

Terrestriality, Bipedalism and the Origin of Language

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Summary. Language is unique to humans, but in the context of the long time span of human evolution it is a fairly recent innovation. All evidence suggests that human brain size and inferred cognitive and linguistic abilities reached their modern norms only within the last quarter of a million years. Foundations for human linguistic and cognitive evolution, however, lie much further back in evolutionary history. Arguments are presented suggesting that these unique human abilities are the legacy of our ancestors' terrestrial and bipedal adaptations. Both terrestriality and bipedalism are directly associated with the unique human propensity for vocal communication, including the range and quality of sound that all humans are capable of producing. Furthermore, terrestriality and bipedalism can also be directly associated with an increase in brain size and cognition. Increases in group size accompanying a committed terrestrial adaptation would have put a premium on social, or Machiavellian intelligence while bipedalism would have been associated with the increased neural circuitry involved in enhanced speed and co-ordination of hand and arm movements. The constricted bipedal pelvis would have also necessitated the birth of less mature offspring, exposing them to a rich environment while the brain was still rapidly growing and developing. A larger brain is not without its costs, however. Energetic arguments are also presented which suggest that a large brain can only evolve in concert with a change to a high quality diet, resulting directly in lifestyle changes for our early ancestors.

All of these features were in place by the appearance of early *Homo erectus* about 1.8 million years ago and underpinned an apparently stable hominine adaptation that lasted for well over 1.5 million years. Modern human cognitive and linguistic talents are rooted in this earlier *Homo erectus* adaptation and may have begun to develop in response to further need for increased group size. Both the costs and the benefits of this later increase in brain size are considered.

INTRODUCTION

LANGUAGE IS SECOND NATURE TO HUMANS. In everyday life we seldom give serious thought to this phenomenal talent for communication and the fact that normal individuals raised in normal cultural environments acquire language easily, without effort and with little, if any, tuition.

One starting point in the study of the evolution of human language is to understand precisely how it differs from the communication systems of our closest living relatives, the non-human primates. Deacon (1992) has outlined three fundamental areas of difference. The first of these concerns the actual physical production of sound. Only humans have a vocal tract that is shaped in such a way as to permit the production of the range of sounds used in human language. Of particular importance is the fact that humans are able to produce consonants which act as 'stops' in the continuous flow of sound. These consonants are essential to our ability to decode, or make sense of, vocal language. We also have the neurological co-ordination that permits the necessary complex articulatory movements of the mandible, lips and tongue in respect to the teeth, palate and pharynx which allows us to produce not only consonants but also a wide range of vowel sounds. An important point is that these articulatory movements have to be learned, they are not innate.

The second unique aspect of human language is that it involves the use of a finite number of sounds to generate an infinite number of meanings. The order of these sounds, or the syntax, is the source of complex meaning in language. The third unique aspect is the symbolic nature of human language. Combinations of sounds, whether at the level of a word, or a string of words, have complex meanings that are easily recognized by the community of speakers of a particular language but are arbitrary in relation to the object or concept that they represent.

The fact that human language is unique in these three major aspects (the physical production of sound, syntax and symbolic content) does not mean that the non-human primates, and particularly African apes, lack all

linguistic ability. Attempts to teach African apes 'non-verbal' language based on either American Sign Language for the Deaf or on computer-based symbol systems have established that they have some of the basic cognitive pre-requisites for language. For example, there seems to be little doubt any longer that African apes, and particularly pygmy chimpanzees, can associate abstract meanings with symbols and use these symbols in novel situations (Savage-Rumbaugh & Lewin 1994; Savage-Rumbaugh *et al.* 1993). This ability should perhaps not seem too surprising in view of the fact that at least one species of monkey is known to produce calls in the wild that have specific symbolic content (Seyfarth *et al.* 1980). Claims for syntactic abilities in non-human primates are arguably more controversial, but apes are capable of producing two-symbol combinations that are analogous to the two-word syntax of very young human children. It is also interesting that they appear to be able to understand some of the more complicated syntax of spoken English (Savage-Rumbaugh & Lewin 1994). This is particularly intriguing in view of the fact that, although they are not capable of producing spoken language themselves, they do have both the auditory abilities and the cognitive capacity to interpret at least some of the continuous flow of sound characteristic of human language.

It is clear that the basic symbolic and syntactic talents of living apes exist in these species without the co-existence of symbolically based, vocal (or for that matter, non-vocal), language systems. These abilities must stem from some other aspect of primate life (Povinelli & Preuss, *in press*). One obvious area for the pre-linguistic use of these talents is social cognition. Work summarized by Tomasello & Call (1994) has shown that there may be little difference between humans and other higher primates in the major aspects of social cognition, and particularly in the basic ability to associate meaning with individuals and to manipulate social situations. The differences that do exist between humans and non-human higher primates more often involve the elaboration and sophistication of basic abilities that exist in other primates than the development of qualitatively new abilities. In particular, Povinelli & Preuss (1995) have recently argued that humans may have specialized in a particular kind of intelligence related to understanding mental states such as desires, intentions, and beliefs.

