The evolution of the human language capacity

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Abstract

The origins and evolution of the linguistic capabilities characteristic of *Homo sapiens* are reviewed. The anatomical and neurological prerequisites for language, and their fossil history, are considered, along with a discussion of the various levels on which selection has shaped the human body, mind, and language, with a synthesis of ideas from biology, neurology, cognitive science, and linguistics. Finally, evidence from the various fields is drawn together to evaluate different theories of language origins, leading to the conclusion that only a subset of the numerous published proposals remain tenable in the face of the evidence.

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1 Introduction

For centuries and millennia, we humans have regarded ourselves as the pinnacle of Creation, placing ourselves closer to our gods than to the other animals on earth. But as we have learnt more and more about animals, we find more and more similarities. The features that have been held up as uniquely human, as proof of the abyss separating us from the animal world, have one by one fallen by the wayside. Human language is one of the very few remaining areas in which it can still be argued that humans are unique in the animal world. No other species has anything remotely approaching our language capability, and many linguists maintain that no other species has any language at all.

Nevertheless, we have overwhelming evidence that we evolved from an ape-like ancestor in just a few million years, and so our language capabilities must have evolved as well, presumably through some sequence of intermediate stages. We share a fairly recent common ancestor with chimpanzees, some five to seven million years ago, and slightly less recent common ancestors with various other primates (reviewed in section 3 below), which provides a starting point for language evolution, but the continuation is not so obvious. Our relatives have their own communication systems, but it is by no means obvious whether any of these are homologous[1] of human language.

The communication systems of some animals, notably monkeys, but also various other, e.g. some rodents, have some basic language-like features, as reviewed in Johansson (2001). For example, the alarm calls of vervet monkeys (Seyfarth et al, 1980) are to all appearances non-iconic and referential, resembling human words. But the other key feature of human language, grammar, is conspicuous by its total absence among the known communication systems of non-humans.

This lack of clear evolutionary transitional forms between non-language and language renders the elucidation of the process difficult, so difficult, in fact, that many scholars have abandoned the problem as intractable, to the point of deriding or even banning any attempt at solving it.

Among linguists, the infamous dictum of the Linguistic Society of Paris in 1866, forbidding speculation on the origin of language (Shupp, 1999; Pinker, 2000), still appears to hold sway in some circles: *"There is a long history of study of origin of language, asking how it arose from calls of apes and so forth. That investigation in my view is a complete waste of time, ..."* (Chomsky, 1988, p 183).

In particular, there has been a remarkable amount of resistance[2] to evolutionary ideas among prominent modern linguists, notably Noam Chomsky (1988;

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[1] "Homologous" is a technical term in biology, roughly meaning "similar due to shared ancestry". It is occasionally used also in linguistic contexts (Pinker, 1998b).

[2] Evolutionary concepts are troublesome not only to linguists. Ferrari & Chi (1998) argue that these difficulties are due largely to the ontological structure of evolutionary explanations, which differs markedly from the event ontology prominent elsewhere in scientific explanations.

1990), but he is far from the only one; see e.g. Piattelli-Palmarini (1989; 2000), Bickerton (1995), Fodor (1998) or the nit-picking in six papers by Botha (1997a; 1997b; 1998a; 1998b; 2000; 2001). A central part of Chomsky's theory of language is a universal grammar, innate in all humans (1965; 1986). This in itself does not exclude the possibility that language evolved (the opposite is argued e.g. by Pinker (1994) and Dennett (1995)), but Chomsky emphasizes the gulf between his system of universal grammar, and any other system of communication, and is openly skeptical about the power of Darwinian evolution to bridge the gap[3], with statements like *"Evolutionary theory is informative of many things, but it has little to say, as of now, of questions of this nature [such as the origin of language]. [...] In the case of such systems as language or wings it is not easy even to imagine a course of selection that might have given rise to them"* (Chomsky, 1988, p 167). Several more quotes in the same vein can be found in Pinker & Bloom (1990). The Chomskian attitude to language is basically Cartesian, with the human language faculty being human-specific, monolithic, and innate (Chomsky, 1990; Mueller, 1996). Taylor (1997) discusses this issue in more detail, comparing Chomsky to the 18th-century Enlightenment philospher Condillac, though Sue Savage-Rumbaugh (1998, p 1) puts it more bluntly: *"Why are we afraid of apes with languages?"*

Other linguists, however, have taken the evolution of language more seriously. Pinker & Bloom (1990) is one seminal paper, followed up by Pinker's (1994) popular book on the subject. But work on the evolution of language within a Chomskian paradigm remains problematic (Uemlianin, 1999). Nevertheless, Pinker (2000) has a point in that *"[t]he study of the evolution of language, ..., has returned to respectability."* [p 441], an observation also made by Carstairs-McCarthy (1996).

Even among those who do work on the issue of language origins, there is a lack of unity of purpose and methods. Linguists often express their disdain or concern when non-linguists tackle the problem: *"We cannot leave the discussion of language origins to those researchers who have yet to understand the concerns of modern linguistics."* (Wilkins & Wakefield, 1995, p27 (online version)). But the issue of language origins is by no means a purely linguistic problem — there is just as much evolutionary biology, neurology, ethology, and social psychology involved. One can equally well reverse the quote: *we cannot leave the discussion of language evolution to those linguists who have yet to understand the concerns of modern evolutionary theory.* Neither aspect can be ignored — both biologists and linguists, and preferably people who understand both fields, are badly needed

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[3] Another aspect of this is "Chomsky's paradox" (Li, 1997), the apparent contradiction between the apparently highly optimized universal grammar, and the generally non-optimized "bricolage" (Duboule & Wilkins, 1999) character of evolved systems (Botha, 1999). But, as Li (1997) shows, this contradiction is only apparent, and not a serious argument against language being a product of evolution. Likewise, Newmeyer (1992) argues that autonomy of grammar does not exclude functional explanations, from which it follows that evolutionary ones are not excluded either. Jackendoff (cited by Botha (1999)) instead resolves the paradox by arguing that language isn't perfect, that it does have the patchwork character typical of evolved systems.

if progress is to be made.

On the biological side, the evolution of language has been discussed on and off ever since the days of Darwin, who proposed a scenario of co-evolution of language and the human brain (1871, chapter 21), remarkably similar to some still-current ideas. The notion of a “language instinct”, in a sense quite similar to the modern Chomskian, can also be found in Darwin (1871), and may well have originated there (Pinker, 1994). In more recent times, the growth of cognitive science, and the first inklings of how the brain actually works, has stimulated research into this area.

I perceive a need for an integration of knowledge from all relevant fields, outside as well as inside linguistics, in a single work. My purpose in writing these theses, the current work together with Johansson (2001), is to bring together the material needed for such an integration, and to take the first steps towards the synthesis needed for a thorough understanding of the evolution of language. Johansson (2001) covered the linguistic and cognitive abilities of our closest relatives, which establishes a starting point for the evolution of human language. Here I cover our own language-related abilities, and move on to discuss the evolutionary path to human language. This thesis may appear dominated by biological issues, but this simply reflects the fact that more data is available on the biological side — I wish to emphasize here that cultural and cognitive issues are likely to have been at least as important as biology for the origin of human language, even though less hard data are available.

The main questions to be addressed in the current work are:

- *The evolution of humans* — what does our general evolutionary history look like, and what implications does this have for the evolution of language? Our family tree, presented in section 3, provides the backdrop against which the story of language origins unfolds, and will enable us to locate important events in time and space, and provide some hints of what the first speakers may have looked like.

- *The bodily equipment needed for language* — what anatomical and neurological structures are necessary bases for the evolution of language, and when did our ancestors acquire them? Which structures were acquired specifically for linguistic purposes, and which ones were had evolved for some other purpose and were later co-opted for language? These issues are addressed in section 4.

- *Hypotheses of language evolution* — among the multitude of hypotheses proposed to explain the origins of language, which classes of hypotheses are inconsistent with the available evidence, and which remain tenable? In section 5.1, hypotheses are classified along five different dimensions, and information from the preceding sections is used to constrain the array of possibilities and exclude some sections of this five-dimensional space.

- *What drove the evolution of language* — what reproductive advantages did language confer on our ancestors, causing “language genes” to increase in frequency? And why did the same factors *not* give chimps language? This is the theme of section 5.2 where a variety of ideas, from politics to sex, concerning why our ancestors found language so useful, are evaluated in the light of what we know about the habits of our ancestors and cousins.
- *Paths of language evolution* — what transitional stages may language have gone through, on the path from ape-like to human-like linguistic abilities? Finally, in section 5.3, we try to trace the actual steps towards language that our ancestors went through, and identify a possible path from ape to human.

2 The theory of evolution

The purpose of this section is to summarize some biological basics that are needed in order to discuss the evolution of language. First the theory of evolution by natural selection is presented as a general concept, and then I discuss some extensions and limitations of evolutionary processes.

2.1 Natural selection as an abstract process

The most important concept in the theory of evolution is natural selection. The process of natural selection, discovered by Charles Darwin (1859)[4], is applicable to a very large class of systems, far beyond the confines of biological evolution for which it was originally intended. The prerequisites for natural selection to work are:

- A class of objects exists, the objects in which are similar but not identical; some variation between objects exists in some features.
- The objects have different rates of reproduction and/or mortality.
- The differences in reproduction/mortality rates have some correlation with the variable features.
- If the objects reproduce, then the features of the copies are correlated with those of the original (parent) object(s).

Given the above conditions, the objects will evolve. Objects with features correlated with higher reproductive rates, or lower mortality rates, will increase in frequency, at the expense of their less successful brethren.

This description of natural selection is intentionally phrased in highly abstract terms. The objects are by no means limited to being living creatures, but can be anything from universes (Harrison, 1995) to religious dogma (Cullen, 1998; Gottsch, 2001); results from evolutionary theory at this level of abstraction can be applied to both. For slightly different, but equally abstract, accounts of natural selection, see Hull et al (2001), Calvin (1997) and Gabora (1997).

In the abstract description above, there is nothing corresponding to the biological distinction between genotype and phenotype. In principle, such a distinction is not needed for natural selection to do its job — but conceptual clarity may be gained by separating the dual functions of what I above called “objects”:

- Storing the information that needs to be transferred to the next generation, in order to maintain the correlation of features between parent and copy.

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[4] For a more recent introduction to evolutionary theory, see e.g. the textbook by Skelton (1993), or any of a number of popular works by Richard Dawkins, e.g. (1976).

- Interacting with the world, and either succeeding or not in producing a copy carrying the above-mentioned information.

Dawkins (1976) generalized the geno-phenotype distinction with his concepts of *replicator* and *vehicle*, where the replicator is the information carrier and the vehicle is whatever equipment the replicator uses to interact with the world in its quest for replication. In biology, the replicators are normally genes, and the vehicles are mainly the bodies of organisms. The 'vehicle' concept was later generalized and renamed *interactor* by Hull (1980, cited in Wilkins (1998a)). It should, however, be noted that the interactor need not be separate from the replicator, and there is no need for "the" interactor to be a single coherent entity like the biological organism — Dawkins' *The extended phenotype* (1982) is an extended argument for the possibility of more distributed interactors, a point he also makes in much briefer form in Dawkins (1994). See Szathmary (2000) for more on replicators.

