



McDONALD INSTITUTE MONOGRAPHS

Modelling the early human mind

Edited by
Paul Mellars and Kathleen Gibson



Measuring Cognition in Extinct Hominids

Robert A. Foley

Any model of the evolution of the human mind should be testable against and consistent with the evidence drawn from the human palaeontological and the archaeological record. Such data are, however, notoriously sparse and incomplete. Here an attempt is made to measure a number of variables from the palaeobiological record that may provide evidence of the pattern of human cognitive evolution: relative brain size, neocortex ratio, duration of technological tradition, complexity of technology and rate of maturation. If these data do reflect cognitive states then they show a pattern of independent evolution, with maturation rate and neocortex ratio showing a relatively early and more continuous pattern than EQ and technology. Debates about the relative cognitive status of extinct hominid taxa should take into account that different skills may evolve independently. It is also argued that changes in life history strategy underpin cognitive evolution.

There are two necessary components of any successful explanation and description of the evolution of the human mind. The first of these must be an adequate understanding of the biological mechanics of cognition and a theory that can account for the range of variation we can see among animals today. The second is to place that theoretical framework into the specific context of the time and place of hominid evolution. Ultimately it is the way we put these two elements together that is crucial. The problem with such an integration, however, lies in the fact that these two components draw on radically different sets of data and theoretical frameworks.

Building a theoretical model of the way a mind works is the field of comparative psychology. The primary source of information here is the study of humans and other animals under laboratory and natural conditions, and an understanding of them in terms of the mechanics of neurobiology. The pre-human mind that emerges from such studies is seldom specific to the particular conditions of phylogeny or environment in which humans evolved. To the comparative psychologist the early human mind floats unanchored in the vast tracts of space and time between the development of the central nervous system and the evolution of human self-reflexivity.

The specifics of hominid evolution, on the other

hand, which are the concern of palaeoanthropologists, do provide details of the context and timing of events in the evolution of human cognition. This evidence, though, tends to be lacking in detail, is sparse and unevenly distributed, and can seldom be directly linked to the cognitive skills of the extinct hominids that would be of concern to psychological models. For the most part palaeobiologically based interpretations of the early human mind are vast inferential arches built on one or two rather eroded foundation stones.

Solutions to these methodological problems will come from a number of directions. For example, rooting behavioural and anatomical characteristics onto phylogenetic structures through cladistics will allow cognitive skills to be assigned to taxa at various evolutionary nodes, thus helping to anchor the psychological and social capacities with the specific events of evolution (Foley 1987; 1989a; see Robson Brown this volume). Another approach would be to secure more firmly the skills involved in technology to broader cognitive models (Mithen this volume). In this paper no attempt is made to infer directly the actual cognitive skills and capacities of the pre-human hominids. Instead what I shall seek to do is to quantify the relative information processing and adaptive intelligence levels of extinct hominid taxa, specifically those of the genus *Homo*. The aim is to

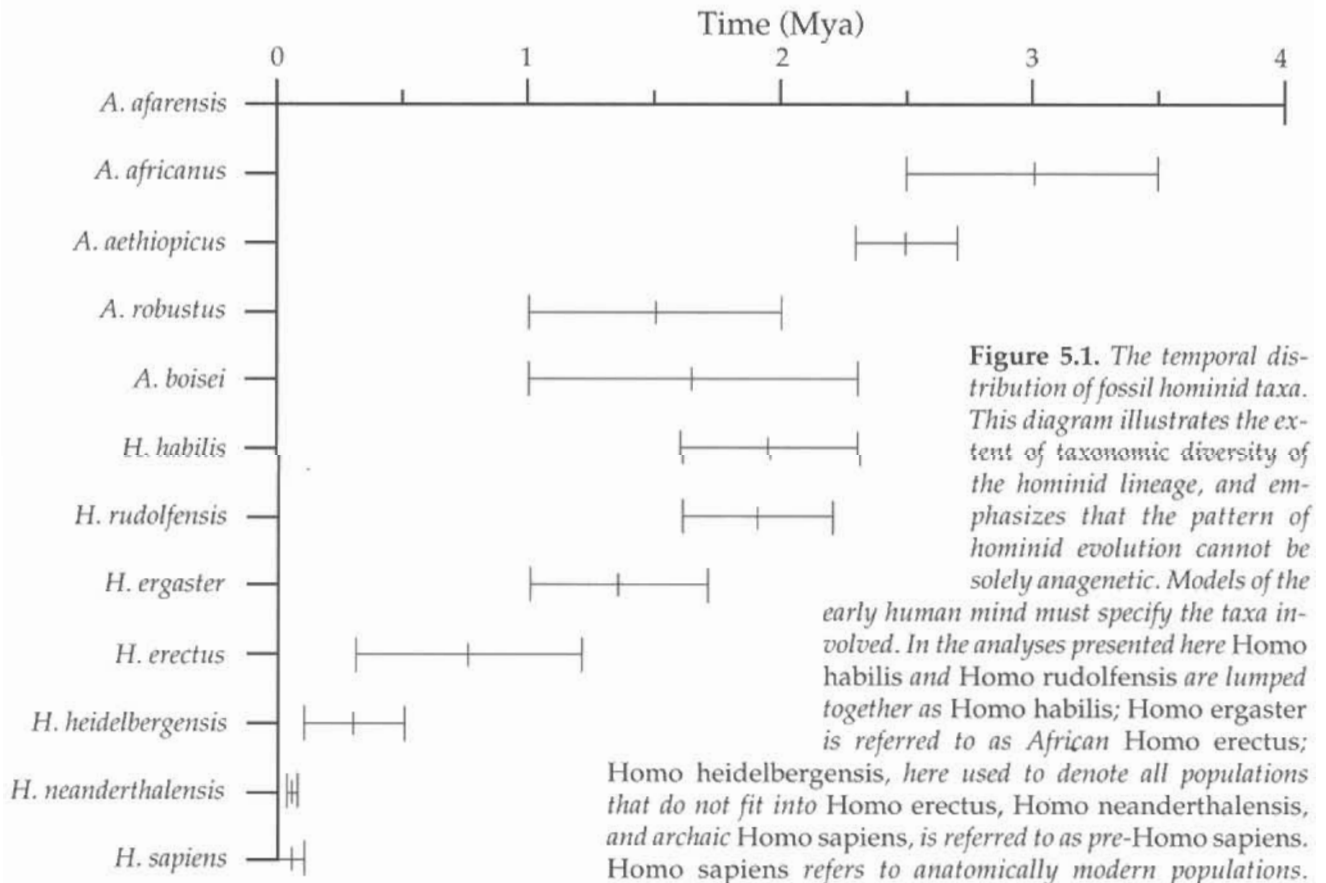
provide a more secure empirical basis for discussions of the relative capabilities of the hominids of the past, using the palaeobiological and archaeological evidence available. In simple terms, are modern humans twice as intelligent as *Homo habilis* as brain size data might imply; was *Homo erectus* two and a half times more intelligent than chimpanzees? The answer to such questions may help to solve some of the debates about the relative cognitive and intellectual capacities of neanderthals and *Homo sapiens*; whether the difference is a quantum leap, or a mere difference in style.

