Evolutionary ecology of spoken language: co-evolutionary hypotheses are testable

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Abstract

Evolutionary ecological frameworks can give us new insights into the emergence of human adaptations such as language and cultural learning. There now exist several well-specified models of the social and ecological conditions in which the human capacity for language came under strong positive selection pressure. We critically review them, and ask how we can test them using archaeological evidence. We identify a series of critical archaeological and palaeontological parameters whose values we must know if we are to discriminate among competing hypotheses of the evolutionary ecology of language.

Keywords

Evolution of language; speech; vocal tract; group size; sexual selection; life history strategy; co-evolution.

Introduction

The questions of why and when language evolved in humans, and of why it did not in other branches of the primate order, have occupied researchers from a wide variety of disciplines, especially over the last few decades. Much work has been carried out on non-human primate vocal communication systems, on human brain evolution, on the evolutionary anatomy of human speech and, more recently, on possible selection pressures related to hominin social strategies (Knight et al. 2000).

Taken alone, no one of these approaches can hope to supply the answers sought. The evolution of language could not have occurred without the co-option of highly complex anatomical and neurological systems to a degree not seen elsewhere in the animal kingdom. But language, more than that, is also a social tool, and this context must be considered to be at least as important when determining the selection pressures for its emergence. This context can be studied using the methods of evolutionary ecology, which

may be described as 'the application of natural selection theory to the study of adaptation and biological design in an ecological setting' (Smith and Winterhalder 1992: 5). This paper will address these issues in an attempt to create a more coherent synthesis of current research into this problem, and to identify the crucial parameters from each area of study that must be defined in order to understand the social context of language evolution.

The first task is to address the emergence of language as a product of natural selection and therefore under the influence of a variety of environmental pressures over the course of evolutionary time. This idea has not been without its controversy, most notably tackled by Pinker and Bloom in an insightful 1990 paper. To many researchers, language has not appeared to show any genetic variation, to exist in any intermediate forms or to confer an obvious selective advantage; and it seems to require more evolutionary time and genomic space than is available (Pinker and Bloom 1990: 707). Prominent opponents of the natural selection impetus behind language are Noam Chomsky and Steven Jay Gould, who both argue that language may be simply a 'side effect' of other evolutionary forces such as an overall increase in brain size (Pinker and Bloom 1990: 708). Gould specifically suggests the term 'exaptation' (Gould and Vrba 1982) to describe the process whereby new uses are made of parts that were originally adapted to some other function (Pinker and Bloom 1990: 709). However, structures produced entirely by non-adaptive mechanisms are generally one-part or repetitive shapes or processes that correspond to simple physical or geometric laws. Spandrels, exaptation and other explanations are the bases of what natural selection has to work with (Pinker and Bloom 1990: 710).

Language has specific features that appear to be highly adaptive. For all the things that a speaker may wish to do with language, such as talk about events and states, distinguish the participants in the event or state according to role, or comment on the time and duration of an event or state, grammar is able to provide that ability. It can map propositional structures onto a serial channel, minimizing ambiguity in context while constrained by the need for high-speed encoding and decoding, according to a code shared by an entire community of potential communicators (Pinker and Bloom 1990: 713). In order for this to have resulted from natural selection, there must have been variability among individuals in terms of their grammatical competence, and the process from no language to language as we speak today must have been gradual, with each step being small enough to have stemmed from a random mutation which conferred enough advantage to have been fixed into the population. Pinker and Bloom argue that our current knowledge of language and of evolution make each of the above postulates plausible (1990: 721).

Moreover, language has costs. Physically, it has been suggested that the distinctive human trait of a lowered larynx in the throat has incurred a higher risk of death from choking, as the downward movement has caused us to lose the ability to swallow and breathe at the same time (in human babies and chimpanzees, the larynx is high enough for the soft palate and epiglottis to meet and close off the trachea while liquid flows harmlessly down the oesophagus (Laitman et al. 1978: 467–8)), as the pharynx is a common pathway for food, liquid and air in human adults (Lieberman et al. 1972: 291). However, it has been suggested recently (Clegg and Aiello 2000: 126) that this increased risk of choking may have been exaggerated somewhat, as it was found that overall mortality from choking on food over the last 100 years averaged 0.6 per 100,000 head of the population.