2.2 Variation, randomness, and mutation

Natural selection is, however, not the only component of evolution. The variability that natural selection acts upon must come from somewhere, usually from random mutations. "Random" is used here in the special sense of random with respect to reproductive success (fitness), with no correlation between the probability of a certain mutation and its effect on fitness. There is, however, no *requirement* that the mutations are random — natural selection works perfectly fine regardless of the source of variation, as long as the rate of introduction of new mutations is not larger than the rate at which natural selection can weed out failed variants. Darwin's major insight was that evolution can work, and generate the appearance of design, *even if* mutations are random and undirected.

Jean Baptiste Pierre Antoine de Monet, Chevalier de Lamarck (1744-1829), formulated his own theory of non-random evolution a generation before Darwin, based on the inheritance of acquired characters. This acquisition of characters can be regarded as non-random mutations. Lamarckian evolution would have worked in biology, even better than Darwinian, if it hadn't been for the empirically observed facts that the pattern of biological mutations is indeed effectively random with respect to fitness, and the interactor's acquired characters aren't transmitted back to the replicator, and are thus not replicated. See Wilkins (2001) for a review of Lamarckism, as well as a critical perspective on the role of Lamarckism in cultural evolution.

There are considerable amounts of randomness elsewhere in the evolutionary process as well, making the outcome non-deterministic, and occasionally causing changes in entities that do not correlate with higher reproductive potential, a process known in biology as "genetic drift". But the random aspects of evolution can never be responsible for the exquisite and complex adaptations that are ubiquitous in living creatures, not least in ourselves. Natural selection is the only reasonable scientific explanation here. But the process is nevertheless subtler than what is usually presented at school.

2.3 Limitations of evolution

Evolution is a remarkably powerful process, displaying the appearance of ingenuity and creativity and design despite its partially random basis. But there are a few limitations of evolutionary processes that may also be worth pointing out:

- *Evolution does not plan ahead.* A feature is selected (or not) on the basis of its *current* utility, nothing else. An ape will not acquire a structure because it in some distant future will be vital for an as yet unattained language capability; it will be selected for only if it's of some use to the ape right then and there (though possibly for some different purpose). This has an important corollary: if a feature evolved because it's useful for language, then language was in place before that feature evolved.

- *Evolution will find local optima only.* The process is limited by the features already present, and will only take routes that are accessible by small steps from the current situation, with every step being advantageous (or at least not harmful). This can lead very far, but not everywhere, and not in a straight line. The process can easily get stuck in functional but suboptimal solutions, and every organism carries a lot of evolutionary baggage, accumulated along its historical path. This means that it's a lot easier and more likely to have an existing structure adapted for a new purpose, than to build a new structure from scratch.

- *Evolution does not take into account "the good of the species" or any other higher-level goals.* In the case of biological evolution, a feature is selected (or not) on the sole basis of whether it promotes the spread of copies of the genes of its individual possessors[5]. A mutation giving an ape some language capacity, will not spread and become common just because it benefits the tribe of that ape — only if it actually benefits that individual ape, and its close relatives carrying copies of the same gene. The same applies in principle to other evolutionary processes such as cultural evolution — a feature will spread and increase in frequency if and only if it increases the fitness of whatever entity carries the feature (though some care is required in identifying the relevant entities).

- *Evolution does not repeat itself.* The evolution of a complex feature is a rare occurrence, so it is very unusual for a complex feature to evolve twice in different organisms. The corollary of this is that if we observe the same

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[5] This applies even in the rare cases of apparent group selection, e.g. Wilson (1997), though the details can be subtle. In theory, group-level features are possible (Price, 1972, cited in Leigh (2000)), but no clear examples are known from real life.

complex feature in two related organisms, we can safely assume that it evolved only once, and that their common ancestor possessed it already (Byrne, 2000). In the case of language, this means that any language-related features displayed by e.g. chimpanzees today, were present already in the common ancestor of us and chimpanzees, and did not evolve for human-level linguistic purposes.

If evolution does appear to repeat itself, with the what appears to be the same complex feature turning up in unrelated animals, this implies either that the similarities are merely superficial, as with the wings of birds and bats, or that the feature isn't as complex as it appears, and is not a difficult evolutionary step.

In principle, this non-repeatability applies also to non-biological evolution, such as cultural evolution (see section 2.4 below). However, the "family tree" of cultural features need not coincide with the biological family tree, and the presence of the same cultural element in two organisms need not indicate that their common *biological* ancestor had that element (or had culture at all, for that matter). But the corresponding cultural conclusion *can* be drawn, that the presence of the same complex cultural feature in two separate cultures indicates the existence of a common *cultural* ancestor.

- *Evolution is not a matter of ascending a ladder towards an ultimate goal.* There are actually three errors in that ladder picture:
  - There is no well-defined notion of "progress" in biological evolution, no up or down on the ladder. Every evolutionary step is in the direction of increased fitness right then and there, but what happens to be more fit here and now is not "better" in any absolute sense, and might be totally unfit in a different environment.
  - The pattern of evolutionary change is rarely a single sequence of ancestors and descendants — the typical family tree looks more like a bush than a ladder, with lots of branches diverging in different directions. Our own history is no exception — two million years ago there were at least four different species of humans alive at the same time. This also means that an ancestral species need not disappear just because a new species evolves — if the speciation event involves only a subpopulation of the ancestral species, the rest of the ancestral species is unaffected. I've heard this used as an argument against human evolution in general: "If we're descended from apes, how come there are still apes around?", an argument that is firmly rooted in this erroneous view of evolution as a ladder.
  - Evolution is not directed towards any goal. As already noted, it takes whatever direction happens to increase fitness here and now. Even in the special cases of goal-directed evolution like artificial breeding of dogs or intentional language change, changes can only be effected

indirectly, by increasing the here-and-now fitness of the desirable dogs and words. In the case of dogs, this is done simply by providing the desirable ones with mates and ample food — directing language change is more tricky. As for evolution “in the wild”, its course has meandered and bifurcated so much over the gigayears that it much more resembles a random walk from a simple starting point, than a goal-directed process with a purpose in mind.

2.4 Cultural evolution

Culture is a concept that is not entirely trivial to define, and there is little consensus among students of culture about what the proper definition should be. But without worrying about the finer details, we can apply ‘culture’ as a label for the complex patterns of social behavior, beliefs, and artifacts that are characteristic of all human societies. The cultural patterns of humans are strongly variable between groups, but are often reasonably homogeneous within groups, and preserved from generation to generation with some degree of fidelity. This cultural continuity within groups can be explained in three different ways (Aunger, 2001):

- Transmission (social learning, memes).
- Genetic inheritance (biological evolution).
- Individual learning (different individuals learning from the same context arriving at the same result).

Human cultural universals may have a genetic basis, but the vast complexity of culture makes it vulnerable to the “poverty of the genes” argument (see p 89), and the wild variability of culture in both space and time is simply too fast to be explained by the slow and cumbersome process of biological evolution (Boyd & Richerson, 2001).

Individual (non-social) learning, including the “ecological inheritance” of (Laland & Odling-Smee, 2001), appears unlikely as an explanation for human cultural continuity, both because it requires a degree of identity between the thought processes of different individuals that is hardly consistent with our observations of learning in non-cultural contexts, and because of the quintessentially *social* nature of human culture. Furthermore, processes that are straightforwardly interpreted as the social transmission of culture are readily observed in the interactions of human adults and children.

The situation may differ in other animal species, where individual learning and imitation may play a significant role in those rudiments of culture that have been observed — but it may be argued that a common behavioral pattern does not qualify as culture, unless it is based on a common understanding, transmitted in a process of social learning. In *Homo sapiens* transmission, cultural learning, clearly emerges as the by far most plausible explanation for cultural continuity within groups and across generations. Tomasello (1999) argues for cultural learning as the main adaptive breakthrough of humans, leading to our cumulative growth of culture and knowledge, and playing a major role in the evolution of human cognition.

The transmission of culture entails the transfer of some kind of information describing the culture to a new member, and the creation of a replica of that information in the mind of the new member. Cultural evolution is the process of evolution by natural selection applied not to the reproduction of biological organisms, but to this transfer of cultural patterns and components of social systems. The application of evolutionary ideas to the study of cultures has a long history, but has remained peripheral in the field. The reasons for this may be both practical — the application is not easy — and cultural — students of culture commonly regard concepts from the natural sciences as foreign, if not with outright hostility — and historical — past attempts at applying evolutionary concepts in cultural studies have a mixed and partially unsavory record.

The core logic of cultural evolution remains the same abstract process of natural selection described on page 9 above, but beyond this any analogies with biological evolution should be handled with care, since there are several important differences between biology and culture. To begin with, the biological concepts relevant to evolution, such as genes, reproduction, mutations, organisms, and species, are reasonably well understood and can be reliably operationalized[6]. The corresponding concepts in cultural evolution, however, remain elusive and difficult to define and operationalize, and it is not at all clear whether all the biological concepts mentioned above actually have relevant correspondencies in culture. Attempts to shoehorn culture into an exact biological template are doomed to fail. But the mere fact that there are differences between biology and culture is not in itself sufficient to invalidate an evolutionary approach to culture, as long as the distinguishing features of culture are taken into account, and the conceptual machinery of Darwin is appropriately adapted.

2.4.1 The three worlds of Karl Popper

One of the aspects making cultural evolution more difficult to study than biological, is that the relevant biological concepts generally correspond to concrete measurable physical objects and events, whereas cultural concepts are of a more abstract nature. Even though aspects of culture may be instantiated in artifacts and minds, it is not really appropriate to say that a culture *is* its artifacts. Artifacts may be manifestations of a certain cultural concept, but the concepts themselves are independent of the artifacts, mainly inhabiting what Popper

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[6] Even though biology is more complex than is often appreciated outside the field (Speel, 1997). For example, the species concept as normally defined is applicable only sexually reproducing organisms, and, as noted by Dawkins (1982), the biological gene is very difficult to define stringently.

(1979) calls “world 3”. Popper’s three-world system distinguishes what might be called three different planes of existence:

- *World 1:* The normal physical universe, inhabited by everything from galaxies to genes.
- *World 2:* Mental space, inside our heads, inhabited by our thoughts and emotions and memories.
- *World 3:* The world of disembodied abstract ideas.

The three worlds are not entirely independent of each other. World 1, the mindless physical universe, is not dependent on the others. World-2 objects, however, do appear to depend on the existence of world-1 brains[7]. World-3 objects, however, are less straightforward. Popper regards a world-3 object as existing regardless of whether it is currently instantiated in either world 1 or world 2 — e.g. a melody keeps on existing as a world-3 object even if all recordings of it (world-1 objects) are destroyed and all memories of it (world-2 objects) are forgotten. In this respect, Popper’s world 3 has much in common with Plato’s world of Ideas or Forms, despite their totally different metaphysical status: *“... Plato was the discoverer of the third world. ... Plato’s third world was divine; it was unchanging and, of course true. Thus there is a big gap between his and my third world: my world is man-made and changing.”* (Popper, 1979, p 122). Furthermore, for Plato, only idea-world objects really exist, objects in the other worlds being mere shadows of them. Popper, on the other hand, does not appear to grant primacy to any of the worlds, but regards all three worlds as in some sense real.

A world-3 object will apparently survive indefinitely, once it is born. But unlike the Ideas of Plato, it is indeed born, created when it is first instantiated in world 2[8] — the first time an idea emerges in a mind, as a world-2 object, the corresponding abstract world-3 object is born. In this sense, the contents of world 3 is a human creation, as stated by Popper in the quote above.