Which pre-human mind? The problem of hominid taxa

One of the primary discoveries of recent years is that the cognitive abilities of animals varies considerably between taxa (see Lee this volume; Byrne & Whiten 1988; Cheney & Seyfarth 1990; McGrew 1992; Parker & Gibson 1979; Savage Rumbaugh *et al.* 1983). Monkeys have very different abilities from apes, and within the Hominoidea there is also much variation. This can be seen in the differences between gorillas and chimpanzees which, despite a very close

phylogenetic relationship, differ very considerably in both level of encephalization and cognitive abilities and styles. Even between the two species of chimpanzee, *Pan troglodytes*, and *P. paniscus*, there may be substantial differences in behavioural potential (Savage-Rumbaugh & Savage-Rumbaugh 1993). There may of course be still further levels of variation within species, such as between sexes and with age, but these will not be addressed here (see Lee this volume; Byrne this volume).

These results are significant for the way in which we approach the evolution of hominid cognition and the specifics of the pre-human mind. In particular, the key question is — which 'early human mind'? It is clear from the fossil record, and recent interpretations of it that the pattern of human evolution is not one of a continuous and gradual anagenesis, but includes distinct species located at particular points in time and space (Fig. 5.1). The antecedents to the human mind therefore cannot be a general and unspecified precursor of that of modern humans, but is likely to have varied between taxa (Lee 1989). Furthermore, not all extinct hominids are ancestral to modern humans. Some, such as the robust Australopithecines, and possibly *Australopithecus africanus* and



Homo neanderthalensis, are distinct evolutionary developments, and cognitively as much as anatomically they are likely to have their own unique traits. It is no longer possible to adopt a progressivist approach to the evolution of human cognition any more than it is to other hominid features.

The aim here will be to establish the relative cognitive capacities of specific hominid taxa. The definitions of these are set out below. Owing to our inability to establish data on very specific taxonomic groups these are relatively generalized, and it is not necessarily the case that the units used here represent real species, nor that they comprise the totality of the hominid record. From the range of taxa shown in Figure 5.1 a number of key units are employed in the analyses presented here. In particular, only the genus *Homo* is included in these analyses as there is no clear evidence for stone technology among the Australopithecines (Foley 1987; Susman 1988) and this limits their use for comparative purposes.

1. Early *Homo*: this refers to *Homo habilis* in the sense used by Tobias (1991) to include all the early African hominids not specifically assigned to *Homo erectus* or the australopithecines (i.e. with enlarged cranial capacity, reduced face and dentition, but lacking the cranial specializations of *Homo erectus*). Many authors, myself included, would prefer to split this material into two species, *Homo habilis* (e.g. the Olduvai hominids + KNM-ER1813) and *Homo rudolfensis* (e.g. KNM-ER 1470), a larger and more robust species (Wood 1991). This hominid occurs in sub-Saharan Africa between 2.3 and 1.6 Myr (Hill *et al.* 1992).
2. Early (African) *Homo erectus*: in the generalized sense the taxon *Homo erectus* occurs in Asia and Africa, from 1.6 Myr to 0.3 Myr. It is possible to distinguish various attributes that are unique to the later Asian forms, and so some authorities recognize an early African taxon (*Homo ergaster*) (Andrews 1984; Wood 1991) and true, later, Asian *Homo erectus*. This distinction is made here, and 'early African *Homo erectus*' refers to the material, such as KNM-ER3733, occurring in Africa between 1.6 and <1.0 Myr.
3. Later (Asian) *Homo erectus* represents the remainder of '*Homo erectus*', and is generally later (<1.0 Mya) and confined to Asia.
4. Pre-*Homo sapiens*: *Homo sapiens* is conventionally used to include all material that post-dates *Homo erectus* and shows cranial expansion (>1000 cc) and a reduction in facial height. This makes the taxon extremely polytypic. Recently it has been argued that the taxon *Homo sapiens* should be

confined to anatomically modern humans (Stringer & Andrews 1988; Tattersall 1986; Foley 1989b). This leaves various problems in assigning the later Middle Pleistocene and early Upper Pleistocene material consistently. Here 'pre-*Homo sapiens*' refers to the, primarily European, later-Middle Pleistocene fossil hominids.

