is around 100 kya (figure 1a,b). Thus, the first traces of modernity coincide with, or shortly precede, the period of a marked change in brain size. However, it is only after population density reached a critical level that there is a clear signal in the archaeological record with the emergence of the Upper Palaeolithic as AMH spread out of Africa (approx. 60 kya).

(c) *Early language*

One widely suggested innovation that could explain the cultural proliferation of the Upper Palaeolithic revolution period post 50 kya is fully functional language. Without language, it is not possible to share symbolic ideas or to impart knowledge about events removed in space or time. It has controversially been proposed that the cultural complexity of the Upper Palaeolithic coincided with a brain mutation that permitted fully blown modernity approximately 50 kya with the advent of the Upper Palaeolithic in Europe [86,87]. However, this idea has been largely dismissed on the grounds that there is no evidence for any correlated brain size changes [88,89]. In contrast, our reanalysis of the fossil data indicates a shift in brain size that *is* contemporary with changes in cranial and vocal anatomy (which, it has been argued, become more like that of contemporary humans at this time [90,91]).

While there are various views on how early or how late language evolved, there is an important distinction between speech (the capacity to vocalise) and language (in the sense of fully grammatical propositions) that needs to be borne in mind [92]. Communication competencies would have successively increased prior to the appearance of fully modern language. Whether these arose through the transfer of gestural forms of communication to verbal ones, or what the structure and sound of early proto-language would have been has been the subject of intense speculation [93]. The anatomical signatures that have been associated with language production (e.g. the thoracic nerve expansion

[94] and, more controversially, the hypoglossal canal [95] coincide with the appearance of archaic humans around 600 kya [92]) are, in fact, equally required for non-verbal forms of human communication such as wordless singing (*sensu* [96,97]). If language complexity is dependent on intentional competences (or whatever relevant aspects of cognition these index) and these in turn are correlated with brain size, then tracing brain size might tell us something about the phases of language evolution. The final step change in brain size that begins at approximately 100 kya may reflect this final phase shift in language complexity. Some evidence to support this comes from a recent study tracing the global distribution of phoneme variation that provides strong evidence that complex language evolved in Africa and spread rapidly from approximately 80 kya [98].

5. CONCLUSION

Our re-evaluation of the enduring mystery about what drove human encephalization has not identified a smoking gun. We suggest that the evidence in support of either the variability or arditiy hypothesis is not compelling and that the relationship between brain size and palaeoclimate is not straightforward. In the light of this, we suggest that the drivers of hominin encephalization are manifold. Environment likely played a part, whether as a direct pressure or by forcing hominins to change their behaviour so as to be able to use more risky and peripheral habitats, to live in larger groups, or to use novel resources. However, the climate variables we have used cannot explain encephalization. Most tantalizing and enigmatic is the role of social evolution in the encephalization process. There remains no direct measure of social grouping structure or complexity from archaeological evidence; yet, social intelligence is fundamental to what makes us human. Evidence from language evolution studies, brain morphology and the appearance of symbolic behaviour, all suggest that language evolution is a key component of human cognitive evolution and that cultural advances may have occurred in a series of steps that mirror changes in brain size and architecture.

REFERENCES

1 Robson, S. L. & Wood, B. 2008 Hominin life history: reconstruction and evolution. *J. Anat.* **212**, 394–425. (doi:10.1111/j.1469-7580.2008.00867.x)

2 Leonard, W. R. & Robertson, M. L. 1992 Nutritional requirements and human evolution: a bioenergetics model. *Am. J. Hum. Biol.* **4**, 179–195. (doi:10.1002/ajhb.1310040204)

3 Aiello, L. C. & Wells, J. C. K. 2002 Energetics and the evolution of the genus *Homo. Annu. Rev. Anthropol.* **31**, 323–338. (doi:10.1146/annurev.anthro.31.040402.085403)

4 Steudel-Numbers, K. L. 2006 Energetics in *Homo erectus* and other early hominins: the consequences of increased lower-limb length. *J. Hum. Evol.* **51**, 445–453. (doi:10.1016/j.jhevol.2006.05.001)

5 Wolpoff, M. H. 1980 *Paleoanthropology.* New York, NY: Knopf.

6 Vrba, E. S., Denton, G. H., Partridge, T. C. & Burckle, L. H. E. 1995 *Paleoclimate and evolution, with emphasis on human origins.* New Haven, CT: Yale University Press.