World-3 objects lead a passive existence within their world 3, and interact only through their world-1 and world-2 instantiations. But when a world-3 idea is instantiated in a mind, as a world-2 object, that mind can communicate the idea to others, planting new instantiations in new minds, either through direct communication or through intermediate world-1 objects (books and other information-storing artifacts). In a new host mind, the idea will interact with other ideas in the same mind, and likely be modified. The modified version is in a sense

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[7] Alternatively, if intentionality, consciousness and meaning can actually emerge in a computer or a robot, e.g. as envisioned by Zlatev (2001a), world-2 objects would instead be hosted by world-1 silicon. But some world-1 substrate is required, unless one postulates the existence of disembodied souls, which would live in world 2 alone, but which would bring us too far into theological territory.

[8] Or even in world 1, at least in special cases — Popper invokes the example of a computer-generated table of logarithms (Popper, 1979, p 115).

a new world-3 object, a descendant of the old one, similar to the parent but not identical. This is something quite close to Darwin's concept of descent with modification. But not all world-3 objects reproduce equally often — some ideas are more likely than others to be communicated, and adopted by new minds. Thus, some world-3 ideas will be fruitful and spread into many minds, generating many descendants, whereas others will be forgotten by all minds and stranded uninstantiated in world 3, for all practical purposes dead.

In the case of scientific hypotheses as world-3 objects, Popper makes the parallel with Darwinism explicit: *"the growth of our knowledge is the result of a process closely resembling what Darwin calls 'natural selection'; that is,* **the natural selection of hypotheses***: our knowledge consists, at every moment, of those hypotheses which have shown their (comparative) fitness by surviving so far in their struggle for existence;..."* (1979, p 261, emphasis in original). This is the basis of Popper's influential evolutionary epistemology, foreshadowed in his seminal work *The Logic of Scientific Discovery* (1959) and fully developed in *Objective knowledge — an evolutionary approach* (1979). Evolutionary epistemology is reviewed and further analysed in Wilkins (1995), who proposes an epistemology even more Darwinian than Popper's.

This evolutionary perspective also resolves the slight tension between the individual and the social in Popper's discussion of world 3. World-3 objects are born out of individual human minds, and are thus not intrinsically social — but their evolution is fundamentally social, requiring an interacting population of world-2 instantiations, just as biological evolution is normally based on an interacting population of organisms, and it is only through this social process that the *objective knowledge* that is the goal (and title) of Popper (1979) can emerge in any meaningful sense.

2.4.2 Memetics

Popper mainly limited his studies of world-3 evolution to the growth of scientific knowledge. **Memetics**, introduced by Dawkins (1976), is an attempt to extend Popper's Darwinian analogy to include not only scientific hypotheses but all inhabitants of Popper's world 3, cultural, linguistic, or whatever, into a reductionist framework usable for micro-level studies of their evolution. The core concept here is the **meme**, intended to be the cultural equivalent of the biological gene, and closely corresponding to Popper's concept of a world-3 object. Other precursors of the meme concept include the 'symbolate' of White (1959, cited in Gatherer (1997)), and there are hints of similar reasoning also in the writings of Peirce (1931 35) on the evolution of symbols (Gatherer, 1997).

The literature on memetics is not entirely clear on the proper meaning of the meme concept, something which has severely hampered progress in the field. Some memeticists call just about anything remotely mental or cultural a meme, diluting the concept into meaninglessness, whereas others insist on strictly operationalizable definitions of memes as something physically tangible, gaining stringency but possibly losing in the process the “soul” of the concept that makes it fruitful. This difficulty of defining a core concept in a way that is both stringent and fruitful is, however, not unique to memetics — in my experience in a variety of fields, concepts acquire their meaning by usage and joint reference, only rarely by formal definition. What hampers memetics is not so much the lack of definitions, as the lack of consistent usage and joint reference — as a physicist, I would be hard put to provide a stringent definition of, say, ‘energy’ that corresponds to actual usage, but the energy concept is nevertheless eminently successful, one of the major unifying concepts in the natural sciences. I would agree here with Wittgenstein, who in a different context argues for the acceptance of fuzzier concepts: *“[A]ll concepts need not be unitary and crisp, but rather that different phenomena falling under the concept may be connected by ’family-resemblances’.”* (Zlatev, 2001a, p 163, citing Wittgenstein (1953)). Similarly Hull (2001) argues for an emphasis more on finding applications where memes are fruitful and less on definitional battles.

There is no total agreement either on which of Popper’s worlds is the appropriate home of memes — see e.g. the exchange between Gatherer (1998), Wilkins (1999) and Speel (1999), where the contest appears to be between world 1 and world 2. In my opinion, a location in world 3, following Popper’s (1979) analysis of the evolution of scientific hypotheses described above, is more appropriate, and lends itself to more fruitful analysis, despite the fact that world 3 is not directly observable — the study of biological evolution was an eminently successful enterprise for a full century before the biological genes were directly observed in any reasonable sense[9]. The effects of genes, before the discovery of DNA, were observable through the resulting phenotypes, and similarly the effects of world-3 memes are observable through their instantiations in world-2 thoughts (as manifested by world-1 behavior) and world-1 artifacts. Thus, knowledge of the biochemical substrate of genes (DNA) was not needed for the development of Mendelian genetics as a science — likewise, the concept of memetics is not rendered incoherent by our inability to identify the substrate of memes; as emphasized by Aunger (1999), Gabora (1997) and Dennett (1995), the evolutionarily relevant aspect of both genes and memes is their information content, not how they are physically encoded: *“What is preserved and transmitted in cultural evolution is* information

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[9] Possibly a parallel with quantum mechanics may be even more illustrative. The wave function ψ plays a role in quantum mechanics that is as vital as that of a gene in biological evolution or a meme in memetics. The history of quantum mechanics is a century of unparalleled success, both as an eminently fruitful research paradigm and as a source of practical applications that include all modern computer equipment, with a rock-solid empirical foundation — but also a century of abject failure in the quest for the identity and nature of the wave function. Some of the brightest minds of the 20th century, including Albert Einstein, spent decades trying to define and operationalize and make sense of the wave function. The end result is that we have still no idea what a wave function really is — but we can state with some confidence that it is *not* a world-1 object in any reasonable sense, not anything tangible or directly accessible. But the fact that physics is worse off than memetics regarding the ontological status of a central concept, does not prevent physics from being an enormously productive science.

— in a media-neutral, language-neutral sense. Thus the meme is primarily a semantic *classification, not a* syntactic *classification that might be directly observed in 'brain language' or natural language."* (Dennett, 1995, p 353-354, emphasis in original). This means, unfortunately, that the molecular-level reductionist revolution in genetics that has been so successful in recent decades is unlikely to have a memetic counterpart in the foreseeable future.

With my placement of memes in world 3, the world-3 entity would be the replicator *sensu* Dawkins (1976) and its world-1&2 instantiations would be interactors (or vehicles). Other authors make different and sometimes contradictory choices here, with e.g. Gabora (1997) arguing for world-2 replicators and world-1 interactors, whereas Gatherer (1998) proposes the opposite.

Whatever the location of memes, it is quite clear that memes need hosts in order to reproduce. This is sometimes interpreted as memes being akin to viruses, who also co-opt host reproductive machinery in order to replicate themselves — but given the very different nature of a meme and its host, I would rather use the less loaded image of a meme needing fertile minds in the same sense as a plant needing fertile soil for its reproduction.

Still, even if we disregard the definitional debates, there are a number of weaknesses in the meme-gene analogy that even proponents of memes recognize (Dennett, 1995):

- Low-fidelity replication, with an effective mutation rate that may be high enough to wash out any selection effects.
- Mutations may be purposely directed by humans, opening the door to Lamarck.
- Blending inheritance, instead of Mendelian particulate genes, washing out innovations.
- Independent invention of the "same" meme may be common.

The first objection, if true, is fatal to the idea of memetic evolution[10]. The second objection simply means that memetic evolution need not be purely Darwinian in a strict sense, which is not a serious problem — culture *is* different from biology. The third objection, blending inheritance, does not invalidate memetic evolution *per se*, but does, if true, hamper the kind of cumulative growth of complexity and adaptedness that is a major strength of Darwinian evolution (Dennett, 1995) and characteristic of human cultural evolution (Tomasello, 1999), rendering memetics uninteresting as a possible explanatory framework for cultural complexity. The fourth objection, independent invention, does not invalidate memetic evolution, but makes the reconstruction of memetic phylogenies very difficult.

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[10] Rose (1998) suggests that the enormous difference in cultural complexity between humans and other animals, discussed in Tomasello (1999), is due to humans crossing a fidelity threshold in social learning, with fidelity getting high enough for cultural evolution to "take off".

Dennett's objections are all empirical claims about the nature of memes. It is likely that his claims are true for at least some classes of cultural phenomena, rendering a memetic analysis of those phenomena unlikely to be fruitful. However, this need not be the case in all areas of culture — the fact that memes are useless in some areas does not prove that they are useless in all (Aunger, 2001). Wilkins (1998a) addresses the concerns of Dennett (1995) in the context of the evolution of scientific theories, and I'll address his concerns as applied to language in section 2.5.1 below.

Within limited domains, some serious and careful empirical work, has been done within a memetic paradigm, notably in the study of birdsongs, e.g. Baker (1996) or Majoros (2002), and suicide[11] (Marsden, 1998). There is also active reasearch on what idea-intrinsic factors determine the transmissibility and memorability of novel ideas, e.g. the studies reviewed in Barrett (2000), as well as Jacobson (1998), concerning religious concepts. Research like this, even though not all of it is done within an explicitly memetic paradigm, is clearly important for placing memetics on a sound empirical footing.

Unfortunately, these modest successes are often overshadowed by the approach seen in the writings of some the more vocal proponents of memetics, e.g. Blackmore (2000), an approach characterized more by enthusiasm than by stringency. This over-enthusiasm has caused a counter-reaction of skepticism against everything memetic, a polarization that does not facilitate progress in the study of cultural evolution. But the skeptics do have a point both in that much work in memetics *is* wildly speculative and conceptually confused, and in that some proponents of memetics are naïve and ignorant about the cultural sciences (Kuper, 2001; Bloch, 2001).

Nevertheless, despite all the weaknesses and problems with memetics in its current state, I would argue that it contains a valuable core idea, that can contribute to our understanding of the evolution of culture and ideas, and language. If the application of evolutionary ideas to culture is ever to become more than hand-waving, something along the lines of memetics will be needed. But before that will happen, memeticists need to get their act together, and demonstrate that the memetic research program can actually produce results that are both novel and empirically supported. Outside limited domains, the empirical basis of memetics remains modest.

2.4.3 The interaction of cultural and biological evolution

Cultural and biological evolution are by no means two completely independent processes. Cultural evolution wasn't even possible until biological evolution had provided us with the requisite cognitive skills, and cultural evolution even today

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[11] Incidentally, the suicide studies may lead to a clear example of a meme enhancing its own fitness at the expense of the reproductive success of its host, something which needs to demonstrated in order to establish the reality memes as independent replicators.

is very likely biased by our biological predispositions.

But there are links in the other direction as well, from culture to biology. For one thing, modern human material culture will keep alive many people who would have died young in a hunter-gatherer tribe, relaxing the selection pressures otherwise weeding out e.g. people like me who need glasses to see that there's a lion hiding in the grass.