If the cognitive talents present in living African apes also characterized the last common ancestor of these apes and ourselves, the evolution of human language would have involved a significant elaboration of abilities for sequencing and syntax as well as a significant increase in symbolic capacity. At the same time, it would have involved the development of the vocal basis for language. Any approach to the evolution of human language must take into consideration both of these aspects, the cognitive as well as the vocal. It also must address the questions of why these changes occurred

and when in the course of human evolution human language became established. It is the purpose of this contribution to examine these issues.

THE WHY AND THE WHEN OF HUMAN LANGUAGE EVOLUTION

In recent years both the why and the when of language evolution have been under considerable debate. The major issue in relation to the why of language evolution has centred on the question of whether human language appeared as the result of natural selection for linguistic ability (Pinker & Bloom 1990; Pinker 1994). The alternative is that it appeared as a side effect of other evolutionary forces such as the increase in brain size or constraints of brain structure and growth (Piattelli-Palmarini 1989). There are a number of quite compelling theoretical arguments that can be put forward to argue that linguistic ability has specifically been selected for in human evolution (Pinker & Bloom 1990; Pinker 1994). These include the extreme improbability that the complex neurological structures underlying a function as complex as human language could have arisen either entirely by chance or as a by-product of some other unrelated function. The fact that children can acquire language extremely rapidly and with minimal, if any, tuition is strong evidence for the predisposition of the human brain not only for the symbolic requirements of language but also for the sequencing and syntactic structure of all human language.

Perhaps the strongest evidence that language ability was specifically selected for in the course of human evolution is the fact that the prefrontal cortex in humans is the only area of the human brain that is disproportionately large in relation to the brains of other primates (Deacon 1992). The prefrontal cortex is that area of the brain that is specifically responsible for many features of language production and comprehension as well as the unique human ability to reflect on one's own mental states and those of others (Povinelli & Preuss 1995). It is difficult to understand why this particular area of the brain would be the only area that was so disproportionately large if the functions it serves were not interrelated and also the object of continued selection during the course of human evolution. Recent work on the relative sizes of cortical areas in primates support this idea by demonstrating that in animals that are active in daylight, the visual cortex is disproportionately large in relation to its size in nocturnal animals (Barton *et al.* 1995). There is little reason to have a disproportionately large visual cortex unless the visual acuity conferred by the enlarged cortex gave a specific reproductive advantage to its owner. The same can be said for language, cognition and the prefrontal cortex.

If it is accepted that language did arise by natural selection during human evolution rather than as an accidental by-product of some other process, what were the selective pressures resulting in its appearance? Did both the cognitive and the vocal aspects of human language develop at the same time and for the same reasons during human evolution, or did one significantly precede the other and serve as an exaptation for language? These questions have received surprisingly little attention in the literature on the evolution of language. Rather the main focus has been on when human language first appeared.

It has become popular in recent years to argue that language is a very recent development in human evolution, accompanying the appearance of anatomically modern *Homo sapiens* and/or the Upper Palaeolithic transition (White 1982; Chase & Dibble 1987; Mellars 1991; Noble & Davidson 1991; Davidson & Noble 1993; Milo & Quiatt 1993). These arguments have been made from the points of view of both the ability to produce human vocalizations (e.g. Lieberman *et al.* 1992) and the presence of evidence of the cognitive capacity for symbolization. The vocally based arguments have centred on the conclusion that only anatomically modern humans have a vocal tract capable of producing the full range of human vowel sounds. Over the years this work has been heavily criticized on the basis of the accuracy of the vocal tract reconstructions for the fossil hominines (see particularly Scherpartz 1993; Houghton 1993). Furthermore, the discovery of the first Neanderthal hyoid bone at Kebara, Israel, and the recognition that it is totally modern in form has convinced the great majority of anthropologists that Neanderthals had a vocal apparatus capable of the production of the full range of sounds needed for human language (Arensburg *et al.* 1989, 1990). At least from the physical point of view vocally based language could have characterized pre-modern hominines.