5. *Homo neanderthalensis*: that part of the 'archaic *Homo sapiens*' category of the conventional classification that has distinct mid-facial prognathism and a number of other unique features, and occurs in Europe during the upper Pleistocene until approximately 35 Kyr, and contemporaneously in the Middle East. It represents the best known non modern hominid, and to many authorities constitutes a distinct species evolving in parallel to modern humans (see Tattersall 1986).
6. *Homo sapiens*: refers to anatomically modern humans, occurring from approximately 100 Kyr in Africa and the Levant. Where associated data relating to *Homo sapiens* is used (see below), late Pleistocene and hunter-gathering modern humans are used.

In the subsequent analyses these taxa constitute the units used.

Quantitative measures of cognitive states in extinct hominids

The fossil and archaeological record contains a number of lines of evidence that have been used to infer the cognitive states of the hominids. These are both anatomical and behavioural. Here only those that are susceptible to quantitative analysis and can be assigned to several of the taxa are used. The following variables may be defined:

1. *Brain size and encephalization quotient*. Overall brain size, which can be calculated from cranial capacity with considerable accuracy, is generally thought to be a good indicator of the overall *information-processing capacity* of a species. However, the primary determinant of brain size is body size. In assessing the significance of brain size it is therefore necessary to factor out the effect of brain size. The relationship between brain size and body size is allometric and a number of models have been developed to describe the relationship. These may be used to calculate the encephalization quotient (EQ), which is the size of the brain relative to expected size for a particular body weight. Two exponents are generally used — two thirds (Jerison 1973) and three quarters (Martin 1983). The

- former scales with surface area, the latter with metabolic rate. Both are presented where available. Use of EQ in the fossil record depends upon the availability of good estimates of body size. The data used here are from Aiello & Dunbar (1993).
2. *Neocortex ratio*. Dunbar (1992) has recently argued that neocortex ratio, rather than EQ is the best estimate of 'significant higher intelligence' and therefore it is the ratio of this to the rest of the brain that needs to be measured. This has been calculated for a number of extinct hominids (Aiello & Dunbar 1993).
 3. *Technocomplex duration*. Once stone tools are made then there is greater access to behavioural information about hominids, and by deduction, their cognitive capacities (Gowlett 1984). Quantifying such information, however, is no easy task. The length of time technological traditions persist, defined here as the length of time from first to last appearance, is one such variable that may be assessed, if assumptions are made about the use of specific artefacts as 'technological apomorphies' (see Foley 1987; 1989c). Pronounced persistence may provide insights into cognition either in terms of limited scope for innovation and introducing variation and novelty, or else in terms of the maintenance of social traditions (McGrew & Tutin 1978). Isaac (1972) produced a similar set of data, and this has been updated here (Table 5.1). The assumption is made here that *Homo habilis* is responsible for the Oldowan and that this technology persists throughout the duration of the species; that the duration of the Acheulean, associated with African and (by inference only) European *Homo erectus* is over 1 million years; that the pebble tool tradition of Asia is associated with *Homo erectus*, with similar levels of longevity. Pre-*Homo sapiens* has been linked here with the technologies associated with the African MSA, while *Homo neanderthalensis* is associated with the Levallois tradition lasting over 200,000 years. For *Homo sapiens* a number of archaeological hunter-gatherer populations were used.
 4. *Technocomplex complexity*. The number of identifiable stone tool types is basic information that can be derived from archaeological data, and from which inferences about cognition may be derived. Clearly these data are subject to a certain amount of subjectivity, but the differences between taxa are often an order of magnitude and therefore the effect of classificatory bias may be insignificant. The data used here are drawn from Isaac (1972), updated from Schick & Toth

(1993) for the earlier phases.

5. *Age of eruption of mandibular M1*. There is growing acceptance that levels of encephalization are related to other life history parameters (gestation length, longevity, age of first reproduction) (Harvey *et al.* 1987). It is also known that the rate of growth and hence age of maturation changes very substantially during the course of hominid evolution (Smith 1992). Recent developments in studies of dental microstructure (Bromage & Dean 1985; Beynon & Dean 1988; Beynon & Wood 1987) now allow the age at which teeth erupt to be determined independently, and as the age of eruption of the first molar correlates with brain size among primates (Smith 1989), this can be used to indicate evolutionary changes in life history strategy that are likely to be associated with cognitive and social traits. Data here are drawn from sources described in Foley & Lee (1991).