7 Potts, R. 1998 Variability selection in hominid evolution. *Evol. Anthropol. Issues News Rev.* **7**, 81–96. (doi:10.1002/(SICI)1520-6505(1998)7:3<81::AID-EVAN3>3.0.CO;2-A)

8 Potts, R. 1998 Environmental hypotheses of hominin evolution. *Am. J. Phys. Anthropol.* **41**, 93–136. (doi:10.1002/(SICI)1096-8644(1998)107:27+<93::AID-AJPA5>3.0.CO;2-X)

9 Trauth, M. H. *et al.* 2010 Human evolution in a variable environment: the amplifier lakes of Eastern Africa. *Quat. Sci. Rev.* **29**, 2981–2988. (doi:10.1016/j.quascirev.2010.07.007)

10 Ungar, P. S., Grine, F. E. & Teaford, M. F. 2006 Diet in early *Homo*: a review of the evidence and a new model of adaptive versatility. *Annu. Rev. Anthropol.* **35**, 209–228. (doi:10.1146/annurev.anthro.35.081705.123153)

11 Kaplan, H., Hill, K., Lancaster, J. & Hurtado, A. M. 2000 A theory of human life history evolution: diet, intelligence, and longevity. *Evol. Anthropol. Issues News Rev.* **9**, 156–185. (doi:10.1002/1520-6505(2000)9:4<156::AID-EVAN5>3.0.CO;2-7)

12 Gamble, C., Gowlett, J. & Dunbar, R. 2011 The social brain and the shape of the Palaeolithic. *Camb. Archaeol. J.* **21**, 115–136. (doi:10.1017/S0959774311000072)

13 Ash, J. & Gallup, G. 2007 Paleoclimatic variation and brain expansion during human evolution. *Hum. Nat.* **18**, 109–124. (doi:10.1007/s12110-007-9015-z)

14 Bailey, D. H. & Geary, D. H. 2009 Hominid brain evolution: testing climatic, ecological, and social competition models. *Hum. Nat.* **20**, 67–79. (doi:10.1007/s12110-008-9054-0)

15 Cowlishaw, G. 1997 Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Anim. Behav.* **53**, 667–686. (doi:10.1006/anbe.1996.0298)

16 Hill, R. A. & Lee, P. C. 1998 Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. *J. Zool.* **245**, 447–456. (doi:10.1111/j.1469-7998.1998.tb00119.x)

17 Pickering, T. R., Clarke, R. J. & Moggi-Cecchi, J. 2004 Role of carnivores in the accumulation of the Sterkfontein Member 4 hominid assemblage: a taphonomic reassessment of the complete hominid fossil sample (1936–1999). *Am. J. Phys. Anthropol.* **125**, 1–15. (doi:10.1002/ajpa.10278)

18 Gilbert, C. C., McGraw, W. S. & Delson, E. 2009 Brief communication: Plio-Pleistocene eagle predation on fossil cercopithecids from the Humpata Plateau, southern Angola. *Am. J. Phys. Anthropol.* **139**, 421–429. (doi:10.1002/ajpa.21004)

19 Wood, B. & Collard, M. 1999 The human genus. *Science* **284**, 65–71. (doi:10.1126/science.284.5411.65)

20 Reed, K. E. 1997 Early hominid evolution and ecological change through the African Plio-Pleistocene. *J. Hum. Evol.* **32**, 289–322. (doi:10.1006/jhev.1996.0106)

21 Shultz, S. & Dunbar, R. I. M. 2006 Chimpanzee and felid diet composition is influenced by prey brain size. *Biol. Lett.* **2**, 505–508. (doi:10.1098/rsbl.2006.0519)