Cognitively based arguments centred on the evidence of symbolism in the fossil record in the form of art or non-utilitarian objects. Noble & Davidson (1991; Davidson & Noble 1993) have been prominent in this debate, arguing that there is no evidence for modern human symbolic, and therefore linguistic, ability until the Upper Palaeolithic transition in Europe (between 30,000 and 40,000 years ago). They do, however, concede that the peopling of Australia at an earlier date of 40,000 years ago (now probably closer to 60,000 years ago, Roberts *et al.* 1990) would mark the most ancient evidence for modern human symbolic ability. The recent discovery of carved harpoons at the Zairian site of Katanda may push the evidence of symbolic behaviour back to about 90,000 years ago (Yellen *et al.* 1995) and the presence of red Ochre and notched bone, engraved ostrich shell and perforated *Conus* shell in southern African sites may push the evidence of symbolic behaviour even further back, to earlier than 100,000 years (Knight *et al.* 1995).

These dates should be taken as the youngest possible occurrence of symbolic language and not the oldest. All that we can be sure of from archaeological evidence is that symbolic behaviour was in place by the time of the particular discovery. It does not tell us how long prior to the date of the discovery that the ability was present. Pinker (1994) makes the very good point that modern human language capability must have been in place by the first appearance of modern humans. This is because we all have the same linguistic abilities and these abilities must have been a feature of the human brain before the spread of modern humans throughout the world. Genetic evidence suggests that the modern human mitochondrial ancestor could be no more than about 500,000 years old (Stoneking 1993). The mtDNA ancestor does not necessarily mark the first appearance of modern humans, only the mtDNA characteristic of modern humans. The mtDNA date of 500,000 years together with the archaeological date of about 100,000 years does allow us, however, to bracket the time that modern human symbolic behaviour was most probably evolving.

It is notable, that the period between 500,000 and 100,000 years ago, the second half of the Middle Pleistocene period, corresponds to a period of very rapid brain expansion in our early ancestors (Figure 1). Recent research suggest that this rapid brain expansion may be directly related to the evolution of modern human language (Deacon 1992). Finlay & Darlington (1995) have argued that selection for a particular behavioural ability, such as language, may result in the co-ordinated enlargement of the entire brain (except for the olfactory system which represents a special case). They base this idea on the fact that the primary determinant of the size of a brain structure is the period of time during which the neurons form in early development (the period of neurogenesis). As a result, selection for a particular cognitive function may be easiest achieved by selection for prolonged neurogenesis that would effect the size of the entire neocortex.

THE SIGNIFICANCE OF TERRESTRIALITY TO HUMAN COGNITIVE AND LANGUAGE EVOLUTION

This argument is interesting as an explanation for the explosive increase in the size of the human brain that occurs in the last quarter of a million years or so. It does not tell us, though, why we have an explosive selection for language at this stage and equally importantly why we do not see a similar run-away development of the brain and linguistic capability in other primate species. The conclusion is unavoidable that there is something specific to the course of human evolution that emphasized the development both of verbally based communication and of the phenomenal development of

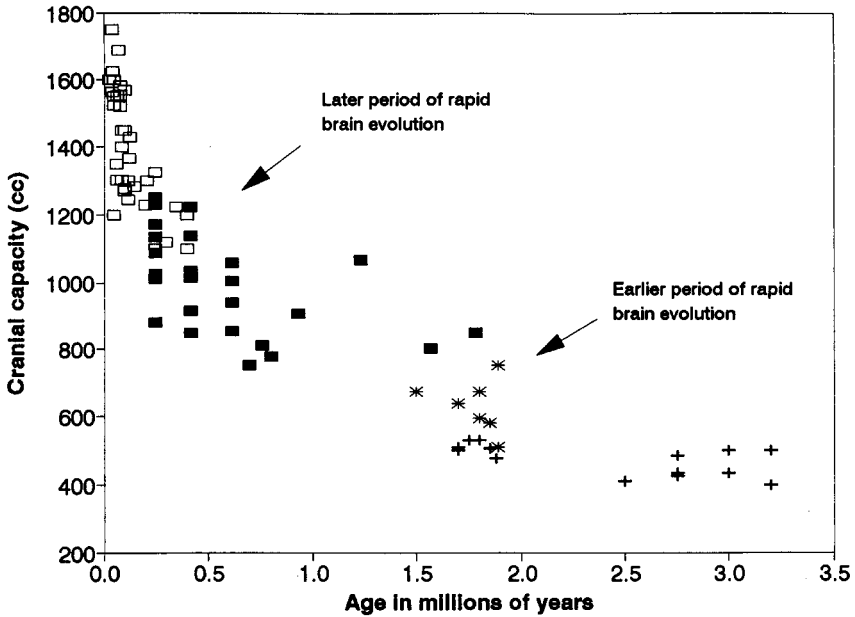


Figure 1. The increase in hominid cranial capacity over the past 3.5 million years (data from Aiello & Dean 1990). Plus = australopithecines, asterisk = early *Homo* (*H. habilis*, *H. rudolfensis*), filled square = *Homo erectus* (including *Homo ergaster*), open square (archaic and modern *Homo*). Note the two periods of rapid increase in brain size, the first occurring between about 2.0 and 1.5 million years ago and the second after 500,000 years ago.

cognitive capacity that accompanied it. One clue to what this might be can be inferred from the pattern of brain size increase in the hominines over the past 4 million years (Aiello, in press). In addition to the exponential increase in the brain of *Homo* in the second half of the Middle Pleistocene period there is also a marked increase in brain size that accompanies the first appearance of the genus *Homo* at approximately 2 million years ago (Figure 1).