Our mate preferences are strongly affected by cultural factors, which means that cultural evolution directly modifies the biological reproductive success of different individuals, changing the course of biological evolution — in a culture where e.g. people with freckles are culturally regarded as particularly attractive, people with freckles will have more opportunities to reproduce, and genes for freckles will spread in the population. Durham (1991, cited in Rose (1998)) proposes that similar meme/gene coevolution may be a significant process in humans.

A subtler effect of culture on biology is the Baldwin effect (Baldwin, 1896; Turney et al, 1996; Steels, 1997), known from various other fields of behavioral evolution:

If a certain behavior is highly advantageous for the members of a species, the behavior may, in a cultural species, first turn up as a cultural innovation, with no biological basis. The first generation of children after the innovation may start out by learning the behavior without innate help other than general learning abilities. But in each new generation, those individuals who acquire the behavior quickly and effectively are favored by natural selection. This is a clear recipe for the evolution of an innate predisposition to acquire the behavior, or even a dedicated acquisition device. In the long run, the behavior may become entirely genetically hardwired, bypassing the acquisition step.

2.5 Evolutionary theory as applied to language

The evolution of language is usually discussed exclusively in terms of the biological evolution of the human language faculty. This is a limited and problematic view, since several other evolving systems are involved, evolving at different rates, and with complex mutual interactions. The most important evolving system here is language itself, considered as a meme-complex in Popper-world 3. Memetic evolution of language will be discussed in section 2.5.1 below. But there are also other evolving systems that are relevant for language:

- **Evolution of other human bodily and mental faculties**, that are now used for linguistic purposes, but may have arisen as adaptations for some other purpose, as exaptations[12]. This is a matter of normal biological

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[12] Exaptation, a word coined by Gould & Vrba (1982), refers to a feature that evolved for some other purpose, or as a simple side effect of the evolution of unrelated features (in which case Gould & Lewontin (1979) call it a spandrel), but turned out to be, quite accidentally, useful for a

evolution, but their evolution need not be connected with emergence of human language, and may well have taken place in our remote proto-ape ancestors, which largely removes the timing constraints discussed below.

- **Evolutionary processes in ontogeny** The ontogenetic development of neural connections in the brain has some parallels with natural selection (Cziko, 1995; Deacon, 1997; Sireteanu, 1999; Chenn & Walsh, 1999). In those cases that have been studied in detail, the neural connections are found not to be genetically preprogrammed. Instead, neurons at first form connections in large numbers, rapidly and to all appearances randomly. As neural input arrives, those connections which are heavily used multiply and are strengthened and those which rarely carry any signals wither and are eventually pruned. The result is a pattern of connections that is adapted to handle the type of input received during this sensitive period.

  It is not entirely obvious how an innate language acquisition device with a genetically determined universal grammar (Chomsky, 1965) could arise through such a process.

- **Evolution of human social systems, both biological and cultural evolution** (Hill, 1997; Laland et al, 1999; Caporael, 1996). Humans, like most other mammals, certainly have a set of biological adaptations for social life, which have evolved in the usual Darwinian fashion. But the wild diversity of social systems in different human cultures demonstrates that our social system — unlike that of most other animals — is *not* genetically biologically determined in any strong sense. Instead, the most important evolutionary process in this context is cultural evolution, with our genetic adaptations for sociality as a more-or-less deeply buried substrate.

2.5.1 Evolution of language *per se*.

Language, as an abstract structure, is not some pre-existing essence, a goal for a teleological evolutionary process to strive towards, *contra* Bever (1982), but instead an evolving entity of its own (Wilkins, 1998b; Keller, 1989; Diller, 1997), a huge and successful system that can be regarded as an entity (or population of entities) in Popper-world 3 (see section 2.4.1 above, as well as Popper (1979)).

The discussion of evolution-like processes in the history of language actually predates Darwin, beginning with the conclusion of Sir William Jones in 1786, that Sanskrit, Latin, and Greek all were descended from a common ancestor through a process of gradual modification. These studies significantly influenced Darwin (1859) as he transferred the concept of descent with modification from linguistics

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new purpose, different from that for which it evolved. The co-opting of exaptations is a recurring theme in the evolution of human language. Previously, exaptations were somewhat misleadingly called preadaptations, a usage still occasionally seen, e.g. in Corballis (1999) and Zlatev (2001a).

to biology (Gatherer, 1997). Within linguistics, the study of the phylogeny of languages has remained a vital field of research ever since, though usually purely descriptive, without explicitly invoking evolutionary parallels except at a very superficial level.

Still, the processes of language change may well be open to evolutionary interpretations. Language can be modeled in terms that closely parallels Popper's (1979) evolutionary epistemology, with scientific hypotheses as evolving world-3 entities. "Language" in the abstract sense would similarly be a world-3 entity, and its implementations in human minds would be world-2 objects, and of course the communicative use of language encodes it into sound patterns and other world-1 objects. This view of language has considerable similarities with memetics as well, and may be analysed within a memetic paradigm, particularly since at least some of the objections against memetics do not apply to language. Returning to the list of Dennett (1995) from page 18 above:

- Low-fidelity replication, *does not apply to language, as language is clearly transmitted from generation to generation with only minor changes.*
- Mutations may be purposely directed by humans, *does apply to language, but does not invalidate an evolutionary approach.*
- Blending inheritance *may apply at the phonetic level, but not at the level of the lexicon or grammar — if two parents use different words for the same concept, their children will learn one or the other (or likely both) but will not blend the words together.*
- Independent invention of the "same" meme *is unlikely to be a problem, given the conventional and arbitrary nature of language.*

Within this Popper-inspired quasi-memetic framework, language evolution can be considered on several different levels. Popper (1979) appears to regard "language" not as just *a* world-3 entity, but as a major part of the framework for world 3, with a role much like the spacetime of world 1 (Einstein, 1915; Johansson, 1998): *"Main thesis: our conscious subjective knowledge (world 2 knowledge) depends on world 3, that is to say on (at least virtually)* **linguistically formulated** *theories."* (Popper, 1979, p 74, emphasis in original).

But 'language-as-spacetime' is not a tremendously useful perspective for language evolution. On less abstract levels, there are several linguistic entities in different worlds that are better candidates for evolutionary considerations.

- *Meme level.* Reductionistically, one may adopt the equivalent of the "gene's eyes view" of Dawkins (1976), which would be the smallest linguistic units that can be coherently replicated, the memes of language. Memes are notoriously difficult to pinpoint in many cultural contexts, but language, being both more coherent and more thoroughly analyzed, may offer some hope of success. A non-exhaustive list of plausible linguistic meme candidates might include:

  - Individual words.
  - Individual grammatical rules (or parameter settings in a Universal-Grammar framework).
  - Generic utterances (Zlatev, 1997).

  This would appear to be a useful level of analysis for the study of contemporary language change, on a rather short time scale. The spread of a newly-coined word, for example, is about as clear an example as one can get of memetic evolution.

- *"Organism" level.* The organism level in biology may be regarded, following Dawkins (1976), as a coherent set of genes working together as a team, forming a common interactor. Individual genes of a human being do not do anything useful on their own — they are meaningful evolutionary units only in the context of all the other genes of our genome. Similarly, individual language memes like the words or rules or utterances mentioned above are not meaningful in isolation, only as parts of a coherent system with, at a minimum, a set of generic utterances and a set of words to fill the slots in them, and more normally consisting of a large battery of grammatical rules and tens of thousands of words as well as all the various other bits and pieces that make up a language. The lowest-level entity in which all these meme-level pieces are gathered together in a coherent whole would be the idiolect of an individual language-user.

  In biology, the lowest-level entity in which all human genes are working together as a coherent whole is an individual human being, as a biological organism. I will regard an idiolect as a "linguistic organism" in the same sense. It is quite accidental that the organism levels of biology and linguistics very nearly coincide, and perhaps unfortunate, as it may invite confusion as well as over-extension of biological analogies; this will have to be kept in mind.

  This organism level may be the most fruitful for the study of the origin of the human language capacity. Very little interaction can be expected between individual language memes and individual human genes, so the meme/gene level is less likely to yield interesting insights into this issue. Direct interaction, and possible co-evolution, may instead be expected at the system level, between the human being as a system, with emergent properties beyond the sum of the genes, and the idiolect as a system of, but similarly beyond the sum of, language memes. This interaction will be discussed more at length in section 2.5.2 below.

- *"Species" level.* In biology, a species can be regarded as a set of organisms that are mutually reproductively compatible. Alternatively, from a gene perspective, a species is a gene pool within which genes can flow freely. A linguistic analogy of the species concept would then be either a population of mutually compatible idiolects, or a "meme pool" within which language memes can flow freely. With either perspective, a linguistic species concept is indicated that is quite close to our everyday notion of a language[13], an analogy that I will pursue in more detail in Johansson (in preparation). This level of analysis is relevant for the study of the historical development of languages and language families, but hardly for the ultimate origins of language.

2.5.2 Co-evolution of linguistic and biological organisms.

Each human has an idiolect, his or her own version of language[14]. The idiolect is for this purpose regarded as one individual organism; the inner structure of this "organism" is presumably built from individual language memes, but need not concern us here. Idiolects reproduce whenever somebody acquires a language — language acquisition does not take place in a vacuum, pre-existing "parent" idiolects[15] are always present as sources of language input. The resulting idiolect of the language acquirer is the descendant of the idiolects that provided input, in the Darwinian sense of "descent with modification" required for an evolutionary process — the "child" idiolect is normally very similar to, but not identical with, the "parent" idiolects.

Language evolution, in this sense, can be seen as a process of natural selection between our individual idiolects, with the most fit idiolects contributing the most to the idiolects of the next generation of people. The features of an idiolect that provides input to many language acquirers become more common in the next generation, whereas the features of an idiolect from which nobody acquires language disappear.

The features mentioned above correspond to the meme-level components of an idiolect. These memes, entities in Popper-world 3, are instantiated in world-2 idiolects, and the evolution of idiolects can reductionistically be regarded as a sequence of changes in the frequency of instantiation of different memes. New linguistic memes are created in individual human minds, same as for other world-3 objects, in the context of the world 2 of that individual mind, including its resident idiolect, but may then spread (or not) in a social process establishing their conventionalized meaning in world 3.

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[13] In biology, our intuitive "folk biology' notion of what a species is, across cultures, corresponds remarkably closely with the biological species concept, much more closely than the correspondance between folk and scientific concepts in other areas and on other levels (Atran, 1998). Our intuitive "folk linguistics" might also be similarly reliable at the species level.

[14] Or several idiolects, in the case of bilinguals or multilinguals

[15] Note that "parent" here does *not* imply that the hosts of the parent idiolects are necessarily the biological parents of the language acquirers, though in practice that is commonly the case, nor does it imply that the number of parent idiolects is necessarily equal to two.

The evolution of idiolects (and individual language memes) is in several respects as much Lamarckian as Darwinian:

- Idiolects can acquire new features during their lifetime, and pass on those features to their offspring. New words are being acquired throughout the entire lifespan, and changes in grammar and phonology are not rare either. A complication here is that there is no clean demarcation between features acquired "at birth" à la Darwin and features acquired later à la Lamarck, but it is nevertheless quite clear that the latter process plays a more prominent role here than in biological evolution.