There are social costs too, perhaps of a more significant nature than the one suggested

above. Language may allow an individual to become part of a social group, through the exchange of information and common symbolic understanding, but this comes at the often-overlooked consequence of being 'locked' into a speech community. When individuals learn a language, they 'construct their system of verbal behaviour to resemble that common to the group or groups with which [they] wish from time to time to be identified' (LePage 1968: 192). The development of dialect and linguistic diversity may function to constrain human mobility. The 'free rider', who moves ruthlessly and exploitatively from group to group, 'could not possibly survive in populations where each local group had its own language or dialect. Each group would be able to tell by his speech that he was an outsider and where he came from' (Nettle and Dunbar 1997: 98).

For language to have developed in the way it did, there must therefore have been social preconditions, as well as the necessary physical modifications. As a social adaptation, language equips individuals with the ability to transfer and receive information, including about people, objects and places not present, and to manage relationships with other individuals. It is likely that anatomical specialization for language evolved in tandem with the social context of language use, as part of a gene-culture co-evolutionary process.

Both sides of the foregoing debate (Pinker and Bloom versus Chomsky and Gould) take it as axiomatic that natural language structure has a genetic basis. An important alternative perspective is the self-organizing systems approach, which argues that a language community is a complex adaptive system in which 'language behaviour becomes canalized because the more members of a community adopt the same convention, the stronger the convention will become' (Steels 1997; see also Kirby (2001) for a recent 'self-organizing' perspective). In this approach, there is no genetically-encoded 'language organ' (whether or not the subject of natural selection); rather, natural language features become fixed by conventionalization, and the evolution of language is in this sense a side effect of cultural transmission and adaptation underwritten by an innate general substrate of cognitive, perceptual and motor abilities. A synthesis of the genetic and the self-organizing perspectives is, however, provided by the hypothesis of a 'Baldwin effect', in which – as language emerges through self-organization and becomes perpetuated by cultural transmission – individual variability in features advantageous to language production and comprehension becomes subject to natural selection, leading to 'genetic assimilation' of linguistic structures.

For our purposes here, the difference of perspective between those favouring a 'language organ' and those favouring genetic assimilation is secondary. In each case, some model of hominin social dynamics is a prerequisite for the emergence of linguistic structure and its anatomical underpinnings. The pure self-organizing perspective (without genetic assimilation) we take to be refuted by numerous independent lines of evidence for adaptation in the vocal production system, reviewed below. The aim of this paper is to determine these social preconditions and how they must have interacted with the evolution of human anatomy in order to make the emergence of language possible, if not inevitable. This will be achieved through the study of independent markers in the fossil and archaeological records of social system evolution and of language/speech evolution (noting that 'language' refers to the cognitive capacity while 'speech' implies the physical ability). By determining the visibility of relevant parameters for language-social system

co-evolution, we hope to highlight areas that need to be further investigated through archaeological research.

Social models of language evolution

Numerous recent studies have proposed social preconditions for the evolution of language (summarized in Table 1). We have organized them along three major dimensions of social variability; they are parenting strategy, status and rank, and co-operation. It seems to us that models can be differentiated according to the emphasis they give to, respectively, the evolution of extended provisioning networks and the costs of rearing large-brained offspring; the sexual selection of high linguistic competence in preferred mates; and the co-evolution of language and social co-operation in stable social groups. In order to simplify our analysis, we shall caricature the options in terms of three extreme models.

The first set of models emphasizes the stabilization of kinship networks and the extension of provisioning effort for the rearing of offspring to include both males and female kin (e.g. 'grandmothers'). In this model, the effectiveness of alliance networks enables a mother to rely on other individuals, envisaged as close kin relations, to assist in the provisioning and nurturing of the female's offspring. The supposed benefit of such a situation is to ensure gene survival over multiple generations. Language serves both to optimize the task of co-operative food search and to enforce social contracts linking provisioning effort to reproductive success.

In the second set of models, the emphasis is on sexual selection of mates who are either verbally adept or who are able to communicate information that is useful to other members of the group. In its extreme form, such a model would see linguistic interaction as a competition for social dominance and for consequent preferential access to fertile mates.