22 Shultz, S. & Finlayson, L. V. 2010 Large body and small brain and group sizes are associated with predator preferences for mammalian prey. *Behav. Ecol.* **21**, 1073–1079. (doi:10.1093/beheco/arq108)

23 van Schaik, C. P. 1983 Why Are diurnal primates living in groups? *Behaviour* **87**, 120–144. (doi:10.1163/156853983X00147)

24 Shultz, S., Noe, R., McGraw, W. S. & Dunbar, R. I. 2004 A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proc. R. Soc. B* **271**, 725–32. (doi:10.1098/rspb.2003.2626)

25 Dunbar, R. I. M. & Shultz, S. 2007 Evolution in the social brain. *Science* **317**, 1344–1347. (doi:10.1126/science.1145463)

26 Jolly, A. 1966 Lemur social behavior and primate intelligence. *Science* **153**, 501–506. (doi:10.1126/science.153.3735.501)

27 Humphrey, N. K. 1976 The social function of intellect. In *Growing points in ethology* (eds P. P. G. Bateson & R. A. Hinde), pp. 303–317. Cambridge, UK: Cambridge University Press.

28 Dunbar, R. I. M. 2011 Evolutionary basis of the social brain. In *The Oxford handbook of social neuroscience* (eds J. Decety & J. T. Cacioppo), pp. 28–38. Oxford, UK: Oxford University Press.

29 Shultz, S. & Dunbar, R. I. M. 2012 Social cognition and cortical function: an evolutionary perspective. In *Action, perception and the brain: adaptation and cephalic expression* (ed. J. Schulkin). Basingstoke, UK: Palgrave Macmillian.

30 Barton, R. A. 1996 Neocortex size and behavioural ecology in primates. *Proc. R. Soc. B* **263**, 173–177. (doi:10.1098/rspb.1996.0028)

31 Dunbar, R. I. M. 1998 The social brain hypothesis. *Evol. Anthropol. Issues News Rev.* **6**, 178–190. (doi:10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8)

32 Aiello, L. C. & Dunbar, R. I. M. 1993 Neocortex size, group-size, and the evolution of language. *Curr. Anthropol.* **34**, 184–193. (doi:10.1086/204160)

33 Dunbar, R. I. M. 2009 The social brain hypothesis and its implications for social evolution. *Ann. Hum. Biol.* **36**, 562–572. (doi:10.1080/03014460902960289)

34 Luria, A. R. 1981 *Language and cognition.* New York, NY: John Wiley & Sons.

35 Deacon, T. W. 1997 *The symbolic species: the co-evolution of language and the brain.* New York, NY: W. W. Norton and Co.

36 Powell, J. L., Lewis, P. A., Dunbar, R. I. M., García-Fiñana, M. & Roberts, N. 2010 Orbital prefrontal cortex volume correlates with social cognitive competence. *Neuropsychologia* **48**, 3554–3562. (doi:10.1016/j.neuropsychologia.2010.08.004)

37 Lewis, P. A., Rezaie, R., Brown, R., Roberts, N. & Dunbar, R. I. M. 2011 Ventromedial prefrontal volume predicts understanding of others and social network size. *NeuroImage* **57**, 1624–1629. (doi:10.1016/j.neuroimage.2011.05.030)

38 Bogin, B. 1997 Evolutionary hypotheses for human childhood. *Am. J. Phys. Anthropol.* **104**, 63–89. (doi:10.1002/(SICI)1096-8644(1997)25+<63::AID-AJPA3>3.0.CO;2-8)

39 Dunbar, R. I. M. & Shultz, S. 2007 Understanding primate brain evolution. *Phil. Trans. R. Soc. B* **362**, 649–658. (doi:10.1098/rstb.2006.2001)

40 Shultz, S. & Dunbar, R. I. M. 2010 Encephalization is not a universal macroevolutionary phenomenon in mammals but is associated with sociality. *Proc. Natl Acad. Sci. USA* **107**, 21 582–21 586. (doi:10.1073/pnas.1005246107)

41 Isler, K. & van Schaik, C. P. 2009 Why are there so few smart mammals (but so many smart birds)? *Biol. Lett.* **5**, 125–129. (doi:10.1098/rsbl.2008.0469)