Patterns in the evolution of hominid cognition

Table 5.1 shows the values obtained for these variables for the fossil hominid taxa. For a number of data points it was not possible to calculate a figure; for EQs this is due to an absence of good body size estimates, and for age of eruption of M1 no material has yet been analyzed for one taxon. It should also be stressed that there may be considerable variance involved and these are taxon means based on single data points or small samples. A further problem lies in the fact that the data for each cognitive variable varies considerably in range, and it is difficult to establish equivalence. Table 5.2 therefore shows the same data expressed as a ratio relative to *Homo habilis*, where *Homo habilis* always equals zero; in Table 3 a ratio relative to *Homo sapiens*, where *Homo sapiens* always equals 1. In Table 5.4 the ratios are calculated in such a way as to root *Homo habilis* at zero and *Homo sapiens* at 1. These data give a better impression of the relative positions of the hominid taxa and the amount of change between them.

The information that can be derived from these data do not relate to the actual cognitive or behavioural skills of the hominids. What they can do is provide a scale of the relative abilities of the hominids, and thus when and in what general areas of cognition evolutionary changes are occurring.

The most obvious point to emerge is that whatever scale is used the various traits change independently, or at least the association is not such that all change is simultaneous. Figures 5.2 and 5.3 show for the two ratios used, the pattern of change for

Table 5.1. Anatomical, behavioural and life history variables of extinct hominid taxa and early *Homo sapiens* from which cognitive states may be inferred. See text for discussion and definition of variables and taxa. See text for details and sources.

Taxon	Encephalization Quotient ('EQ') (Jerison)	Encephalization Quotient ('EQ') (Martin)	Neocortex Ratio	Duration of archaeological technocomplex (Myr)	Archaeological complexity (number of tool types)	Age of eruption of mandibular M1 (years)
<i>Homo habilis</i>	4.31	3.38	3.44	1.20	6.00	4.00
<i>Homo erectus</i> (African)	4.40	3.34	3.66	1.20	11.00	4.60
<i>Homo erectus</i> (Asian)	4.40	3.34	3.79	1.00	7.00	5.40
Pre- <i>Homo sapiens</i>	–	–	3.95	0.10	19.00	–
<i>Homo neanderthalensis</i>	–	–	4.06	0.21	42.00	6.60
<i>Homo sapiens</i>	8.07	6.28	4.12	0.02	69.00	6.10

Table 5.2. Ratio of behavioural and neurobiological characteristics of *Homo* species. In all cases *Homo habilis* = 0.

Taxon	Jerison's Encephalization Quotient	Neocortex Ratio	Archaeological Longevity	Technological Complexity	Age of Maturation
<i>Homo habilis</i>	0.00	0.00	0.00	0.00	0.00
<i>Homo erectus</i> (African)	2.00	6.00	0.00	7.00	9.00
<i>Homo erectus</i> (Asian)	2.00	9.00	0.00	1.00	23.00
Pre- <i>Homo sapiens</i>	–	13.00	17.00	19.00	–
<i>Homo neanderthalensis</i>	–	16.00	7.00	52.00	42.00
<i>Homo sapiens</i>	47.00	17.00	98.00	91.00	34.00

Table 5.3. Ratio of behavioural and neurobiological characteristics of *Homo* species. In all cases *Homo sapiens* = 1.

Taxon	Jerison's Encephalization Quotient	Neocortex Ratio	Archaeological Longevity	Technological Complexity	Age of Maturation
<i>Homo habilis</i>	0.53	0.83	0.02	0.09	0.66
<i>Homo erectus</i> (African)	0.55	0.89	0.02	0.16	0.75
<i>Homo erectus</i> (Asian)	0.55	0.92	0.02	0.10	0.89
Pre- <i>Homo sapiens</i>	–	0.96	0.19	0.28	–
<i>Homo neanderthalensis</i>	–	0.99	0.09	0.61	1.08
<i>Homo sapiens</i>	1.00	1.00	1.00	1.00	1.00

Table 5.4. Ratio of behavioural and neurobiological characteristics of *Homo* species. In all cases *Homo habilis* = 0 and *Homo sapiens* = 1.

Taxon	Jerison's Encephalization Quotient	Neocortex Ratio	Archaeological Longevity	Technological Complexity	Age of Maturation
<i>Homo habilis</i>	0.00	0.00	0.00	0.00	0.00
<i>Homo erectus</i> (African)	0.04	0.35	0.00	0.08	0.26
<i>Homo erectus</i> (Asian)	0.04	0.53	0.00	0.01	0.68
Pre- <i>Homo sapiens</i>	–	0.76	0.17	0.21	–
<i>Homo neanderthalensis</i>	–	0.94	0.07	0.57	1.24
<i>Homo sapiens</i>	1.00	1.00	1.00	1.00	1.00

each of the variables, and it can be seen clearly that, for example, technological parameters alter very little for most of the non-modern hominids. It is only with *Homo sapiens* that there is much change, and then it is very dramatic. In contrast, neocortex ratio shifts gradually and relatively continuously across the taxa. An attempt can be made to assess the degree of association statistically, although the small samples and unknown error levels rule against using these measures to assess statistical significance. However, Table 5.5 shows the correlation coefficients for the relationship between the cognitive variables. The strongest associations are between archaeological complexity and EQ ($r = 1$); archaeological duration and EQ ($r = -.99$); maturation rate and neocortex ratio ($r = .96$); and archaeological duration and neocortex ratio ($r = -.91$). It should be remembered for the first two associations there are no EQ data for two of the taxa. If the ratios are used to calculate the

correlation coefficients (in order to remove scaling effects) the level of association drops although the rank order remains the same.