In the third set of models, language is seen as dependent on the co-operative interactions of members of the proto-linguistic community. In one extreme form, it has been suggested that language evolved as a time-efficient means of servicing affiliative relationships in groups whose size had become too large for social grooming to have remained an effective strategy for social cohesion.

We may note at once some significant contrasts in the predictions derived from each such group of models. In the kinship-oriented models, there is no supposition of unusually large group sizes, while the emphasis on parenting effort precludes any emphasis on intense male-male competition for mating opportunities (which would tend rather to favour adaptations to mating effort). In the competition models, the emphasis is on verbal displays of reproductive fitness, and the expected correlate would be intensified agonistic interactions among members of the same sex and an emphasis on mating rather than parenting effort. In the group size models, the emphasis is on social manipulation in increasingly complex social groups under time constraints, and there is no assumption of any linkage either to more intense parenting effort and co-operative provisioning or to more intense mate competition.

Table 1 Models of the social context for spoken language evolution

<i>Factor</i>	<i>Principal exponents</i>	<i>Theoretical position</i>
<i>Parenting strategy</i>	Cavalli-Sforza and Feldman (1983)	Cultural interactions within the nuclear family can be important in fostering the evolution of communication.
	Deacon (1997)	Language co-evolved with the need for enforceable social contracts committing males to invest parenting effort in the rearing of costly offspring.
	Knight (1996), Power and Watts (1996)	Metaphorical language (symbolism in the special sense used by symbolic anthropologists) originated in female coalitionary behaviour, as performed through symbolic rituals to guarantee male parental investment in the rearing of costly offspring.
	Nowak et al. (1999)	Parental learning and role model learning are effectively indistinguishable. With language, children inherit a device for acquiring a language from others in the population. Thus, the language that they learn depends on what others are doing and is therefore frequency dependent.
	Livingstone and Fyfe (2000)	A communication system with costs can evolve only among individuals with high levels of shared experience (close kin).
<i>Status/rank</i>	Burling (1986)	Leaders are admired for their linguistic skills; better speakers become leaders and leaders raise more children.
	Mazur and Cataldo (1989)	Dominance and deference are a normal part of human and primate social interactions, and a feature of conversational exchanges.
	Dunbar (1993, 1996); Aiello and Dunbar (1993)	Conversational language was an efficient mechanism of affiliation and social bonding in increasingly large and complex hominin social groups.
	Dessalles (2000)	Within-group coalitionary behaviour gives advantages in between-group competition; status became related to the communication of information relevant to the interests of other group members.
	Locke (2001)	Initially, the performative functions of vocal displays in promoting rank and relationships facilitated conflict avoidance and resolution, collaboration, and reciprocal sharing of needed resources. This led to the elaboration of the speech communication system.
	Gil-White (2002)	Natural selection favours preferential imitation of individuals with above-average quality of information, such that the distribution of variance in prestige (freely conferred deference) co-evolves with language and social transmission.

Table 1 Continued

<i>Factor</i>	<i>Principal exponents</i>	<i>Theoretical position</i>
<i>Co-operation</i>	Steels (1998)	Many features of natural language may emerge as the communication patterns of interacting agents evolve towards stability. An experimental set-up consisting of two robotic heads that watch static or dynamic scenes and engage in language games, in which one robot describes to the other what they see, elicited the emergence of distinctions, of a lexicon and of primitive syntactic structures.
	Nowak and Krakauer (1999)	Signal-object associations form only when information transfer is beneficial to both speaker and listener. Otherwise, communication requires co-operation between individuals. Thus, co-operation may be a prerequisite for language.
	Bickerton (2000)	Symbolic reference emerges from stimulus-stimulus linkages and is latent in many animals, while syntax emerges from the argument structures inherent in the social calculus associated with reciprocal altruism. The large quantities of neurons unique to <i>Homo</i> permit more complex message structures, and longer and more complex trains of thought.
	Grassly et al. (2000)	Social or geographic structuring of populations promotes the stability of small sign communities and consequently fosters lexical diversity. Population structure can ensure the stability of sign systems even in the face of deceit. This is because pay-offs are determined by local interactions, thereby promoting the emergence of co-operative or honest sign systems through a mechanism of repeated encounters.
	Lachmann et al. (2001)	Recent game theoretic models have shown that several key features of language could plausibly arise and be maintained by natural selection when individuals have coincident interests. However, honest signalling can evolve even when interests conflict, and fully coincident interests are not a prerequisite for linguistic communication.