42 Martin, R. D. 1981 Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature* **293**, 57–60. (doi:10.1038/293057a0)

43 Milton, K. 1999 A hypothesis to explain the role of meat-eating in human evolution. *Evol. Anthropol. Issues News Rev.* **8**, 11–21. (doi:10.1002/(SICI)1520-6505(1999)8:1<11::AID-EVAN6>3.0.CO;2-M)

44 Leonard, W. R. & Robertson, M. L. 1996 On diet, energy metabolism, and brain size in human evolution. *Curr. Anthropol.* **37**, 125–129. (doi:10.1086/204476)

45 Wrangham, R. W., Jones Holland, J., Laden, G., Pilbeam, D. & Conklin-Brittain, N. 1999 The raw and the stolen: cooking and the ecology of human origins. *Curr. Anthropol.* **40**, 567–594. (doi:10.1086/300083)

46 Foley, R. & Gamble, C. 2009 The ecology of social transitions in human evolution. *Phil. Trans. R. Soc. B* **364**, 3267–3279. (doi:10.1098/rstb.2009.0136)

47 Gould, S. J. & Eldredge, N. 1977 Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* **3**, 115–151.

48 Cronin, J. E., Boaz, N. T., Stringer, C. B. & Rak, Y. 1981 Tempo and mode in hominid evolution. *Nature* **292**, 113–122. (doi:10.1038/292113a0)

49 Lee, S.-H. & Wolpoff, M. H. 2003 The pattern of evolution in Pleistocene human brain size. *Paleobiology* **29**, 186–196. (doi:10.1666/0094-8373(2003)029<0186:TPOEIP>2.0.CO;2)

50 Rightmire, G. P. 1981 Patterns in the evolution of *Homo erectus*. *Paleobiology* **7**, 241–246.

51 Ruff, C. B., Trinkaus, E. & Holliday, T. W. 1997 Body mass and encephalization in Pleistocene *Homo*. *Nature* **387**, 173–176. (doi:10.1038/387173a0)

52 Rightmire, G. P. 2004 Brain size and encephalization in early to Mid-Pleistocene *Homo*. *Am. J. Phys. Anthropol.* **124**, 109–123. (doi:10.1002/ajpa.10346)

53 Beals, K. L., Smith, C. L. & Dodd, S. M. 1984 Brain size, cranial morphology, climate, and time machines. *Curr. Anthropol.* **25**, 301–330. (doi:10.1086/203138)

54 Leigh, S. R. 1992 Cranial capacity evolution in *Homo erectus* and early *Homo sapiens*. *Am. J. Phys. Anthropol.* **87**, 1–13. (doi:10.1002/ajpa.1330870102)

55 Lestrel, P. E. & Read, D. W. 1973 Hominid cranial capacity versus time: a regression approach. *J. Hum. Evol.* **2**, 405–411. (doi:10.1016/0047-2484(73)90020-1)

56 Lestrel, P. E. 1976 Hominid brain size versus time: revised regression estimates. *J. Hum. Evol.* **5**, 207–212. (doi:10.1016/0047-2484(76)90022-1)

57 Godfrey, L. & Jacobs, K. H. 1981 Gradual, autocatalytic and punctuational models of hominid brain evolution: a cautionary tale. *J. Hum. Evol.* **10**, 255–272. (doi:10.1016/S0047-2484(81)80063-2)

58 Rightmire, G. P. 1986 Statis in *Homo erectus* defended. *Paleobiology* **12**, 324–325.

59 Green, R. E. *et al.* 2010 A draft sequence of the Neandertal genome. *Science* **328**, 710–722. (doi:10.1126/science.1188021)

60 Krause, J., Fu, Q., Good, J. M., Viola, B., Shunkov, M. V., Derevianko, A. P. & Paabo, S. 2010 The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. *Nature* **464**, 894–897. (doi:10.1038/nature08976)