A related point is that the baseline of change is very different for the different taxa. *Homo habilis* possesses over four-fifths of the neocortex ratio of *Homo sapiens*, about half of the EQ, and matures at about two-thirds of the rate found in modern humans. In contrast, the archaeological/technological measures show less than 10 per cent of the capabilities found in early modern humans.

Furthermore, change is not always unidirectional towards greater complexity, reaching a peak in modern humans. For example, the Asian *Homo erectus* display less technological complexity compared to earlier African *Homo erectus*. In the case of Neanderthals and modern humans there is considerable complexity. Neanderthals share some technological characteristics with early *Homo sapiens* (Skhül

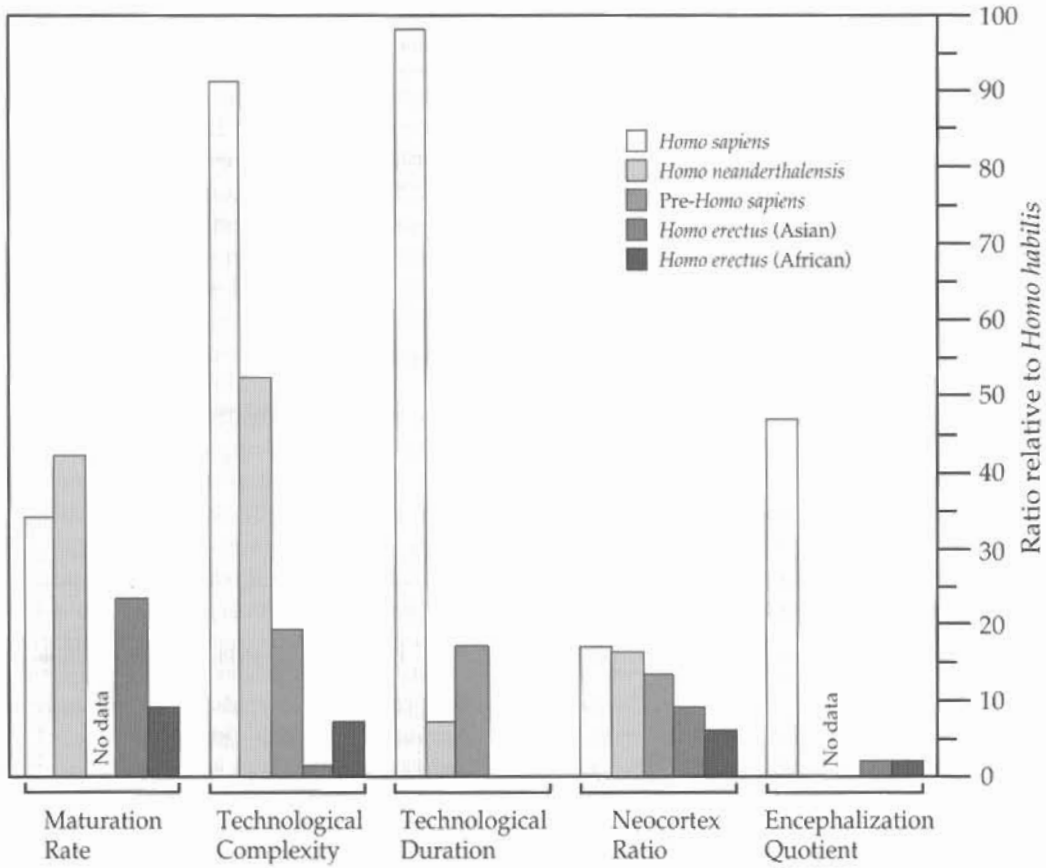


Figure 5.2. Histograms representing the 'cognitive variables' for the hominid taxa. To ease comparison all data are expressed as a ratio relative to *Homo habilis* which equals zero (and hence is not shown).