The evolution of hominin social systems

We now turn to a consideration of the anatomical and archaeological evidence for the evolution of hominin social systems. Again, these diagnostic markers may be clearly separated into three distinct emphases: parenting strategy; competition level; and group size (see Tables 2 and 3). The division into anatomical and archaeological evidence allows us to assess the different pressures focused on in a range of models.

Classically, palaeoanthropologists emphasize the evolution of life history in the hominins, with an emphasis on the implications of encephalization for maternal energetic costs in child rearing, and thus for parenting strategy. Large brains imply extended periods of immaturity (secondary altriciality), while the prolongation of foetal brain growth rates into the first year of postnatal life imposes a substantial energetic burden on lactating mothers. One of the major questions in hominin evolution relates to the timing of the evolution of cultural strategies for extension of provisioning effort to others than the biological mother. Similarly, much archaeological work has focused on the question of whether or not early African Palaeolithic sites represent home bases or central places to which foragers brought food resources (notably, animal carcass elements) for sharing, as a proto-human strategy (in Isaac's (1989) sense) of group provisioning.

With respect to intensification of mate competition, hominin fossil anatomy points to a reduction in adult sexual dimorphism of body mass and canine size (and hence of male-male competition), which does not suggest that male-male competition for mates was a driver for the evolution of social communication strategies. In the archaeological record, Kohn and Mithen (1999) have argued that Lower Palaeolithic handaxes – the first clearly elaborated and standardized stone artefact tradition – served to advertise the fitness of their makers in a context of intense male-male competition. However, Steele (1994) has suggested, on the basis of simulations of cultural diffusion, that stability of artefact form in space and time of the order seen in the Acheulean handaxe tradition implies functional adaptiveness in their design. Shennan and Steele (1999) have proposed that the cultural transmission of complex craft skills is a form of parental investment in the extractive foraging capability of offspring, such that the handaxe tradition – if it gives functional advantages to its practitioners in food processing – should be seen not as a sign of runaway sexual selection of a non-adaptive cultural display, but as a sign of increased parenting effort. Thus, the archaeological evidence for intensification of mate competition hinges on the interpretation of this artefact tradition as involving non-adaptive investment in standardization, elaboration and symmetry of form. If such traits give a functional advantage in extractive foraging tasks (notably, animal carcass resource processing), then Kohn and Mithen (1999) are refuted.

With respect to group size and the 'vocal grooming' argument, testing the hypothesis relies upon the single anatomical marker of relative neocortex size, as predicted from endocranial volume, which is intended to stand as a proxy for average group size and social complexity, and hence as a marker for the number of social relationships that an individual can keep track of. However, it has been shown (Steele 1996) that the correlation between endocranial volume and social group size in primates is fairly weak, to the extent that hominin group sizes cannot reliably be predicted from brain capacity measures.

Table 2 Diagnostic markers for the evolution of hominin social systems: anatomy

Factor	Anatomical trait	Key contributors	Theoretical position
Group size	Absolute brain size	Dunbar (1993, 1996), Aiello and Dunbar (1993), Steele (1996)	In primates, average group size is positively correlated with relative neocortex size (and thus with absolute brain size); in hominins, by the appearance of early African <i>Homo</i> , group sizes (as predicted from cranial capacity) would have crossed a threshold beyond which language was the only viable mechanism of relationship maintenance. However, the prediction equations used to derive these estimates are subject to very considerable error.
Competition level	Sexual dimorphism of body mass and canine size	McHenry (1996), Plavcan (2000)	In primates, the degrees of adult sexual dimorphism in canine size and in body mass correlate with levels of mate competition. In hominin evolution, canine reduction is an early-appearing trait. Paradoxically, early Australopithecines (<i>A. afarensis</i>) had high body mass dimorphism, but this diminished by the time of appearance of <i>Homo ergaster</i> . This implies relatively low levels of mating competition in the genus <i>Homo</i> .
Parenting strategy	Life history traits, relative brain size	Kaplan et al. (2000), Clegg and Aiello (1999)	The energetic costs of rearing large-brained offspring mandated a social shift favouring provisioning effort by male parents and/or by kin of the mother. Hunting of large packets of high-quality animal food may have provided the basis for this expansion of the care-giving network, and modern human growth patterns may have originated with <i>Homo ergaster</i> .