61 Strait, D. S. & Grine, F. E. 2004 Inferring hominoid and early hominid phylogeny using craniodental characters: the role of fossil taxa. *J. Hum. Evol.* **47**, 399–452. (doi:10.1016/j.jhevol.2004.08.008)

62 Shultz, S. & Dunbar, R. I. M. 2010 Species differences in executive function correlate with hippocampus volume and neocortex ratio across nonhuman primates. *J. Comput. Psychol.* **124**, 252–260. (doi:10.1037/a0018894)

63 Deaner, R. O., Isler, K., Burkart, J. & van Schaik, C. 2007 Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain Behav. Evol.* **70**, 115–124. (doi:10.1159/000102973)

64 Wolpoff, M. H. 1984 Evolution in *Homo erectus*: the question of statis. *Paleobiology* **10**, 389–406.

65 McHenry, H. M. 1994 Behavioral ecological implications of early hominid body size. *J. Hum. Evol.* **27**, 77–87. (doi:10.1006/jhev.1994.1036)

66 Hublin, J. J. 2009 The origin of Neandertals. *Proc. Natl Acad. Sci. USA* **106**, 16 022–16 027.

67 Endicott, P., Ho, S. Y. W. & Stringer, C. B. 2010 Using genetic evidence to evaluate four palaeoanthropological hypotheses for the timing of Neanderthal and modern human origins. *J. Hum. Evol.* **59**, 87–95. (doi:10.1016/j.jhevol.2010.04.005)

68 Pearce, E. & Dunbar, R. Latitudinal variation in light levels drives human visual system size. *Biol. Lett.* **8**, 90–93.

69 Miller, K. G. *et al.* 2005 The Phanerozoic record of global sea-level change. *Science* **310**, 1293–1298. (doi:10.1126/science.1116412)

70 deMenocal, P. B. 1995 Plio-Pleistocene African climate. *Science* **270**, 53–59. (doi:10.1126/science.270.5233.53)

71 Trauth, H. H., Larrasoaña, J. C. & Mudelsee, M. 2009 Trends, rhythms and events in Plio-Pleistocene African climate. *Quat. Sci. Rev.* **28**, 399–411. (doi:10.1016/j.quascirev.2008.11.003)

72 Bobe, R. & Behrensmeyer, A. K. 2004 The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **207**, 399–420. (doi:10.1016/S0031-0182(04)00049-5)

73 Donges, J. F., Donner, R. V., Trauth, M. H., Marwan, N., Schellnhuber, H.-J. & Kurths, J. 2011 Nonlinear detection of paleoclimate-variability transitions possibly related to human evolution. *Proc. Natl Acad. Sci. USA* **108**, 20 422–20 427. (doi:10.1073/pnas.1117052108)

74 Tobias, P. V. 2006 Longevity, death and encephalisation among Plio-Pleistocene hominins. *Int. Congress Ser.* **1296**, 1–15. (doi:10.1016/j.ics.2006.03.034)

75 Aiello, L. C. & Key, C. 2002 Energetic consequences of being a *Homo erectus* female. *Am. J. Hum. Biol.* **14**, 551–565. (doi:10.1002/ajhb.10069)

76 Buchsbaum, D., Bridgers, S., Weisberg, D. S. & Gopnik, A. 2012 The power of possibility: causal learning, counterfactual reasoning, and pretend play. *Phil. Trans. R. Soc. B* **367**, 2202–2212. (doi:10.1098/rstb.2012.0122)

77 Joffe, T. H. 1997 Social pressures have selected for an extended juvenile period in primates. *J. Hum. Evol.* **32**, 593–605. (doi:10.1006/jhev.1997.0140)

78 Smith, T. M., Tafforeau, P., Reid, D. J., Grün, R., Eggins, S., Boutakiout, M. & Hublin, J.-J. 2007 Earliest evidence of modern human life history in North African early *Homo sapiens*. *Proc. Natl Acad. Sci. USA* **104**, 6128–6133. (doi:10.1073/pnas.0700747104)

79 Brothers, L. 1990 The social brain: a project for integrating primate behavior and neurophysiology in a new domain. *Concepts Neurosci.* **1**, 27–51.