- "Mutations" of an idiolect are not necessarily random, but can be directed towards increased fitness. This includes both failure to acquire features that are difficult to learn, and the addition of features, e.g. new words, that enhance communication.

The fitness of an idiolect is to some extent determined by the biological fitness of its host, i.e. the host's reproductive success, since your biological descendants commonly have your idiolect as a major source of language input. High reproductive success means having many surviving children, which indirectly also means that your idiolect will be a primary source of input data for language acquisition for as many new idiolects as you have children.

Apart from the reproductive success of the host, a large number of social and cultural factors will also likely influence the reproductive success of an idiolect.

More interesting in a linguistic context are factors that are intrinsic to language, and that may affect the reproductive success of an idiolect (as opposed to the reproductive success of its host). Some selection for communicative functionality can be expected (Bates & MacWhinney, 1982; Nettle, 1999), largely because an idiolect that's more efficient for communication enhances the biological fitness of its host, but also because others may be more likely to adopt memes from a communicatively superior idiolect, and language learners may be more likely to learn from (and get a larger fraction of their idiolect from) a better communicator. But since mutations of idiolects are commonly in the direction of increased functionality as well, due to human design, it is difficult to distinguish selection effects.

In the transmission process itself, there will be severe selection for learnability — an idiolect that is difficult for children to acquire, will not be passed on effectively; either the children will acquire some other idiolect (from the other parent or from someone else) or they will acquire a modified idiolect that's not identical to the parent's, presumably modified in the direction of improved learnability. Creole formation may be an extreme example of such modification, with the pidgin of the parents being modified into the creole of the children.

This selection for learnability applies regardless of whether the children have an innate language acquisition device or not — the evolution of idiolects will be driven towards learnability with whatever cognitive equipment children happen to have (Newport, 1982). Johansson (1997) presents a computer simulation of such evolution towards learnability.

At the same time as idiolects are subject to learnability selection, children are subject to selection for the ability to acquire an idiolect, and parents for the ability to ensure that their children learn. Language is so vital in human society that failure to acquire an idiolect that is communicatively usable will severely reduce biological reproductive success, both directly, and through other learning being hampered by the lack of communication.

Within modern human societies, with well established languages, selection relating to language, both biological and memetic, may be expected to be largely stabilizing, since our idiolects are already quite well adapted to their ecological niches, and humans are likewise well adapted to language acquisition[16]. This means that main effect of selection is to gradually weed out "failures" — such as SLI children on the biological side, or functionally detrimental inventions on the idiolect side. Ordinary diachronic language change over the few thousand years for which we have solid data, basically resembles a random walk around roughly the same level of functionality — there is no support either for claiming that the fitness of Italian idiolects is higher or lower than that of Latin ones, or for claiming that modern Italians are better or worse at language acquisition than Romans.

Significant directional evolution is observed mainly in the formation of new Creole languages from pidgins. But in the distant past, before either language or the human language capacity had attained their modern level of refinement, significant idiolect evolution can be expected to have occurred. As soon as our species-unique capabilities for cultural transmission (in which I include idiolect transmission) had reached the threshold needed for cumulative cultural evolution (Tomasello, 1999), this cultural evolution of language would pick up speed as well, growing from whatever primitive communication systems were in use at the time (which must nevertheless have been non-trivial, or cultural transmission would be ineffective) towards modern human language.

The general "cultural explosion" would have both provided the cognitive tools for rapid idiolect evolution, as well as considerable selection pressure towards improved communication concerning more and more complex issues. Rapid growth of the size and complexity of idiolects would result, straining the abilities of learners and speakers, and placing selective pressure on our biological language equipment as well.

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[16] Note that I am not implying here anything with respect to innate language acquisition devices à la Chomsky, an issue to which we'll return in section 5.1.5, only that human beings have what it takes to acquire a language, whatever that may be.

2.6 The time scale of evolution

Biological, classical Darwinian, evolution of human beings is by far the slowest of the various levels of evolution discussed in this section, with many generations required for notable changes to occur. Cultural evolution, including memetic language evolution, is orders of magnitude faster, not least because it is basically Lamarckian — variations can be directed, and acquired characters can be transmitted and inherited[17].

Cultural evolution also permits large-scale horizontal transmission of information (Takahasi, 1999), unlike traditional Darwinian evolution where normally only your direct descendants inherit your genes[18]. Loanwords is a linguistic example of horizontal transmission.

The evolution-like processes taking place during ontogeny are, of course, the fastest, as they need to be completed on a timescale of months or years.

The issue of time scales is highly relevant, as it has been argued by various people, from Chomsky (1990) to religious fundamentalists[19], that the time elapsed during human evolution is insufficient for the Darwinian gradual evolution of such a complex system as human language. Worden (1995) makes the same argument, in more quantitative terms, and with more real biology behind it than either Chomsky or the fundamentalists can muster. Worden's argument is not completely watertight, but he does have a point in that the emergence of language would be remarkably rapid if it were a pure process of biological evolution gradually, step by step, producing a highly complex innate, genetically determined, language acquisition device. From this it can be concluded that such arguments *"depend on inaccurate assumptions about biology or language or both."* (Pinker & Bloom, 1990, p 707) and that *"the claim that linguistic principles are innate or genetically programmed is an oversimplification with little precise meaning."* (Mueller, 1996, p 25, online edition). The latest version of Chomskian grammar (Chomsky, 1995; Berwick, 1997) might appear to offer a way out, in that his "Minimalist program" actually proposes a very simple core grammar, with basically just a single rule — but the complexities involved in the application of this "simple" rule mean that any such hopes are vain.

In any case, this complex interplay of evolution at different levels is not a unique feature of the evolution of language, but is a general, if often neglected, feature of the evolution of complex traits, particularly those with a behavioral component (Vancassel et al, 1996; Lipp, 1996; Laland et al, 1999). And even the biological part of the evolutionary process need not be straightforward, but may take a variety of routes (Thornhill & Ussery, 2000).

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[17] But see Wilkins (2001).

[18] Though evidence is accumulating that horizontal transmission is not rare in biological evolution either, particularly among bacteria (Poelarends et al, 2000; Brown & Doolittle, 1999).

[19] Chomsky's rhetoric here is frequently quoted with some glee by these fundamentalists, e.g. Morris (2001), in supposed support of their own anti-evolutionary and anti-scientific agenda.

3 Human origins and evolution

An overview of our family tree is given here, as there will be frequent reason further on to refer back to various branching points in the phylogeny. In this section, I shall dwell mainly on our own line of descent through the fossil record, with scant attention paid to other branches. I have chosen to start with the origin of mammals, because several relevant organs (notably brains and ears) underwent significant restructuring at that time. The history of life before that point is treated at length in any number of textbooks (e.g. Cowen (1995)) and popular works (e.g. Fortey (1997)), to which the reader is referred.

Likewise, there is no shortage of books about human evolution, from Darwin (1871) onwards. As a serious textbook, Lewin (1993) can be recommended. Popular works abound; Johanson & Edey (1981), Johanson & Shreeve (1989), Trinkaus & Shipman (1993), Walker & Shipman (1996), Leakey & Lewin (1993), Tattersall (1995) and Sagan & Druyan (1992) are but a few examples. Most of them contain detailed accounts of recent fossils of human or near-human beings, together with large or small doses of speculation about our origin and evolution.

The study of human evolution, touching as it does upon our own reasons for existing, is a highly emotional subject for many people. Tempers run high also among professional paleoanthropologists (Lewin, 1987), and a sizeable fraction of the general population even today refuse to recognize our kinship with the other primates. The issues in human evolution thus appear more contentious in the literature than is really motivated by the magnitude of the actual scientific disagreements, which are generally minor[20].

3.1 Mammals

Mammals arose during the Triassic, some 200-odd[21] million years ago, from a group of reptiles, in parallel with the evolution of dinosaurs from another group of early reptiles. The transition from reptiles to mammals is a smooth sequence, amply documented in the fossil record, with numerous intermediate forms, so closely similar anatomically that it is difficult to select one of them and say “Here is the first mammal.” One of the important skeletal differences between reptiles

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[20] One source of unnecessary confusion comes from the naming of fossil species. Living species are moderately well-defined, but the partitioning of a set of fossils into different species involves a degree of intrinsic arbitrariness. Particularly in the case of so-called chronospecies, where a single lineage changes through time, the divisions are purely a matter of taste. Different paleoanthropologists use different names for the same fossils, and the same names for different fossils; do not mistake naming conflicts for genuine disagreements about the course of human evolution (for an example of a pure naming conflict, see e.g. the exchange between Kennedy (1999) and Wood (1999), and the comments of Groves (1999)). I shall endeavor to be consistent in my own use, and to note where confusion may arise.

[21] The exact age is undetermined, and largely a matter of definition at that (Rowe, 1988). Jenkins et al (1997) argue for a somewhat older (Mid-Triassic) age than most authors, based on recent fossil finds indicating considerable diversity already 200 million years ago.

and mammals lies in the inner ear, where reptiles have just a single bone, and mammals have three, significantly improving the frequency range and sensitivity of their ears; see section 4.2.

A detailed review of the reptile-mammal transition, with references to the primary paleontological literature, can be found in Rowe (1988) (but see also Wible (1991) for some critical perspectives on Rowe (1988)). More accessible, and possibly more complete, is the fossil review of Hunt (1997).

The early Mesozoic mammals were all small, and most likely nocturnal, superficially resembling modern-day shrews but belonging to groups that are now extinct. The diversification of placentals[22] into the familiar orders of today's mammals, from perissodactyls to primates, did not take place until almost 150 million years after mammals first appeared, around the time of the mass extinction at the Cretaceous-Tertiary (KT) boundary[23]. The exact timing of events is unresolved, but shortly after the dinosaurs were gone, the mammals (as well as the birds) underwent a major adaptive radiation. All modern orders, including our own, can trace their origin to this period. The rapidity of the diversification is unfortunate, since it makes the relationships between major groups of mammals difficult to resolve, though some progress has been made recently (Murphy et al, 2001).

3.2 Primates

Our own order of mammals can also trace its roots to the post-KT radiation. According to some authorities, primates are members of a larger grouping, *Archonta*, which also includes *Chiroptera* (bats), *Dermoptera*, and *Scandentia* (tree shrews), but the evidence remains inconclusive (Allard et al, 1996; Miyamoto, 1996). Unambiguous primate ancestors are recognizable already from the early Paleocene[24], with a sometimes extremely detailed fossil record (Gingerich, 1980; Gingerich, 1983). Some recent finds from this earliest period are reviewed in Ringe (2002), and a nice overview of both fossil and extant primate groups can be found in Shoshani et al (1996).

The extant primates can be divided into two major groups[25]: the *Strepsirhini* (lemurs) and *Anthropoidea* (monkeys, apes, and us). The split between the two

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[22] The placentals (or more formally *Eutheria*) are mammals equipped with a placenta, and thus capable of nourishing their young inside the body for an extended period, unlike the marsupials and the egg-laying monotremes.

[23] Mostly famous for the demise of the dinosaurs, even though they formed only a small minority of all the animals that went extinct at the same time. For more on the KT extinction, see e.g. Burke et al (1994). Benton (1995) reviews the general history of mass extinctions.

[24] The first geological period after the KT extinction, from 65 to 55 million years ago.