Table 3 Diagnostic markers for the evolution of hominin social systems: archaeology

Factor	Archaeological marker	Key contributors	Theoretical position
Group size	Site area (no. of hearths, etc.)	Hassan (1981)	Forager band sizes averaged twenty persons during the Pleistocene.
	Lithic transport distances as a marker of group range area	Foley (1987), Steele (1996), Gamble and Steele (1999), Leonard and Robertson (2000)	Lithic raw material transfer distances (from rock outcrop to site) indicate a progressive expansion of home ranges during the Palaeolithic, although it is unclear how far this was determined by increasing group mass as opposed to shift into a higher (carnivore-mode) trophic level.
	Stable transmission of skilled tool-making traditions	Mithen (1994, 1996)	Large group sizes with high intensity of social interaction may have promoted the stable social transmission of highly skilled technological traditions (such as Acheulean handaxe manufacture).
Competition level	Elaboration of skilled artefact production as a display of male fitness	Kohn and Mithen (1999)	Handaxes are pervasive in the archaeological record because throughout the Pleistocene hominids frequently lived in large, socially complex and competitive societies in which sexual selection pressures and inter-male competition for mates were intense: handaxes functioned in the social domain as indicators of health and intelligence and as aesthetic displays.
Parenting strategy	Lithic and animal bone accumulations indicating repeated occupancy of a site	Isaac (1989), Potts (1992)	Accumulations of stone artefacts and of animal bones from the African Early Palaeolithic may indicate use of a central place by foraging bands analogous to that seen in modern hunter-gatherers, with transport of animal carcass elements to that place as part of a group provisioning strategy. However, plausible alternative hypotheses also exist for the mechanisms of such accumulation.

Table 3 Continued

<i>Factor</i>	<i>Archaeological marker</i>	<i>Key contributors</i>	<i>Theoretical position</i>
	Stable transmission of skilled tool-making traditions	Shennan and Steele (1999)	Ethnographic comparisons show that complex craft skills are predominantly transmitted from parent to same-sex offspring, as a form of parental investment. The involvement of males in such vertical cultural transmission is a hominin innovation that may derive from the increasing role of male hunting in group provisioning.
	Symbolic strategies (ochre use)	Knight (1996), Power and Watts (1996)	Ritualized displays of social solidarity associated with increased male provisioning effort, and originating in the African Middle Stone Age associated with early modern <i>Homo sapiens</i>
	Long-distance transport of artefacts signifying long-distance alliances	Gamble (1996, 1998)	Social network extension as a risk-buffering mechanism, associated with the cultural construction of kinship categories, and originating with early modern human societies in marginal environments.

The archaeological evidence for hominin social group sizes includes site area and the number of hearths, and home range area (as a function of group biomass). The first of these sources relies on the supposition that a greater number of hearth sizes indicates a larger social grouping and therefore an opportunity for language evolution, if the 'vocal grooming' hypothesis is followed. This may not be a wholly reliable estimator of the level of activity on a site, as the habitual use of a site by a particular group over time will ultimately expand the size of the area because of overlap caused by a lack of precision in the location of recurrent activities. However, what evidence we do have suggests that co-residential social groups were relatively small throughout the Pleistocene. Group home ranges, as indicated by lithic transport distances, certainly far exceed those seen in contemporary non-human primates and become progressively greater through the Palaeolithic; however, the possible association with enlarged social groups is confounded by the shift in this period to greater dietary dependence on animals (Gamble and Steele 1999). Carnivores tend to have home ranges an order of magnitude greater than those of primates, while carnivores in high latitudes range yet more widely – due to the sparser concentration of feeding resources respectively at the higher trophic level and in the less productive and more seasonal environments. The reliance on animal-based protein and hunting would have selected for smaller, more mobile groups, overall reducing the plausibility of the evolutionary existence of large co-residential social groups, which are therefore an unlikely driver for the evolution of language. Mithen (1994, 1996) has proposed a third source of indirect evidence for large social groups, namely the social transmission of skilled, complex technological traditions. However, the validity of this proposal rests on the correlation between such Lower Palaeolithic artefact traditions and habitat characteristics favouring large social aggregations, and this has been undermined by demonstrations of the occurrence of the artefact traditions in environments antithetical to those which Mithen suggests would have selected for intense sociality (McNabb and Ashton 1995; McNabb 1996).