This increase in brain size is correlated with one major feature in hominine adaptation, a transition to a fully terrestrial lifestyle. By the appearance of early *Homo erectus* (*Homo ergaster*) at approximately 1.8 million years ago in East Africa all evidence of any type of committed arboreal adaptation has been lost from the hominine postcranial skeleton. Early *Homo erectus* has modern limb proportions rather than the relatively short legs of the australopithecines and also lacks the specific skeletal morphology of the australopithecines that has been interpreted as indicative of at least a partial arboreal lifestyle (Walker & Leakey 1993). These arboreal adaptations include, among others, a funnel-shaped thorax (Schmid 1983, 1991; Hunt 1994), curved hand and foot phalanges (Stern

& Susman 1983) and features of the upper limb skeleton that are associated with forelimb strength and mobility (Aiello & Dean 1990). *Homo habilis*, an earlier member of the genus *Homo*, may still retain some climbing adaptations in its skeleton (Hartwig-Scherer & Martin 1992), but the palaeoecology of Bed I at Olduvai Gorge where it is found, indicates an adaptation to a mosaic lake-shore environment, which would include open country habitats (Plummer & Bishop 1994).

TERRESTRIALITY, GROUP SIZE AND LANGUAGE

Adaptation to an open-country, terrestrial environment has a number of perhaps unsuspected implications for an increase in brain size in general and for the origin of language in particular. One of the most important of these is that a terrestrial, open-country adaptation is correlated in primates with large group sizes (Foley 1987). This correlation can best be explained by the increase in predator pressure in such open environments and the protection from predators that is gained through larger group numbers (Aiello & Dunbar 1993). Primates that live in large groups also tend to have relatively larger neocortices than those living in smaller groups (Dunbar 1992, 1993). The neocortex is that part of the brain that deals with cognitive (among other) functions. Dunbar explains the relationship between large group size and relatively large neocortex sizes by the increased sophistication in social cognition needed to maintain the increased number and complexity of social relationships in a larger group. Following this line of logic, larger group sizes would not only be associated with larger neocortex sizes but also, and perhaps surprisingly, with a greater reliance on vocally based communication.

The connection between large group sizes and vocally based communication comes in the context of the maintenance of social cohesion. Non-human primates reinforce their social networks through mutual grooming and there is a strong correlation between group size and time spent in such grooming behaviour. The larger the group the more time must be spent in grooming to maintain group cohesion. But if too much time is spent grooming there will be insufficient time for other activities such as feeding, resting or travelling. Dunbar has suggested that the maximum time that can be spent grooming is about 20% of the daily time budget. Any more than this and other activities will suffer and this will ultimately affect individual survival and fitness.

Following this line of reasoning, one can predict when the early hominines might have begun to experience time-budget pressures. Neocortex size, can be predicted from total brain size, group size can be predicted from neocortex size and percentage grooming time can be predicted from group size (Aiello & Dunbar 1993). Although this three-step process of

inference compounds error, the results do suggest that early *Homo*, and particular early *Homo erectus*, would have been the first of the hominines to have to find a solution to the problem of maintaining group cohesion. Increased emphasis on vocalization as seen in living Gelada baboons, could serve as a supplement to mutual grooming by reaching more individuals than the specific focus of the grooming activity. At this stage, such vocalizations would not have necessarily had to have any specific symbolic content, but could be seen as something as simple as 'vocal grooming'. Control of the voice in tone and pattern would have been sufficient to spread a feeling of mutual content and well being. At this early stage, such vocalization may have been analogous to the chattering observed today in Gelada baboons, which have some of the largest group sizes of any living primates.

The importance of this to the evolution of human language is that it would have been a means by which conscious and co-ordinated control of vocalization could have become established. And importantly it would have been a way of establishing vocally based communication in our hominine ancestors without presupposing any necessary symbolic or other advanced cognitive capacity.