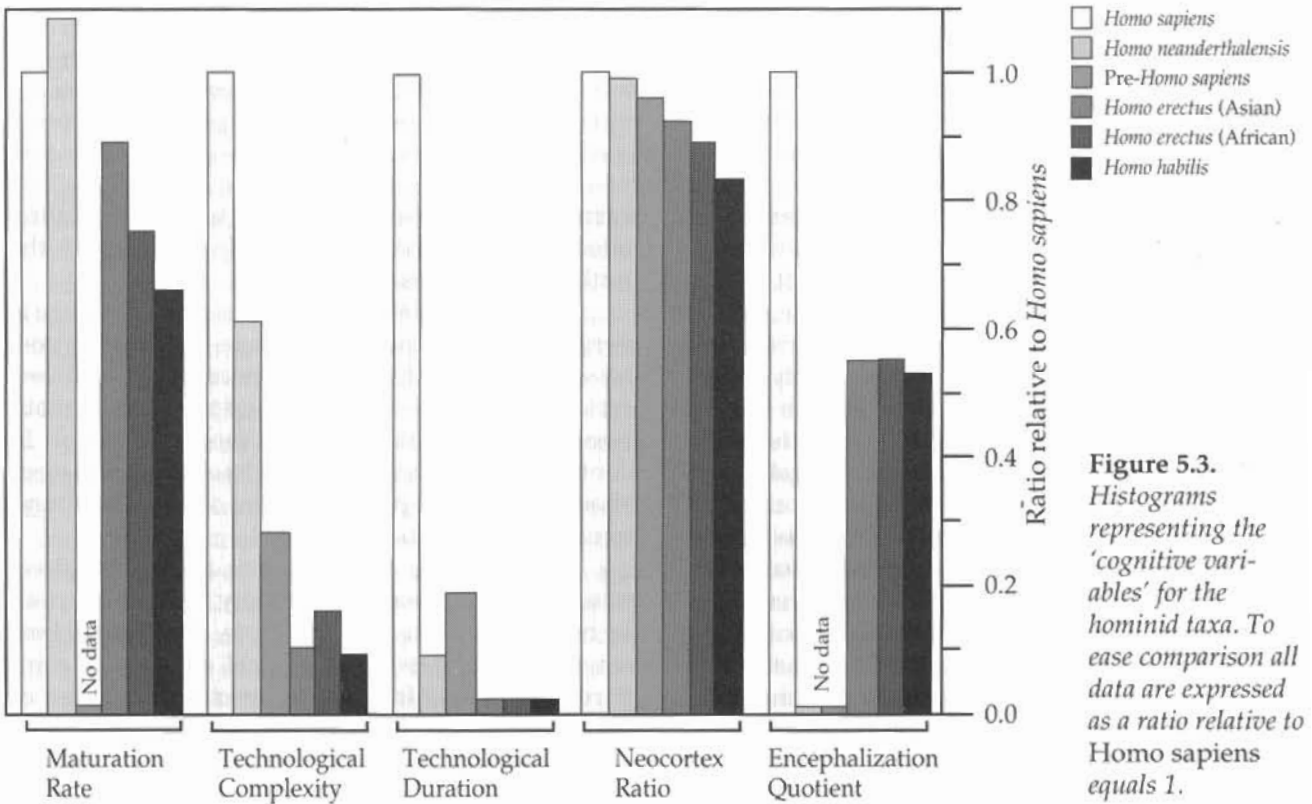


Figure 5.3. Histograms representing the 'cognitive variables' for the hominid taxa. To ease comparison all data are expressed as a ratio relative to *Homo sapiens* equals 1.

Table 5.5. Correlation coefficients between behavioural and neurobiological variables.

	Encephalization Quotient				
Encephalization Quotient	1.00		Neocortex Ratio		
Neocortex Ratio	0.87		1.00	Archaeological Longevity	
Archaeological Longevity	-0.99		-0.91	1.00	Maturation Rate
Maturation	0.79		0.96	-0.89	1.00
Technological Complexity	1.00		0.82	-0.79	0.76
					1.00

and Qafzeh), and also show increasing complexity at the end of their time span (Châtelperronian, Szeletian, etc.). Conversely complex and 'modern' technology (cf. Upper Palaeolithic) is not always associated with modern *Homo sapiens*. It is the case, however, that in Europe at the transition between Neanderthals and *Homo sapiens* there is an increase in technological complexity (Mellars this volume).

These three observations together have important implications for debates about the abilities and cognitive states of extinct hominids relative to modern humans. The level of difference between modern humans and other species depends upon the measure used. Technology will exaggerate the differences, while neocortex ratio will emphasize continuity. EQ and maturation rate indicate an intermediate position. The simplest conclusion to be drawn is that different skills and capacities evolved at different rates at different times, and therefore that the various extinct hominids may have had genuinely different combinations of behavioural and intellectual traits.

From the relative patterns of these various traits it is perhaps more interesting to see whether any biological insights can be gained from the pattern of change, rather than being concerned with the relative rankings of the taxa. These may provide a better understanding of the evolutionary processes that led to the evolution of modern humans.

For the earliest part of the hominid evolutionary history, the rate of maturation appears to change most significantly. This pattern would be seen even more strongly if comparisons with Australopithecines were made. This implies that changes in life history strategies and their underlying patterns of parental effort and investment are the first shifts to occur. These are associated with a gradual change in neocortex ratio. Dunbar (1992) has argued that this change reflects increasing group size, and it may be argued here that the conjunction of these two variables implies an ecological and energetic change in the earlier phases of hominid evolution, resulting in a change in social strategy and hence both the conditions under which encephalization may occur and

the selective pressures leading to such a change. Subsequent to these life history and neurological changes there are associated, possibly threshold, effects in EQ and technology. These, however, occur later (with pre-*Homo sapiens*) and also very rapidly.

It should be remembered that the analyses presented here have been based on comparisons between taxa, and these do not necessarily relate to the actual rates of change through time. Figure 5.4 shows the extrapolation from this data of the possible rates of change for these variables. Such extrapolations would support the notion that for neocortex ratio and maturation rate there is an earlier, more extended and gradual pattern of change than is found in the technological record.

Conclusions

The primary purpose of this paper has been to argue that any attempt to examine the evolution of human cognition must be based on the palaeobiologically observable pattern of hominid evolution. Models that seek to map and explain the evolutionary pathways from the pre-human mind to the abilities of modern humans must be consistent with the only direct evidence of the timing of this evolution and the conditions under which it occurred. Such an argument in turn places the onus on palaeobiologists to provide data on the cognitive abilities of extinct hominids that allows comparison between taxa. Some steps in this direction are made here, but it needs to be stressed that the data presented are based on sparse and small samples, and analysis has only been possible using pooled taxonomic information that ignores any within-group variance or time-transgressive trends.