Thus, it remains to conclude that the most plausible social explanation for the evolution of language is intensely negotiated co-operation within small stable groups, based on family or kinship ties. Language enhances efficiency in co-operative foraging tasks, particularly where this involves monitoring resource condition across dispersed patches at large space scales ('topographic gossip', Widlok 1997), or where this involves the social transmission of categorical distinctions that enable discrimination of food items by their nutritional value (Cangelosi et al. 2000). Language also enables the negotiation of food sharing – according to Eibl-Eibesfeldt (1989: 525–6), the majority of all !Kung conversations centre on food, and many ethnographically documented food conversations are concerned with social aspects – 'who gives what to whom, and criticisms of those who do not share their food'. Social stability is reinforced by the symbolic development of classificatory kinship terms that discriminate between degrees of relatedness and therefore degree of co-operation. Language is consequently vital to distinguish between members of the kinship group and the importance of their relatedness to an individual – and the social contracts that are entailed in relations between individuals of defined kinship categories.

Evidence for the capacity for language

Finally we come to a review of the anatomical and archaeological markers for the evolution of language (see Tables 4 and 5). The existing literature remains unclear over the nature of the adaptations that took place in hominin evolution. There is no consensus over whether the brain underwent remodelling in favour of selection for language or whether existing elements were co-opted or modified from existing functions. This pits the idea of a novel 'language organ' against the observed conservatism of the mammalian brain, and anatomical studies so far have not identified a unique language-related structure within the human brain that would be preserved in fossil hominids, so the argument must continue for the time being. Perhaps the clearest indicator available that there has been some kind of significant reorganization (whether quantitative or qualitative) of the human brain is lateralization of function, seen in human population-level right-handedness (McGrew and Marchant 1997). No other primate demonstrates the human condition to anywhere near the same degree, and it is sometimes argued that this is an artefact of selection for a specialized speech area in the left hemisphere. Predominant right-handedness is evident as far back as *Homo ergaster*, and certainly by the time of the Neanderthals. However, and perhaps paradoxically, the brain morphological asymmetries that have been associated with this functional trait do not appear to be evolutionarily novel in the hominin line (Steele 2000, in press).

While evidence for language selection within the brain is not easy to interpret, it is more clearly seen that other features of the anatomy necessary for speech in its modern form were under natural selection. Traits of the human vocal articulatory system that have been interpreted as the focus of past selection pressures include vocal tract morphology (the descended larynx), speech-related musculature (the presence of slow tonic muscle fibres in the larynx, pharynx and tongue) and motor innervation of speech-related structures including the thoracic wall, tongue and jaw. These traits are interrelated: for instance, the denser motor innervation of the tongue is matched by the variance between humans and chimpanzees in the angles of inclination of the tongue and larynx muscles, which limit the number and quality of articulatory target areas that the chimpanzee tongue can reach, when compared to humans (Duchin 1990). Studies of fossil hominin anatomy indicate the emergence of these adaptations within the genus *Homo*, although debate continues regarding individual traits' presence or absence in *Homo ergaster*, *Homo erectus* and Neanderthals.

The descent of the human larynx is considered crucial to the investigation of language evolution because it creates a pharyngeal cavity separate from the buccal cavity, with the result that a greater range of vowel sounds can be produced. The position of the hyoid bone is a marker of laryngeal position and thus of vocal tract morphology. However, there have been difficulties in reconstructing the condition in past hominins. The supralaryngeal vocal tract does not fossilize, but it is thought to be affected by the degree of flexion of the basicranium. It appears likely that the basicranium was not flexed to a sufficient degree until the emergence of *Homo sapiens*, but it should not be assumed that this automatically means that Neanderthals were incapable of speech: evidence suggests that cranial base flexion is not a reliable predictor of hyoid position in humans or other primates, and so cannot be extrapolated back into the past.