[25] There is also a third, minor, group, the tarsiers, which are small nocturnal animals from Southeast Asia. Traditionally, they have been placed with the lemurs, but most recent authors classify them with the *Anthropoidea* in *Haplorhini* (Goodman et al, 1998; Kay et al, 1997), a classification that has received some recent fossil support (Ducrocq, 2001), though see also Shoshani et al (1996).

appears to have occurred quite early on, around 50–55 million years ago, or possibly even earlier (Goodman et al, 1998). At that time, there were two prominent fossil groups, the adapids and the omomyids. The adapids have lemur affinities, and the omomyids (Rasmussen, 1996) are probably ancestral to tarsiers, and may be ancestral to us as well (Ross et al, 1998), though some authors, like Shoshani et al (1996) are not convinced.

Our own suborder, the anthropoids, which includes monkeys as well as us and the other apes, is characterized by a larger brain than most other mammals of similar size, by adaptations to a diurnal, largely arboreal lifestyle, as evidenced by binocular vision with a fovea[26], and by grasping feet, obviously adapted for climbing rather than for the leaping common among strepsirhines and tarsiers.

The earliest anthropoids are found in Eocene deposits, around 40 million years old. *Eosimias* may possibly be the earliest monkey fossil (Kay et al, 1997; Ducrocq, 2001), but the evidence is not conclusive; the early primates are not all that different from each other, and most of the fossils are fragmentary, making it hard to tell who is the ancestor of whom. Furthermore, there is a general shortage of mammalian fossils from the relevant time frame (Hunt, 1997), with gaps in many lineages, aggravating the problem of tracing the early lines of anthropoid descent. The split between the *Catarrhini* (Old World monkeys and apes) and *Platyrrhini* (New World monkeys) also occurred in this time frame. The platyrrhines do not further concern us here; for more on their origin and phylogeny, see e.g. Houle (1999) or Bauer & Schreiber (1997).

After that gap, the anthropoids do have a fairly clear fossil record. *Aegyptopithecus*, living in Egypt some 31 million years ago, is a good candidate for the most recent common ancestor of all extant catarrhines (Goodman et al, 1998; Kay et al, 1997; Shoshani et al, 1996), though some authors propose a different, more gibbon-like (so far hypothetical) ancestor (Köhler & Moya-Sola, 1997b). An Old World monkey, distinct from apes, first turns up with *Victoriapithecus*, 15 million years ago (Benefit & McCrossin, 1997; Köhler & Moya-Sola, 1997b).

The apes, or hominoids, more formally known as superfamily *Hominoidea*, are first represented by a diverse group of Miocene fossils, of which *Proconsul* is the best known representative (Rae, 1999). Apes appear to have been significantly more widespread and common during the Miocene than they are today with somewhere around thirty known species then (Gibbons & Culotta, 1997) against less than ten surviving species today (but see Jablonski & Kelley (1997) for a dissenting view). Overviews of the fossils can be found in e.g. Pilbeam (1996) or Shoshani et al (1996), with a historical perspective in Mann & Weiss (1996).

An interesting early ape, which appears to have gone partway along the human route towards bipedality and hand use, is *Oreopithecus*. The morphology of its feet and pelvis is remarkably similar to that of early hominids (Köhler & Moya-

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[26] A spot in the eye with a denser concentration of photoreceptors, improving visual acuity in daylight, at the expense of some night vision.

Sola, 1997a; Rook et al, 1999), and its hands appear capable of the kind of precision grip ("opposable thumb") that is often regarded as typically human (Moya-Sola et al, 1999). *Oreopithecus* lived on a Mediterranean island in what is now Italy, and may have evolved bipedality as an adaptation to insular conditions, with an absence of large predators (cf. the flightless birds formerly common on oceanic islands). It appears unlikely that we are descended from *Oreopithecus*, but it may nevertheless cast light on the evolution of our own anatomical adaptations.

Otherwise, the Miocene scene is complex, and several different candidates have been proposed as ancestors of the living apes and humans (Gibbons & Culotta, 1997; Pilbeam, 1996; Ward et al, 1999; Gibbons, 1998c). Gibbons split off at an early stage, and there is fairly solid evidence of a separate lineage leading to orangutans dating back to at least 15 million years ago[27](Pilbeam, 1996).

3.2.1 Who is our closest living relative?

With the orangutan on a separate branch in the family tree, we are left with ourselves, the gorilla, and the chimpanzee. According to the vast majority[28] of recent work on the subject (Lewin, 1993; Shoshani et al, 1996; Mann & Weiss, 1996; Pilbeam, 1996; Goodman et al, 1998, among many others), we three form a monophyletic group of African apes, with a common ancestor around ten million years ago. *Kenyapithecus* (Gibbons & Culotta, 1997) and *Morotopithecus* (Gebo et al, 1997) are both candidate fossils of the lineage leading to that common ancestor.

The closest relatives within this African group are the two chimpanzee species *Pan troglodytes* (common chimp) and *Pan paniscus* (pygmy chimp, or bonobo)[29]. Beyond that, the relationship between chimps, gorillas, and humans is very nearly an unresolved trichotomy; the family tree split into three branches at the same time, or nearly so (Deinard & Kidd, 1999). Considerable efforts have gone into determining whether the chimpanzee or the gorilla is our closest relative, but the results have not been conclusive. Traditionally. the similar gross morphology and habitat of the chimp and gorilla have been considered sufficient grounds for grouping them together, to the exclusion of humans (Pilbeam, 1996;

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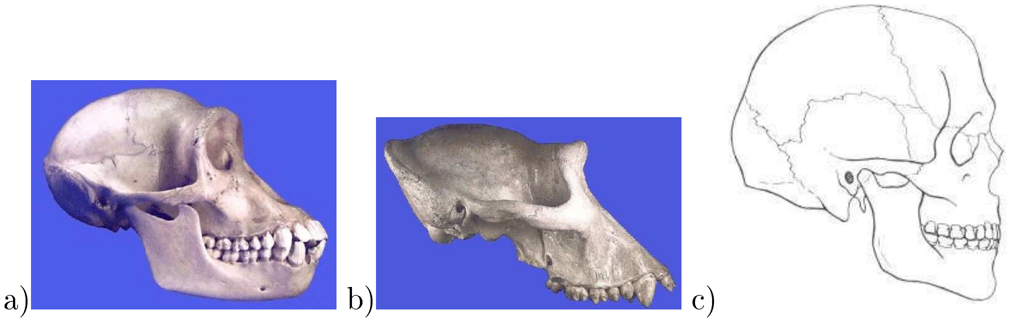
[27] The orangutan lineage includes the genera *Sivapithecus, Ramapithecus*, and *Gigantopithecus* (which are sometimes conflated into a single genus). *Ramapithecus* was once, in the 1930s–1950s, erroneously interpreted as a human ancestor, on the basis of fragmentary fossils. When a complete face was subsequently found, the orangutan affinities became clear. *Gigantopithecus* survived into fairly recent times, co-existing with early humans (Ciochon et al, 1996), and makes a plausible "abominable snowman" or "bigfoot", in the unlikely case that such creatures aren't completely fictional.

[28] Schwartz (1987; 1984) is, as far as I can determine, quite alone in considering the orangutan our closest relative; see also Shoshani et al (1996, table 1 on p 113).

[29] In the following, there will be frequent references to chimps of both species. When referring to identified individuals, "chimpanzee" (or chimp) means *Pan troglodytes*, but "chimpanzee" will also be used as a collective label for both species, when referring to their branch of the family tree in general — in a phrase like "the language abilities of chimps", bonobos are implicitly included.



(Foley, 1997)

Figure 1: Skulls of extant apes, intended for comparison with the various fossil skulls shown in the next section. a) Chimpanzee b) Gorilla c) Human.

Mann & Weiss, 1996; Lewin, 1993). More recent morphological analyses, however, taking into account a larger number of more informative characters, may reach different conclusions; Shoshani et al (1996), for example, present morphological support, albeit weak, for a *Pan-Homo* clade, and with soft-tissue characters included as well Gibbs et al (2000) find that they can firmly exclude a *Gorilla-Pan* connection. Also, the oldest fossils from the human line do show some similarities with chimpanzees (White et al, 1994; Wood, 1994). Pilbeam (1996) gives a review of the situation.

From the 1960s onwards, molecular data have been increasingly used for resolving phylogenetic issues. Molecular comparisons (immunological, protein sequence, chromosome pattern (Williams, 1999), or direct DNA (Gibbons, 1998d; Kaessmann et al, 1999) comparisons) among the hominoids have been published by the dozen, with a strong majority supporting the grouping of chimps with humans, to the exclusion of gorillas (Pilbeam, 1996; Arnason et al, 1996). There are, however, dissenters, such as Deinard et al (1998), who still prefer a *Pan-Gorilla* grouping, and there is some molecular support for that position (Barbulescu, et al, 2001). The current situation is summarized by Pilbeam (2000).

We can conclude that the preponderance of the evidence points towards the **chimpanzee** being our closest living relative.

3.3 Hominids

Our own exclusive branch of the family tree, usually known as the family *Hominidae*[30], separated from the branch leading to the chimpanzees a bit more

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[30] Yet another example of a rather uninteresting naming conflict is the perennial disagreement about which Linnaean rank we should be accorded. Do we have just our own genus *Homo*, or our own subtribe *Hominina*, or our own tribe *Hominini*, or our own subfamily *Homininae*, or are we a full family? Traditionally, we have been placed in our own family (and the great

than five million years ago. Unfortunately, hominoid fossils are sparse from this period, and we do not have any fossils that clearly belong to the last common ancestor of us and chimps, though the Lukeino molar from Kenya is a possible candidate (Ungar et al, 1994), as are the 6-million-year old bones found recently, also at Lukeino (Senut et al, 2001; Pickford & Senut, 2001; Holden, 2000; Balter, 2001), and assigned to *Orrorin tugenensis.* Other small fossil fragments that may belong near the branching point in the family tree have been found in several places in Kenya, but they are too fragmentary for firm conclusions (Schick & Toth, 1993).

Nevertheless, if we look at what traits, both physical and behavioral, we and chimps and gorillas and earlier apes have in common, we can make some plausible inferences about the probable characteristics of this ancestor. Basically, we can expect it to be rather similar to a chimpanzee, an inference that is borne out by the earliest human fossils (Lewin, 1993).

3.3.1 Bipedal apes

The oldest known fossils that with some confidence can be assigned to the human line[31] are those named *Ardipithecus*[32] *ramidus* (White et al, 1994; Wood, 1994; Haile-Selassie, 2001), from 4 - 6 million years ago, found in Ethiopia[33]. Some aspects of their anatomy[34], particularly the teeth, are very nearly halfway between chimps and humans, but some details in the arms and skull base indicate that it was probably bipedal. This is a general theme in early human evolution; ape-like features in the head and teeth (including an ape-sized brain; see section 4.3), but a human-like postcranial (below the neck) skeleton, adapted for bipedal walking. Obviously, the legs evolved first, probably right after we split from the apes, and the quintessential human quality that we call intelligence didn't evolve until a few million years later (McHenry, 1994).