Such data, however, do provide some tentative insights into the pattern of human cognitive evolution. The first of these is that no single variable can represent the character of cognition, and when several variables are used a level of independence can be observed. It is possible to show that different abilities evolve at different rates at different times.

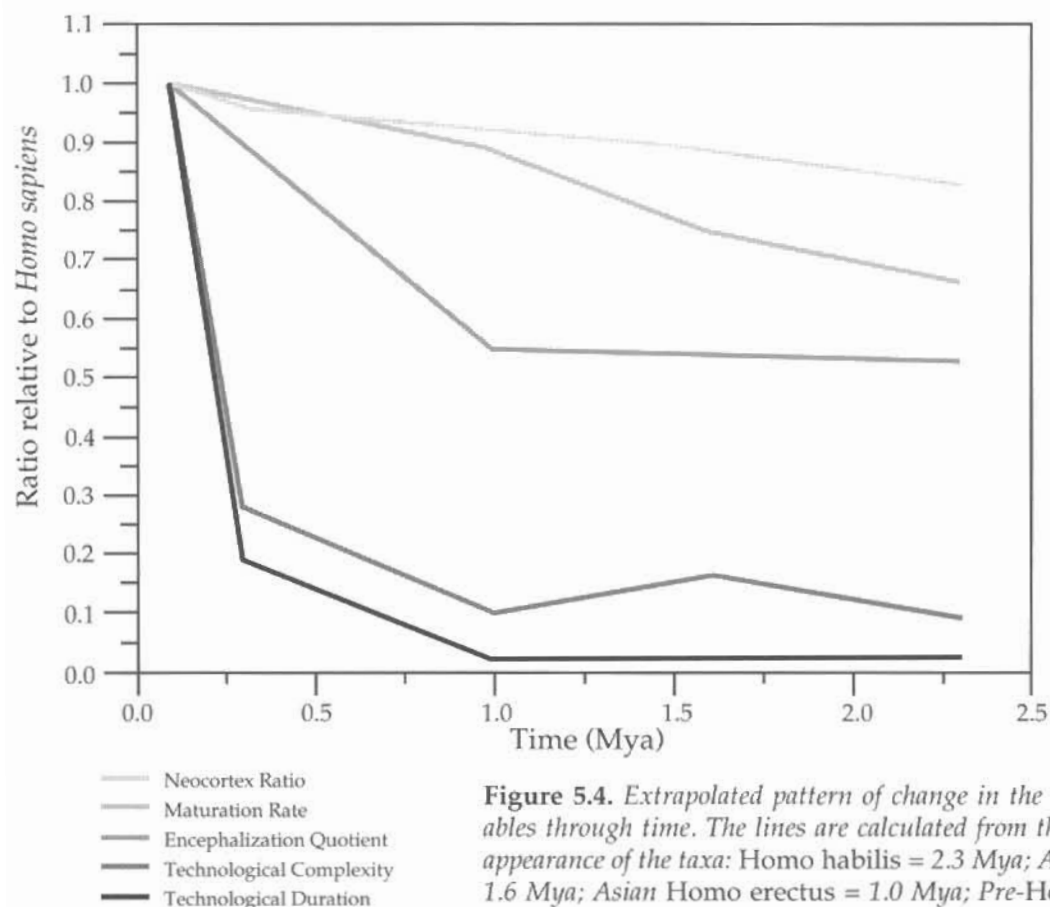


Figure 5.4. Extrapolated pattern of change in the cognitively related variables through time. The lines are calculated from the estimated date of first appearance of the taxa: *Homo habilis* = 2.3 Mya; African *Homo erectus* = 1.6 Mya; Asian *Homo erectus* = 1.0 Mya; Pre-*Homo sapiens* = .5 Mya; and *Homo sapiens* = .1 Mya. Neanderthals are excluded from the extrapolation on the grounds that they do not appear to be part of the evolutionary lineage leading to *Homo sapiens*, but appear later. The values associated with them are shown by the letters M (Maturation Rate), N (Neocortex Ratio), C (Technological Complexity), and D (Technological Duration). Data used are ratio data where *Homo sapiens* = 1.

tion on the grounds that they do not appear to be part of the evolutionary lineage leading to *Homo sapiens*, but appear later. The values associated with them are shown by the letters M (Maturation Rate), N (Neocortex Ratio), C (Technological Complexity), and D (Technological Duration). Data used are ratio data where *Homo sapiens* = 1.

An important implication that would require further investigation is whether this means that the cognitive characteristics of the modern human mind evolved as a response to a number of different selective pressures, or whether there is a greater degree of integration both neurobiologically and in terms of selection. Answering this question may provide some insights into the debate about specific versus general intelligence (see various papers, this volume). It may also help to resolve some of the debates about the relative levels of cognitive skills of extinct hominids and the question of whether there is a 'revolution' with the appearance of modern humans (Mellars & Stringer 1989) or whether neanderthals are only trivially different to *Homo sapiens*. The answer to this question may well depend upon what is being compared.

Perhaps the most provocative suggestion that may be made on the basis of the limited data presented here is the apparent precedence in time of

changes in the rate of maturation. If correct this underpins arguments (Humphrey 1976) that even if social complexity provides the key selective pressure leading to greater levels of encephalization in humans in particular and mammals in general, nonetheless this social complexity is predicated upon the energetic feasibility of specific reproductive strategies, and hence upon the pivotal links between social strategies and ecological ones. It also means that the evolution of the human mind cannot be divorced from the evolution of our more basic biological traits.