Is there any specific, empirical evidence that early *Homo* might have had an enhanced reliance on voluntary vocal communication as postulated by this scenario. The answer is yes. Endocranial casts demonstrate that early *Homo* has a reorganization and elaboration of the sulci of the left inferior frontal lobe of the brain in the region of Broca's area (Falk 1983). Broca's area and the adjacent ventral prefrontal cortex are the precise areas of the brain associated with (among other things) voluntary control and co-ordination of the tongue, lips and pharynx in the production of vocalizations (Deacon 1992). Early *Homo* also has brain asymmetries typical of modern humans (Tobias 1987). The most important of these to the current discussion is the relatively low position of the left Sylvian sulcus which separates the parietal from the temporal cortex and seems to suggest an expanded parietal cortex. Work on the neural organization of language functions suggests that the parietal cortex, together with the temporal cortex is involved in the voluntary production of sound as well as in speech comprehension (Deacon 1992).

The important point here is that this type of brain organization is seen for the first time in early *Homo* and can be interpreted in the context of the co-ordination necessary for the voluntary production of complex vocalization which is both a prerequisite for human language and predicted by the group-size model for the origin of language. This reorganization accompanies a modest increase in relative size of the hominine brain, but it is important to note that the size of the early *Homo* brain is still $\frac{1}{2}$ to $\frac{1}{3}$ smaller,

both in relative and absolute terms, than the modern human brain (Aiello & Dean 1990). This pattern is precisely what might be expected if the evolution of language proceeded through a phase of voluntary production of relatively elaborate vocalizations, lacking the symbolic, syntactic, or cognitive sophistication of modern human language.

TERRESTRIALITY, BIPEDALISM AND LANGUAGE

The group-size hypothesis for the expansion of the human brain and the evolution of language has many compelling aspects, but it cannot be the whole story. Other terrestrial primates living in large groups have not developed brains the size of modern human brains nor have they developed language. One of the reasons for this may be connected with another unique human adaption, bipedal locomotion. Bipedalism is one of the earliest, if not the earliest, hominine adaptation to appear in the fossil record (White *et al.* 1994; Leakey *et al.* 1995). There is no current consensus over the reasons why bipedalism evolved in the human line (Wheeler 1994; Hunt 1994; Jablonski & Chaplin 1993; also see Rose 1991 for a review), or why the postcranial skeletal and inferred bipedal capabilities were apparently so different in the australopithecines on the one hand and early *Homo erectus* (*Homo ergaster*) on the other. But we can be sure that bipedalism was not an evolutionary option for other primarily terrestrial primates such as baboons or macaques. The reason for this is that these primates are Old World (cercopithecoid) monkeys that have a limited component of below branch, or suspensory, postures in their repertoires (Rose 1973). As a result, they have skeletons that are very different from those of the apes in features associated with mobility and truncal erectness (Andrews & Aiello 1984). Primates that engage in suspensory postures, and particularly vertical climbers, are very similar to bipedal humans in joint excursion, muscle usage and kinematics (Kimura *et al.* 1979; Prost 1980; Fleagle *et al.* 1981; Ishida *et al.* 1985; Kimura 1985; Okada 1985). This type of positional behaviour is found in chimpanzees and is also inferred for the immediate proto-hominine. It would have made bipedalism a distinct possibility for the early hominines where it was not an option for the Old World monkeys entering the same niche.

Bipedalism may have had at least four direct effects of the evolution of language and cognition, two of these specifically related to the ability to produce human speech sounds and two generally related to the evolution of increased brain size and cognition. In relation to the production of human speech sounds, bipedalism was most probably directly related to the descent

of the human larynx (Negus 1929). In humans the larynx lies much lower in the throat than it does in apes and the part of the throat above the larynx, whose anterior border is the rear of the tongue, is necessary for the formation of both human vowels and consonants. In bipedal hominines the spinal cord enters the brain case from below rather than from behind, constricting the space for the larynx between the spinal cord and the mouth. This together with the reduction of the face in early *Homo erectus* (see below) in relation to the australopithecines would be expected to necessitate a lower larynx particularly in these later terrestrially committed bipedal hominines.

Bipedalism may also have been directly related to sound quality (Aiello, in press). Humans have a valvular larynx that allows the airway to be closed off. In speaking this permits pressure to build up below the larynx to be released during phonation. A valvular larynx also may have a locomotor function. It is found in mammals with prehensile forelimbs (Negus 1929). Air pressure below a closed larynx stabilizes the chest to provide a fixed basis for the arm muscles. This is why we tend to hold our breath when exerting ourselves with our arms. Negus (1929) has suggested that one difference between ourselves and climbing mammals is that human vocal folds (vocal cords) are less cartilaginous. The more membraneous human vocal folds allow the production of a less harsh, more melodious sound. This change may have been associated with a relaxed selective pressure on the locomotor function of the valvular larynx in a committed terrestrial bipedal. If this proves to be true it would be possible to speculate that the more arboreally adapted early hominines (including *Australopithecus afarensis*, *Australopithecus africanus* and *Ardipithecus ramidus*), retained the ancestral cartilaginous larynx and a harsher voice than would have characterized later members of the genus *Homo*.