80 Behrens, T. E. J., Hunt, L. T. & Rushworth, M. F. S. 2009 The computation of social behavior. *Science* **324**, 1160–1164. (doi:10.1126/science.1169694)

81 Mithen, S. 1999 Imitation and cultural change: a view from the Stone Age, with specific reference to the manufacture of handaxes. In *Mammalian social learning: comparative and ecological perspectives* (eds H. O. Box & K. R. Gibson), pp. 389–400. Cambridge, UK: Cambridge University Press.

82 Goren-Inbar, N., Alperson, N., Kislev, M. E., Simchoni, O., Melamed, Y., Ben-Nun, A. & Werker, E. 2004 Evidence of hominin control of fire at Gesher Benot Ya'aqov, Israel. *Science* **304**, 725–727. (doi:10.1126/science.1095443)

83 d'Errico, F. & Stringer, C. B. 2011 Evolution, revolution or saltation scenario for the emergence of modern cultures? *Phil. Trans. R. Soc. B* **366**, 1060–1069. (doi:10.1098/rstb.2010.0340)

84 Mellars, P. 2006 Why did modern human populations disperse from Africa ca. 60,000 years ago? A new model. *Proc. Natl Acad. Sci. USA* **103**, 9381–9386. (doi:10.1073/pnas.0510792103)

85 Powell, A., Shennan, S. & Thomas, M. G. 2009 Late Pleistocene demography and the appearance of modern human behavior. *Science* **324**, 1298–1301. (doi:10.1126/science.1170165)

86 Klein, R. G. 1995 Anatomy, behavior, and modern human origins. *J. World Prehistory* **9**, 167–198. (doi:10.1007/BF02221838)

87 Klein, R. G. 2000 Archeology and the evolution of human behavior. *Evol. Anthropol. Issues News Rev.* **9**, 17–36. (doi:10.1002/(SICI)1520-6505(2000)9:1<17::AID-EVAN3>3.0.CO;2-A)

88 Holloway, R. L. 1996 Evolution of the human brain. In *Handbook of human symbolic evolution* (eds A. Lock & C. R. Peters), pp. 74–116. Oxford, UK: Blackwell.

89 Holloway, R. L., Broadfield, D. C. & Yuan, M. S. 2004 *Brain endocasts: the paleoneurological evidence. The Human Fossil Record.* New York, NY: Wiley.

90 Lieberman, P. 2007 The evolution of human speech: its anatomical and neural bases. *Curr. Anthropol.* **48**, 39–66. (doi:10.1086/509092)

91 Schwartz, J. H. & Tattersall, I. 2010 Fossil evidence for the origin of *Homo sapiens*. *Am. J. Phys. Anthropol.* **143**, 94–121. (doi:10.1002/ajpa.21443)

92 Dunbar, R. I. M. 2009 Why only humans have language. In *The prehistory of language* (eds R. Botha & C. Knight), pp. 12–35. Oxford, UK: Oxford University Press.

93 Sterelny, K. 2012 Language, gesture, skill: the coevolutionary foundations of language. *Phil. Trans. R. Soc. B* **367**, 2141–2151. (doi:10.1098/rstb.2012.0116)

94 Maclarnon, A. & Hewitt, G. 2004 Increased breathing control: another factor in the evolution of human language. *Evol. Anthropol. Issues News Rev.* **13**, 181–197. (doi:10.1002/evan.20032)

95 Kay, R. F., Cartmill, M. & Balow, M. 1998 The hypoglossal canal and the origin of human vocal behavior. *Proc. Natl Acad. Sci. USA* **95**, 5417–5419. (doi:10.1073/pnas.95.9.5417)

96 Mithen, S. 2006 *The singing Neanderthals*. London, UK: Weidenfeld & Nicholson.

97 Dunbar, R. I. M. 2006 *The human story*. London, UK: Faber & Faber.

98 Atkinson, Q. D. 2011 Phonemic diversity supports a serial founder effect model of language expansion from Africa. *Science* **332**, 346–349. (doi:10.1126/science.1199295)