But the transition to pure bipedalism wasn't instantaneous; apelike body proportions, with long arms and short legs, persist in some hominid fossils for another two million years, as do various climbing adaptations (Shreeve, 1996; McHenry & Berger, 1998; Oliwenstein, 1995; Clarke & Tobias, 1995), and apelike balance organs (Spoor et al, 1994). The early hominids, of the genera *Ardipithecus*

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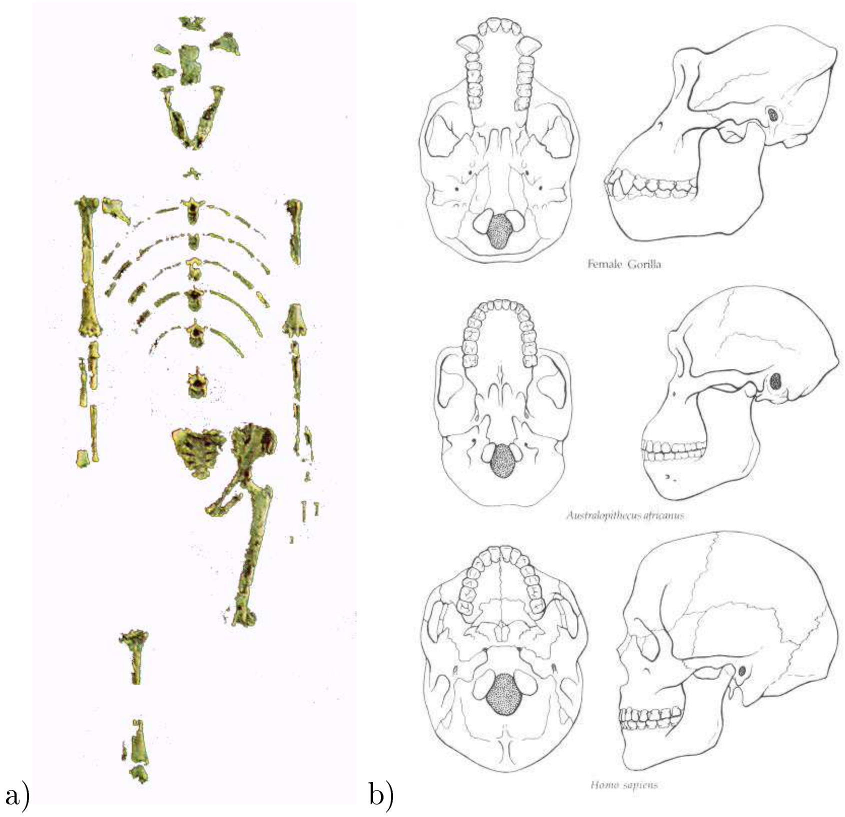
apes in a family of their own as well, the *Pongidae*), but as evidence of the close relationship between us and chimps has accumulated, it has become more and more clear that it's not really appropriate to place us in separate families.

[31] The discoverers of *Ardipithecus* and of the above-mentioned *Orrorin* both consider their own fossil to be a human ancestor, and the other to be a chimp ancestor (Gee, 2001). I find the case for *Ardipithecus* to be more compelling.

[32] Formerly assigned to *Australopithecus.*

[33] The very early history of our lineage is an exclusively African affair, which is not very surprising (it was foreseen already by Darwin), considering that our nearest relatives still live there.

[34] For a really thorough discussion of the evolution of human anatomy, with explanations of all anatomical terms, see Aiello & Dean (1990).



(Foley, 1997)

Figure 2: Fossils of *Australopithecus afarensis*. a) AL 288-1, "Lucy" b) Reconstructed skull of *A afarensis*, shown in side view and bottom view, between the skulls of a gorilla and a modern human, for comparison.

and *Australopithecus*, did walk on two legs, and their gait (Lincoln, 1998) and footprints[35] look very much like ours. Likewise, the load-bearing patterns in their hipbones (Macchiarelli et al, 1999; MacLatchy & Bossert, 1996; MacLatchy, 1996) and spines (Sanders, 1998) are consistent with bipedalism, if not identical to ours. The evidence hints at a lifestyle mixing bipedal walking[36] on the ground, with some modest amount of tree climbing. By three million years ago, the evidence indicates a diet obtained from more open terrain, possibly including meat from grass-eaters (Sponheimer & Lee-Thorp, 1999; Vogel, 1999), implying less climbing.

Just beyond 4 million years of age is the next fossil species, *Australopithecus*

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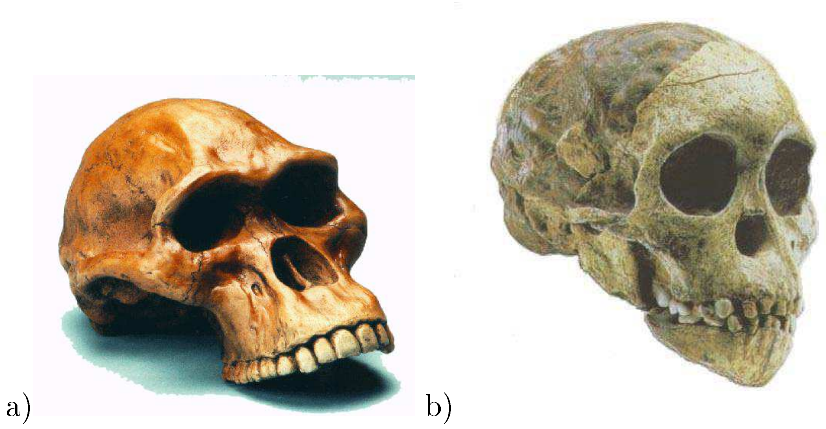
[35] A fossil trail, 3.7 million years old, with very humanlike footprints from at least two individuals, was found at Laetoli, Tanzania (Leakey & Hay, 1979).

[36] As opposed to the quadrupedal knuckle walking of the chimps and gorillas (Dainton & Macho, 1999). The hands of australopithecines do however show faint traces of having evolved from knuckle walking ancestors (Richmond & Strait, 2000; Corruccini & McHenry, 2001; Richmond & Strait, 2001).



(Foley, 1997)

Figure 3: Fossils of *Australopithecus africanus*. a) Reconstructed skull, composite of several individuals. b) “Taung child”.

anamensis (Leakey & Walker, 1997; Leakey et al, 1998; Ward et al, 2001). It is in many ways similar to *Ardipithecus ramidus* from which it may be descended (or maybe just a close cousin), but slightly more humanlike, particularly in the teeth. The changes in the teeth, with thicker enamel, larger molars but smaller anterior teeth, and different wear patterns, can be interpreted as adaptations for eating harder and more abrasive food than the soft fruits eaten by chimpanzees. *A anamensis* was definitely bipedal, with sufficient finds from the legs to demonstrate directly their mode of locomotion, unlike the indirect indications found in *Ardipithecus* and *Orrorin*.

After *anamensis* comes what may be most famous individual fossil of them all: “Lucy” (Johanson & Edey, 1981), more formally known as *Australopithecus*[37] *afarensis*, shown in figure 2. Lucy was found as one fairly complete female[38] skeleton; many other fossils from the same species have subsequently been found. It is closely related to, but more humanlike than, *A anamensis*. The oldest fossils of *A afarensis* are just a few thousand years younger than *A anamensis* (Kappelman et al, 1996). Anatomically, she follows the same pattern as the two previous species, with a lower body adapted for bipedality, but with an apelike

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[37] A few people (Senut, 1996; Strait et al, 1997; Wood & Collard, 1999) prefer to call her *Praeanthropus africanus*. For three reasons, I do not think such a change is well motivated:

- *Australopithecus afarensis* is in common and popular use
- It invites confusion with *Australopithecus africanus*
- The difference between Lucy and the other australopithecines is nowhere near large enough to motivate a genus-level distinction.

See also Groves (1999).

[38] Her gender has been questioned (Häusler & Schmid, 1997), but female remains the most likely interpretation (Wood & Quinney, 1996).

skull. Her brain is just marginally larger than that of a chimpanzee.

Lucy's species appears to have been fairly widespread in East Africa from four to three million years ago. The other hominid species mentioned so far also come from the same region, so it would appear that East Africa is the cradle of humanity. There may, however, be other explanations for the lack of fossil finds elsewhere in Africa:

- Early success in East Africa prompted paleoanthropologists to concentrate their efforts there.
- Fossil-bearing strata of the right age may not exist, or may not be accessible elsewhere in Africa.
- The environments elsewhere may not have been as conducive to fossilization[39] as those of East Africa.

An expedition a few years ago to Chad, 2500 km west of where Lucy was found, did nevertheless surprise everybody by finding an australopithecine fossil. It was named *Australopithecus bahrelghazali*, but the finds made so far are too fragmentary to draw any firm conclusions about its evolutionary significance (Leakey & Walker, 1997)[40]. It does, however, show that the history is more complicated than just a straight-line evolution from *ramidus* through *anamensis* to *afarensis*, and onwards, a complexity confirmed by another contemporary fossil species, *Kenyanthropus platyops* (figure 4), made public even more recently (Leakey et al, 2001; Lieberman, 2001). There may well be many more branches on the family tree than previously thought, also at this early date.

The situation after Lucy, around 2–3 million years ago, is certainly very complex, with several coexisting species (Tattersall, 2000). First on the scene is *Australopithecus africanus*, a gracile hominid basically similar to Lucy, and a plausible descendant of hers, with a few more humanlike traits (figure 3). This was the first australopithecine to be found, in the 1920s in South Africa (Dart, 1925), a find first greeted with considerable skepticism (Tattersall, 1995), as it fit poorly with then-current theories of human evolution. As the human brain is our most important adaptation, it was considered most logical that the large brain would have evolved first, with other human traits, like bipedality and reduced teeth and jaws, coming later. The australopithecines demonstrate the opposite path, with their basically humanlike bodies and teeth, and ape-sized brains (Lewin, 1993).

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[39] How and under what circumstances fossils become fossils is an entire science of its own, named taphonomy. One of its conclusions is that the likelihood of an individual becoming a fossil is strongly dependent on the environment. In some environments, like rain forests or mountains, fossilization is exceedingly rare. Any jungle or mountain dwelling hominids are thus highly unlikely to be found. This may explain the dearth of chimp and gorilla fossils.

[40] There are fresh (August 2001) unconfirmed reports of further finds in Chad, that may clarify the issue.

(Foley, 1997)

Figure 4: *Kenyanthropus platyops*.

But as more bits and pieces of australopithecines were collected, particularly after the Piltdown forgery was debunked, the debate was settled. South Africa remained the main home of *A africanus* — the first semi-complete skeleton of which was found there recently (Clarke, 1998) — as well as of a different, more robust species, *Australopithecus robustus*.

Today, three different species of robust australopithecines are known: *A robustus, A boisei* and *A aethiopicus*. The relationships between the three are unclear; they are similar enough that many researchers regard them as a clade[41] (Strait et al, 1997), and some, e.g. Susman (1998), even place them in their own genus, *Paranthropus*[42]. Others, however, argue that the similarities are just due to parallel evolution of adaptations to a similar lifestyle that involves heavy chewing (Skelton & McHenry, 1998; Morell, 1999; McCollum, 1999). Whatever their relationships, the robusts were quite successful, spreading over most of Africa and persisting for 1,500,000 years (Kullmer et al, 1999). They thus coexisted for quite some time with early *Homo*, before going extinct[43], possibly out-competed by their brainier cousins.

There are also some disagreements concerning the relationships between the robusts and other hominids (Wood & Collard, 1999). Humans, in the stricter

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[41] A clade is a group consisting of a common ancestor, and *all* that ancestor's descendants.