In relation to the general evolution of increased brain size and cognition, committed bipedalism has the obvious effect of freeing the forelimb from locomotor function. Dedicated use of the forelimb for object manipulation would be expected to be associated with enhanced hand-eye co-ordination and an associated increase in neural circuitry. The failure of living apes to produce stone tools as sophisticated as even the earliest Oldowan artifacts (Schick & Toth 1993) may attest to the increased hand-eye co-ordination even in pre-erectus members of the genus *Homo*. Furthermore, Calvin (1983, 1992, 1993) has argued that speed and coordination of arm movement in hammering, throwing and presumably tool manufacture, would require increased neural capacity and integration. He also argues that the neural adaptations necessary for sequencing which would also be important for accurate throwing could serve as a preadaptation for linguistic sequencing, or syntax (Calvin 1992).

The final way in which bipedalism could be related to general cognitive evolution has to do with the structure of the bipedal pelvis (Wills 1995). In relation to a quadrupedal ape pelvis, a bipedal pelvis (whether australopithecine or *Homo*) structurally has to be much more compact. This results in a considerably more restricted birth canal (Berge *et al.* 1984; Tague & Lovejoy 1986). At the same time the evolution of the large human brain would presuppose a relatively large birth canal through which a large-brained infant could be born. Modern humans bear infants at a relatively premature (or secondary altricial) stage in relation to apes, while the brain is still growing at its rapid fetal rate (Martin 1990). This exposes the rapidly growing brain of the infant to the complex environment outside the womb which would have been a very important selective pressure for brain evolution. There is fossil evidence dating back to approximately 1.6 million years ago that suggests that by this time the human pelvis was so constricted and the brain of the infant potentially so large that it would have had to have been born at a less mature stage than is the case in living apes (Shipman & Walker 1989).

Therefore a terrestrial environment together with bipedalism would have resulted in a larger brain size (larger group size, freeing of the forelimb) and secondarily altricial offspring as well as specific factors which predisposed the early hominines to vocal communication (vocal grooming, membranous vocal cords and descended larynx). But there is still one other implication of the expanding brain size at this stage of evolution that has direct relevance to the evolution of linguistic ability in our ancestors. This has to do with dietary change.

TERRESTRIALITY, DIET AND LANGUAGE

Brain tissue is energetically among the most expensive tissues in the body, consuming over 22 times more energy than muscle tissue at rest (Aschoff *et al.* 1971). It follows that the larger the relative brain size, the greater the energetic demand would be on the organism and, everything else being equal, the greater difficulty that organism would have in meeting its daily food requirements. In this context, a relatively big brain would potentially be detrimental to an organism because it would significantly increase the total energy budget of that organism. There are a variety of ways in which an organism could compensate for the increased energy demands of an encephalized brain, but the hominines seem to have done this by reducing the size of one of the other energetically expensive tissues in the body, the gastro-intestinal tract. In humans, there are five organs that make up only about 7% of the total body weight but consume over 75% of our basal

metabolic rate. These organs are the brain, gastro-intestinal tract, heart, liver and kidneys. Of these the heart, liver and kidneys are tied closely to overall body weight because of their physiological functions. The gastro-intestinal tract is the only 'expensive' organ other than the brain that can vary significantly in size in animals of any given body weight. This is because its overall size, and hence energy requirements, is dependent not only on the size of the organism but also on the digestibility of the food eaten.

Aiello & Wheeler (1995) have demonstrated that humans have hearts, livers and kidneys of a size expected for an average primate of our body weights. They have also demonstrated that human guts have reduced in size by precisely the amount that would balance the energy requirements of our expanded brains. As a result, and in spite of our encephalized brains, the average human basal metabolic rate is at a level that would be expected for an average primate of our body weights. The negative correlation between expanded brains and reduced guts is also apparent in non-human primates. The implication of these results is that no matter what was selecting for a relatively large brain in humans (and in other primates) a high quality, easy to digest diet would be a necessary concomitant of encephalization. For our early ancestors, the most obvious source of such a high quality diet would be animal-based products. This suggests that it is no mere coincidence that early *Homo* is the first of the hominines to be associated with significant amounts of animal bones in the sites in which it is found.

The connection between this necessary change in diet and the origin of language comes through the mechanics of mastication. A diet rich in animal products would not only be easier to digest but also easier to masticate. Early *Homo* is the first of the hominines to show a significant reduction in not only the size of the dentition (McHenry 1988) but also the size of the mandible in relation to body mass. Duchlin (1990) has demonstrated that the geometry of the mandible is crucial to the production of sounds used in human speech. It must be shaped in such a way as to give the muscles that move the tongue proper leverage to position it within the oral cavity in the variety of ways necessary to produce the sounds employed in all human speech. The long and relatively narrow mandible of the chimpanzee precludes such movement of the tongue while the mandible of *Homo erectus* is short enough, deep enough and broad enough to potentially allow the proper muscle leverage. Therefore, the change in diet which accompanies the expansion of the brain in early *Homo* is directly associated with an change in mandibular geometry which facilitates the production of the sounds necessary for human speech. Dietary change can also feed back to brain expansion. High quality diets require increased complexity of foraging behaviour and this would be expected to be another selective pressure for brain enlargement (Aiello & Wheeler 1995; Milton 1995).