Table 4 Diagnostic markers for the evolution of language: anatomy

Factor	Key contributors	Theoretical position
<i>Brain – size of neocortex and its lobes</i>	Deacon (1988a, 1988b)	When cortical structures are related to nuclear, humans deviate from the primate trend, with cortical structures proportionately larger than nuclear ones; humans have twice as much prefrontal cortex as expected from non-human primate scaling trends, as a function of relative brain enlargement.
	Rilling and Insel (1999)	The human prefrontal cortex is considerably more gyrified than expected for a non-human anthropoid of the same brain size.
	Finlay and Darlington (1995), Finlay et al. (2001)	The order of neurogenesis is highly conserved, with disproportionately large growth in late-generated structures as brains enlarge; human cortical structures are no larger than would be expected for a primate of our absolute brain size.
	Semendeferi and Damasio (2000)	There is homogeneity in the relative sizes of large sectors of hominoid brains, and the human frontal lobe is not disproportionately enlarged.
	Bookstein <i>et al.</i> (1999)	Frontal lobe external curvature comparable to that of modern humans found in cranial vault analysis of hominins throughout the last 0.5 million years, including Neanderthals.
<i>Brain–laterality</i>	Steele (1998, 2000, in press)	Human morphological brain asymmetries are conserved hominoid features, but human functional asymmetries are derived and may relate to selection for lateralized speech processing. Skeletal adaptations to loading suggest an emergence of predominant right-handedness in <i>Homo ergaster</i> , and its clear presence in Neanderthals.
	Buxhoeveden and Casanova (2000)	The columnar arrangement of human Tpt in the left hemisphere is unique. No fossil anatomical correlates.
<i>Brain–cranial motor nerves</i>	Kay <i>et al.</i> (1998), DeGusta <i>et al.</i> (1999)	Humans have relatively enlarged hypoglossal nerves (as indicated by the size of the hypoglossal canal), suggesting denser motor innervation of the tongue as a speech adaptation, and this enlargement is seen first in Neanderthals and archaic <i>Homo sapiens</i> . Disputed by DeGusta <i>et al.</i>
	Coward and Steele (n.d.)	Humans have a relatively marked enlargement of the mandibular branch of the trigeminal nerve, but not of the facial nerve (as indicated respectively by the sizes of the foramen ovale and of the stylomastoid foramen), suggesting denser motor innervation of the muscles of mastication as a speech adaptation. Traits not yet examined in fossil material.

Table 4 Continued

Factor	Key contributors	Theoretical position
Oral cavity	Duchin (1990)	Chimpanzees cannot articulate because their tongues cannot reach target areas, due to inclination angles of muscles; however, <i>Homo erectus</i> , Neanderthals and modern humans have relatively similar oral cavity morphology.
Supra-laryngeal vocal tract (larynx and hyoid)	Lieberman (1984), Lieberman <i>et al.</i> (1992)	The distinctively human lowered larynx creates a pharyngeal cavity that is separate from the buccal cavity (the oral cavity bounded on the sides by the cheeks); this configuration permits the production of a greater range of vowel sounds (and thus greater generativity in phonological elements of the speech signal). Basicranial flexion is a hard tissue marker of this trait, and is present in human form in some <i>Homo sapiens</i> but not in Neanderthals.
	Houghton (1993), Arensburg (1994)	No reason to suppose on the basis of head and neck morphology that Neanderthals had less linguistic capability than modern humans.
	Lieberman (1994), Lieberman <i>et al.</i> (1998)	Analysis of the Kebara hyoid (Neanderthal) cannot be used to reconstruct the fossil's supralaryngeal airway; variations in cranial base flexion do not predict hyoid position in humans or other primates.
Laryngeal musculature	Han <i>et al.</i> (1999), Sanders (2002)	Slow tonic muscle fibres in the human larynx, pharynx and tongue may represent an adaptation for speech. No fossil anatomical correlates.
Pulmonary function	MacLarnon and Hewitt (1999)	Modern humans and Neanderthals have an expanded thoracic vertebral canal compared with australopithecines and <i>Homo ergaster</i> , suggesting selection for enhanced control of 'speech breathing'.