Robert A. Foley
Human Evolutionary Biology Research Group
Department of Biological Anthropology
University of Cambridge
Downing Street
Cambridge
CB2 3DZ

References

- Andrews, P.J., 1984. An alternative interpretation of the characters used to define *Homo erectus*. *Courier Forschungsinstitut Seckenberg*, 167–75.
- Aiello, L.C. & R.I.M. Dunbar, 1993. Neocortex size, group size and the evolution of language. *Current Anthropology* 34, 184–93.
- Beynon, A.D. & M.C. Dean, 1988. Distinct dental development patterns in early fossil hominids. *Nature* 335, 509–14.
- Beynon, A.D. & B.A. Wood, 1987. Patterns and rates of molar crown formation times in East African hominids. *Nature* 326, 493–6.
- Bromage, T.G. & M.C. Dean, 1985. Re-evaluation of the age at death of Plio-Pleistocene fossil hominids. *Nature* 317, 525–8.
- Byrne, R. & A. Whiten (eds.), 1988. *Machiavellian Intelligence*. Oxford: Clarendon Press.
- Cheyney, D.L. & R.M. Seyfarth, 1990. *How Monkeys See the World*. Chicago (IL): University of Chicago Press.
- Dunbar, R.I.M., 1992. Neocortex size as a constraint on group size in primates. *Journal of Human Evolution* 22, 469–93.
- Foley, R.A., 1987. Hominid species and stone tool assemblages: how are they related? *Antiquity* 61, 380–92.
- Foley, R.A., 1989a. The evolution of hominid social behaviour, in *Comparative Socioecology*, eds. V. Standen & R.A. Foley. Oxford: Blackwell Scientific Publications, 473–94.
- Foley, R.A., 1989b. The ecology of speciation: comparative perspectives on the origins of modern humans, in Mellars & Stringer (eds.), 298–320.
- Foley, R.A., 1989c. Alternative models of Pleistocene cultural evolution. *Antiquity* 63, 159–62.
- Foley, R.A. & P.C. Lee, 1991. Ecology and energetics of encephalization in hominid evolution. *Philosophical Transactions of the Royal Society*, London Series B 334, 223–32.
- Harvey, P.H., R.D. Martin & T.H. Clutton-Brock, 1987. Life histories in comparative perspective, in *Primate Societies*, eds. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker. Chicago (IL): University of Chicago Press, 181–96.
- Hill, A., S. Ward, A. Delno, G. Curtis & R. Drake, 1992. Earliest *Homo*. *Nature* 355, 719–22.
- Humphrey, N.K., 1976. The social function of intellect, in *Growing Points in Ethology*, eds. P.P.G. Bateson & R.A. Hinde. Cambridge: Cambridge University Press, 303–17.
- Jerison, H.J., 1973. *Evolution of the Brain and Intelligence*. New York (NY): Academic Press.
- Lee, P.C., 1989. Comparative ethological approaches in modelling hominid behaviour. *Ossa* 14, 113–26.
- McGrew, W.C., 1992. *Chimpanzee Material Culture*. Cambridge: Cambridge University Press.
- McGrew, W.C. & C.E.G. Tutin, 1978. Evidence for a social custom in wild chimpanzees. *Man* 13, 234–51.
- Martin, R.D., 1983. *Human Brain Evolution in an Ecological Context. 52nd James Arthur Lecture on the Evolution of the Brain*. New York (NY): American Museum of Natural History.
- Mellars, P.A. & C.B. Stringer (eds.), 1989. *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*. Edinburgh: Edinburgh University Press.
- Parker, S. & K. Gibson, 1979. A developmental model for the evolution of language and intelligence in early hominids. *Behavioural and Brain Sciences* 2, 367–408.
- Savage-Rumbaugh, E.S. & D.M. Savage-Rumbaugh, 1993. The emergence of language, in *Tools, Language and Cognition in Human Evolution*, eds. K.R. Gibson & T. Ingold. Cambridge: Cambridge University Press, 86–108.
- Savage-Rumbaugh, E.S., J.L. Pate, J. Lawson, S.T. Smith & S. Rosenbaum, 1983. Can a chimpanzee make a statement? *Journal of Experimental Psychology* 112, 457–92.
- Smith, B.H., 1989. Dental development as a measure of life history in primates. *Evolution* 43, 683–8.
- Smith, B.H., 1992. Life history and the evolution of human maturation. *Evolutionary Anthropology* 1(4), 134–42.
- Stringer, C.B. & P.J. Andrews, 1988. Genetic and fossil evidence for the origin of modern humans. *Science* 1263–8.
- Susman, R.L., 1988. Hand of *Paranthropus robustus* from Swartkrans Member 1, fossil evidence for tool behavior. *Science* 240, 781–4.
- Tattersall, I., 1986. Species recognition in human palaeontology. *Journal of Human Evolution* 15, 165–75.
- Tobias, P.V., 1991. *Olduvai Gorge*, vol. 4: *Homo habilis — Skulls, Endocasts and Teeth*. Cambridge: Cambridge University Press.
- Trinkaus, E. (ed.), 1989. *The Emergence of Modern Humans*. Cambridge: Cambridge University Press.
- Wood, B.A., 1991. *Koobi Fora Research Project*, vol. 4: *Hominid Cranial Remains*. Oxford: Oxford University Press.