THE LINGUISTIC ABILITY OF *HOMO ERECTUS*

By time of the appearance of early *Homo erectus*, the hominine line had experienced a unique set of circumstances that resulted in a series of interconnected adaptations, providing the foundation for both verbally based communication and further cognitive development. But what were these hominines like? How similar or different were they to modern humans in their linguistic and cognitive abilities? The material remains that they left behind suggest they were considerably different from any modern humans. Perhaps most obviously, there is no clear evidence in the fossil record of symbolic behaviour at this stage of human evolution. The only features that have been interpreted in this fashion are the beautifully fashioned bi-facial tools called hand axes that are part of the Acheulian tool tradition that lasted from about 1.4 million (Asfaw *et al.* 1992) until about 150,000 years ago (Gowlett 1992). Schick & Toth (1993) argue that these stereotypic tools may indicate that low levels of symbolic communication or language skills were used to enhance or solidify the ideas that underline their production. However, they also suggest that because of the stylistic uniformity of these tools over almost 1.5 million years *Homo erectus* may have relied primarily on imitation and not verbal instruction. The only thing that is reasonably sure is that there appears to be a marked absence of innovation in material culture throughout the long duration of the Acheulian. Furthermore, although fire was known (Bellomo 1994), there is no evidence of its consistent use and there is only controversial evidence of the construction of shelters. It is perhaps not a coincidence that this period of stasis in material culture correlates with the long period of time where there is little or no significant increase in brain size (Figure 1) (Rightmire 1981; Leigh 1992). It is true that *Homo erectus* was the first hominine to move out of Africa and into Asia and Europe. However other carnivores such as lions, leopards and hyenas also moved out of Africa at about the same time. The geographical expansion may have had more to do with the hunting skills of *Homo erectus* than with any particular increase in intelligence, language or cognitive ability (Schick & Toth 1993).

There are also two features of the anatomy of the most complete *Homo erectus* skeleton that suggest vocally based symbolic communication may not have been developed beyond the most rudimentary stage at this time. This skeleton (KNM-WT 15000) is from the West Turkana region of Kenya and dates to about 1.6 million years ago (Walter & Leakey 1993). Importantly, it lacks the expansion of its neural canal in the mid-thoracic region of its spinal column (MacLarnon 1993). The mid-thoracic expansion is unique to humans and is thought to relate to the local enervation of the thoracic and abdominal muscles which would be associated with fine control

of respiration. This is highly important in the context of sustained vocalization associated with human speech. The fact that KNM-WT 15000 lacks this expansion suggests that it had not yet developed the muscular control that would be associated with human language.

KNM-WT 15000 is a juvenile male and its stage and pattern of development also suggest that hominines at this time may not have developed symbolically based verbal communication (Smith 1993). This idea is based on the inference that *Homo erectus* growth and development may have lacked the adolescent growth spurt that is characteristic of modern humans. The inferred dental age at death of KNM-WT 15000 (10–11 years) does not correlate with its inferred age based on epiphyseal closure (13–13.5 years) or stature (15 years). The fact that age inferred from epiphyseal closure (and stature) is in advance of dental age suggests that the growth of the skeleton is in advance of dental development, a pattern found in living chimpanzees which lack the adolescent growth spurt. Bogin (1988, 1990) has suggested that the function of the adolescent growth spurt is primarily to reduce the rate of growth of children to keep them in a greater state of dependency for a longer period of time to facilitate the transfer of symbolically-based cultural knowledge. The inferred absence of the growth spurt in *Homo erectus* may therefore also suggest the absence of symbolically based learning in this species (Smith 1993).

These speculations suggest that although better pre-adapted to symbolically based verbal communication than any other primate, *Homo erectus* was yet to develop true human language. Its terrestrial and bipedal heritage may have preadapted it to increased vocalization, but evidence of syntactic and symbolic skills, with all of their cultural manifestations, is lacking. It is a fallacy to view *Homo erectus* simply as a transition to ourselves. This stage of human evolution represents a long standing, and highly successful hominine adaptation. Perhaps the most significant unanswered question in human evolution is why *Homo erectus* ultimately gave way to larger brained and cognitive more advanced hominines.