Table 5 Diagnostic markers for the evolution of language: archaeology

Factor	Key contributors	Theoretical position
<i>Technological analogy: skilled motor control</i>	Toth (1985), Ludwig and Harris (1994), Pobiner (1999)	Pattern of flaking shows clockwise core rotation, to imply right-handed knapping, in assemblages from the African Lower Pleistocene, although experimental work shows that there are complicating effects of expertise level and of inter-session variability. May imply selection for language lateralization in <i>Homo ergaster</i> .
	Semenov (1961, 1964)	Right-handed preference in use of bone retouchers by Middle Palaeolithic hominins in Europe (Neanderthals).
	Steele <i>et al.</i> (1995)	Fine motor control (as seen experimentally in knapping of highly standardized artefacts) may be a marker for potential levels of articulatory control in speech, due to common neural substrates.
<i>Technological analogy: generativity</i>	Isaac (1976), Gowlett (1996)	Rule systems – determining elaboration and differentiation of artefact forms – become increasingly complex through the Pleistocene.
	Wynn (1991)	Rule systems for the production and use of tools are not reliable markers of grammatical competence.
<i>Technological analogy: imposition of arbitrary form</i>	Dibble (1989)	Imposition of arbitrary form on raw materials in artefact production does not indicate symbolic language capabilities in Middle Palaeolithic hominins, since much of the variability previously interpreted as due to typological distinctions and mental templates may simply reflect stages in the use-life of artefacts.
<i>Effects of language use</i>	Ohnuma <i>et al.</i> (1997)	Levallois reduction techniques can be acquired by human novices through observation and imitation of experts, without verbal tutoring; thus this lithic tradition is not a reliable marker of the presence of language in Neanderthals.
	Gamble (1995), Roberts (1995)	Conversational groups have a distinctive spatial signature; the absence of structured campsites, with hearths and ‘conversation rings’ of debris, indicates that people of the Lower Palaeolithic in Europe did not use spoken language. Disputed by Roberts.
<i>Symbolic culture</i>	Noble & Davidson 1991	The constituent signs of language are used symbolically, so the point of origin of language must therefore be the point at which the symbolic property of signs (i.e. arbitrariness and convention) was first discovered. There are no signs of symbols in the archaeological record prior to about 32,000 years ago, so language according to this definition cannot have existed before then.
	Chase 2001	‘What usually goes under the rubric of “symbolism” is actually two phenomena that are logically separable – referential symbolism, the purely referential use of symbols in communication, and symbolic culture, the creation of complex systems of symbolic concepts, beliefs and values that play a major role in determining how we think and in how we behave. The paleontological record provides evidence concerning the evolution of the former, while the archaeological record provides evidence of the latter. Chronological discrepancies between the paleoanthropological and archaeological evidence for symbolism may simply indicate that the two phenomena did not evolve simultaneously and in tandem’ (Chase 2001:199).

Unfortunately, the archaeological record does little to confirm or deny the presence of language. Technological analogies such as manipulative skill, right-hand preference, symmetry or standardization of form are not direct markers of the emergence or presence of language. While it is possible or probable that there are homologies of skilled movement and of the organization of production in the technological and in the linguistic domains, the evolution of features in the former can tell us only about the potential for elaboration of homologous features in the latter. Directly, they function only to indicate the development of skills, or lateralization, or different methods of tool production. These can tell us only about the priorities of the toolmaker, or selection pressures acting upon the mode of production. As such, they cannot be interpreted as indicators for the presence or otherwise of language.

We are still a long way from reliable recognition of more direct indications of everyday language use in pre-*sapiens* hominin societies, such as evidence for verbal transmission of craft skills or for spatial structuring of campsite activities indicative of conversational spacing. Thus it is the anatomical record of the evolution of articulatory ability, and not the archaeological record of technological traditions, that is most likely to give us reliable controls on the chronology of language evolution.

Discussion

Our review of social models of language evolution has suggested that three extreme variants can be proposed, which focus (respectively) on the social correlates of hominin life history strategy, of intensified mate competition and of increased group sizes. Our review of the anatomical and archaeological markers of social evolution suggests that neither intense mate competition nor the management of affiliative ties in very large co-residential social groups were the drivers of language evolution. We are left with the hypothesis of life history strategy as the prime mover, and co-operative foraging and provisioning as the selective context for spoken language abilities. Our archaeological focus must therefore be on the co-evolution of the human life history strategy and of speech adaptations in the genus *Homo*.

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