COGNITIVE AND LINGUISTIC EVOLUTION AFTER *HOMO ERECTUS*

Increased cognitive ability accompanied by symbolic and syntactic verbal language has generally been viewed as being such an advantage to human adaptation that the evolution of these features need little explanation. But the considerable costs of larger brain sizes and verbally based symbolic communication need to be weighed against the benefits of information transfer and increased social cohesion. When this is done the increase in

brain size (and by inference cognitive capacity and linguistic ability) that gets underway midway through the Middle Pleistocene period seems all the more remarkable.

There is one major cost of increased brain size and another of symbolically based verbal communication that undoubtedly not only radically changed the social organization of the hominines but also set up a feed-back loop which continued to select for increased cognitive ability throughout this time period. Increased brain size would place an increasing metabolic cost particularly on the females (Foley & Lee 1991; Leonard & Robertson 1992). Power & Aiello (in press) have argued that the Middle Pleistocene increase in hominine brain size would have increased this stress to the point that it would have required considerable paternal investment in the offspring to insure survival. This necessity for long term paternal investment could have marked the beginning of modern human family social organization. It also could have been one of the important factors underlying the origin of human ritual symbolism (Knight *et al.* 1995; Power & Aiello, in press).

Whether symbolically based verbal language evolved in response to the postulated changes in hominine inter-gender social organization (Power & Aiello, in press) to other factors involving general social cohesion and information transfer (Aiello & Dunbar 1993) or to a combination of these, language also had a major cost. It escalated the possibility of cheating which potentially could have significantly lowered individual reproductive fitness. As a result, it would have increased the selection pressure on the development of cognitive ability and particularly on the development of one's ability to reflect on one's own mental states and those of others. From this perspective it may be no coincidence that the human prefrontal cortex is responsible not only for this ability which is considered by some researchers to be unique to humans (Povinelli & Preuss 1995) but also for many features of language production and comprehension.

We have very few clues as to why brain size began to rapidly increase in the middle part of the Middle Pleistocene and why, by inference, the linguistic and cognitive abilities of our ancestors also began to change. The only thing that is apparent from the fossil record is that the long stasis in the Acheulian culture also begins to break down about 250,000 years ago when improvements in manufacturing techniques and specialization of flake tools that foreshadowed the later Mousterian and Middle Stone Age traditions began to appear (Gowlett 1992). This is undoubtedly a consequence of increased brain size (and inferred intelligence) rather than a cause. One of the best explanations at the present time for the increase in brain size is that it was in response to the necessity for increased group size, the same explanation put forward for the earlier Lower Pleistocene increase in brain

size (Aiello & Dunbar 1993). Over the long period of *Homo erectus* existence a virtually imperceptible annual increase in population numbers could produce a seeming population explosion (Foley, in press). As a result, living group size may have been forced to increase in response to population numbers in an 'evolutionary arms race' to provide protection against other human populations (Alexander 1989; Aiello & Dunbar 1993). A related possibility might have to do with the dispersed nature of human populations and the advantages of a nomadic or migrating lifestyle. This may have been increasingly important as the hominines adapted to more severe habitats in the later Middle and early Upper Pleistocene.

CONCLUSIONS

In the context of the long time span of human evolution, the last quarter of a million years in which human brain size, cognitive and linguistic abilities reached their modern norms is a relatively very short time. The arguments present here suggest that although the foundations for human language and cognition extend back over the past 4 to 5 million years of human evolutionary history, during the great majority of this period hominines did not possess either the cognitive or the linguistic talents that we would recognize as human. A terrestrial lifestyle and bipedal locomotion provided our evolutionary ancestors with unique preadaptations to human cognitive and linguistic ability, but it was not until the middle part of the Middle Pleistocene period that the increase in absolute brain size and escalating change in material culture suggest that human abilities may have at last begun to appear.

In trying to understand the reasons behind human cognitive and linguistic evolution we also have to recognize that anatomically modern humans were not the only large brained hominine in existence. Up until as recently as 29,000 years ago Neanderthals were still present in Spain at the site of Zafarraya. Neanderthals were therefore co-existing with anatomically modern *Homo sapiens* that first appeared in Europe about 40,000 years ago and in Africa and the Near East about 100,000 years ago (Aiello 1993). The inferred behavioural differences between Neanderthals and modern humans attest to the fact that selection for increased brain size alone did not necessarily presuppose the development of human cognitive and symbolic abilities. Although there are no physical reasons why Neanderthals could not have produced human language, the difference in material culture between Neanderthals and Upper Palaeolithic modern humans suggests that there were marked differences in their cognitive abilities. The conclusion that can be drawn from this is that, building on the exaptations of our *Homo*

erectus ancestors, human cognitive and linguistic abilities most probably had as much to do with the particular social environment in which brain expansion was taking place as with the brain expansion itself.

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