[42] It can be a bit confusing when the names are mixed, like in Delson's (1997) review of Suwa et al (1997).

[43] Allen (1988) speculates on the possibility of their *not* going extinct, in his novel *Orphan of Creation.*

sense, have traditionally been regarded as descendants of gracile australopithecines[44], with the robusts as just a side branch. There is, however, some recent support for associating some or all of the robusts with the main human lineage, to the exclusion of *A africanus* (Strait et al, 1997; Skelton & McHenry, 1998; Braga, 1998). Apart from the details in the skull and teeth considered by the preceding authors, Susman (1994; 1998) found, interestingly enough, that *A robustus* possesses anatomical structures in the hand that are regarded as human adaptations for tool use (Aiello, 1994), and bone tools have been found in association with *robustus* remains, tools that were apparently used for digging into termite nests (Backwell & d'Errico, 2001; Shipman, 2001)

Among the gracile australopithecines, *A africanus* is a possible ancestor of later humans, but not all the details fit. A direct link from *A afarensis* to *Homo* , bypassing *A africanus*, has been a fairly popular view, but there is a significant gap in both time and morphology to be bridged in that case. A new fossil species, *Australopithecus garhi,* discovered quite recently (Asfaw et al, 1999), has attracted a lot of attention, since it fits quite neatly into that gap, in both time and space and morphology. But the evidence is still insufficient for any firm conclusions — the ancestor of *Homo* is almost certainly found among australopithecines, but we cannot tell which one without more fossil evidence.

In conclusion, the australopithecines[45] were the main proto-human group from around 5 to 2 million years ago, with a rich diversity of species. The australopithecines had roughly human-like bodies, walking upright, but had ape-like skulls and brains. We have little indication of their having any culture beyond that of chimpanzees, and no reason to believe they possessed language.

3.3.2 Growing brains

Contemporary with the later robust australopithecines, and slightly younger than *Australopithecus garhi,* are the first fossils classified within our own genus, *Homo*[46]. These early *Homo* fossils were originally believed to represent a single species, and named *Homo habilis.* As more fossils were discovered, this simple picture became untenable, and the diverse assemblage of semi-human fossils from this period, a few examples of which are shown in figure 5, is now divided into at least two separate species, *H habilis* and *rudolfensis*[47], by many workers in this field. For convenience, "habiline" is often used as a generic term for any of them. The oldest habiline fossils are a bit more than 2 million years old. The

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[44] The graciles include *A afarensis, africanus* and *garhi*, which lack the heavy-duty jaws and teeth of the robusts.

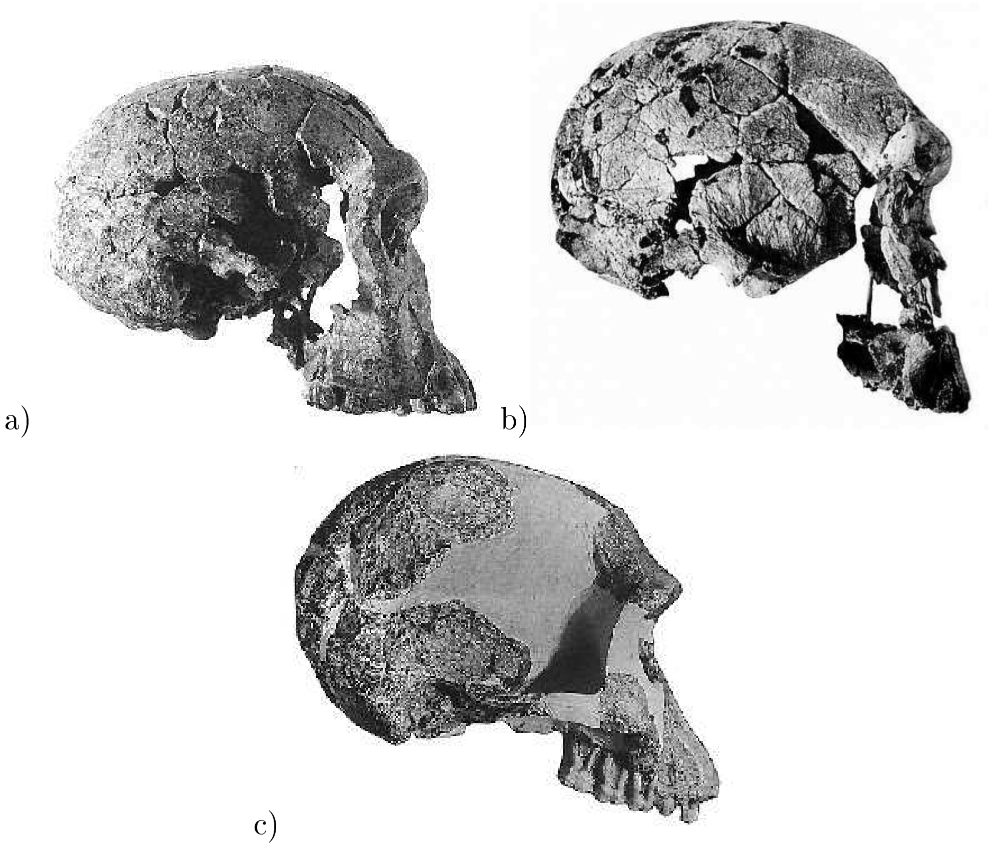
[45] In which I include *Ardipithecus, Kenyanthropus, Praeanthropus* and *Paranthropus*, which are all so similar that they hardly deserve genera of their own.

[46] Wood & Collard (1999), however, argue for placing them in *Australopithecus.* On the other hand, Wood (1992) argued forcefully for retaining them in *Homo.* (Yes, it's the same Wood in both cases; seems he changed his mind.)

[47] Also *Homo leakeyi* has been used (Grine et al, 1996), but to my knowledge not by anybody outside the Leakey family and their friends.

Species	**Significance**	**Time (millions of years ago)**	Location	Famous fossils
Ardipithecus ramidus	Earliest reasonably unambiguous bipedal hominid	6–4	East Africa	
Australopithecus aethiopicus	Very robust, small brain, plausible ancestor of *A boisei* and possibly *robustus*	2.6–2.3	East Africa	Black Skull
Australopithecus afarensis	Early hominid with good fossil record	4–3	Ethiopia and Kenya	Lucy, First Family
Australopithecus africanus	First real ape-human intermediate to be found, in 1925	3–2	Southern Africa	Taung Child
Australopithecus anamensis	Likely ancestor of *A afarensis*	4.5–4		
Australopithecus bahrelghazali	Fragmentary fossils, may well be *A africanus* or *garhi*	2.5	Chad	
Australopithecus boisei	Robust, "Nutcracker man", coexisting with early *Homo*	2.1–1.1	East Africa	Zinj
Australopithecus garhi	Plausible intermediate between *Australopithecus* and *Homo*	2.5	East Africa	
Australopithecus ramidus	(see *Ardipithecus ramidus*)			
Australopithecus robustus	Robust. May have used tools	2–1.5	South Africa	
Homo antecessor	Likely Neanderthal ancestor, claimed to be the common ancestor of us and Neanderthals	0.7	Spain	
Homo erectus	Human body but slightly smaller brain	1.8–0.2(–0.025?)	Africa, Eurasia	Peking Man, Java Man
Homo ergaster	Intermediate between habilines and *erectus*	2–1.5	East Africa	Turkana Boy
Homo habilis	Resembles *Australopithecus*, but slightly larger brain and indications of tool use	2.3-1.8	East and South Africa	
Homo heidelbergensis	Intermediate between *H erectus* and *sapiens*	0.5–0.2	Africa, Europe	
Homo helmei	(see *H heidelbergensis*)			
Homo neanderthalensis	Large-bodied large-brained Ice Age hunter. Coexisted with modern humans for millennia	0.5–0.03	Europe, Middle East	
Homo rudolfensis	Close relative of *H habilis*, formerly believed to belong to that species	2	East Africa	
Homo sapiens	Go look in a mirror!	0.2–0	Earth and Moon	Cro-Magnon
Homo sapiens (archaic)	(see *H heidelbergensis*)			
Homo sapiens neanderthalensis	(see *H neanderthalensis*)			
Homo sapiens sapiens	(name sometimes used to distinguish strictly modern humans from neanderthals and archaic *sapiens*)			
Kenyanthropus platyops	Recently discovered, possible *Homo* ancestor	3.5	East Africa	
Orrorin tugenensis	Possibly bipedal, close to the common ancestor of humans and chimps	6	Kenya	
Paranthropus	(see robust *Australopithecus*)			
Pithecanthropus erectus	(see *Homo erectus*)			
Praeanthropus africanus	(see *Australopithecus afarensis*)			
Sinanthropus pekinensis	(see *Homo erectus*)			
Zinjanthropus boisei	(see *Australopithecus boisei*)			

Table 1: Overview of the various hominid species discussed in the text, including alternate names for the same fossils. The usage varies in the literature; the names designated as primary in the table are the ones I use in the text.



(Foley, 1997)

Figure 5: Three different habiline skulls. a) KNM-ER 1813, *Homo rudolfensis?* b) KNM-ER 1470, *Homo habilis?* c) Stw-53, *Homo habilis*

find of Kimbel et al (1996) may be the oldest *Homo* yet, at 2.3 million years. The dating of another find, KNM-ER 1470, caused a major controversy (Lewin, 1987), but when the dust had settled the consensus view converged on a younger date (but see Fitch et al (1996)).

Habilines generally have somewhat larger brains than australopithecines, and have more humanlike teeth. But the differences between habilines and australopithecines are slight, and might not have been considered significant, were it not for two factors:

- Stone tools turn up in the archaeological record at about the same time as habiline fossils (Wood, 1997b; Semaw et al, 1997; Kimbel et al, 1996), and keep on looking much the same throughout the tenure of the habilines (Semaw, 2000).
- Habilines (some of them, at least) are plausible ancestors of later, more clearly human, fossils.

Of the various habilines, the group sometimes called *H rudolfensis* is the least humanlike (Lieberman et al, 1996), with a small brain (around 600 cm^3) and rather apelike body proportions (Johanson & Shreeve, 1989; McHenry & Berger, 1998, but see also Korey (1990)). *Homo habilis sensu stricto* has clearer human affinities according to most authors (though Strait et al (1997) disagree), and is the probable ancestor of later humans.

After the habilines, evolution towards a more human form is rapid. *Homo erectus*, present in the fossil record from 1.8 million years ago, is indubitably human, with a body below the neck that is barely distinguishable from ours. Early African transitional forms between habilines and *erectus* (Walker & Shipman, 1996; Leakey & Lewin, 1993) are often called *Homo ergaster* (figure 7), a usage which I will adopt in this work, even though there is no clear dividing line between *ergaster* and *erectus*, just a gradual increase in brain volume, from about 900 cm^3 to 1100 cm^3. The brain size, and associated skull shape, is the main character distinguishing *erectus* from *sapiens*. Other differences are minor, though some, like the prominent brow ridges above the eyes, are pretty obvious.

Homo erectus is also the first in the human family to spread beyond Africa[48], possibly as much as 1.7 million years ago (Gabunia et al, 2000), though Goguitchaichvili & Pares (2000) argue for caution in interpreting that dating. Fossils of *erectus* are widespread in Asia ("Peking Man" (Tattersall & Sawyer, 1996; Grün et al, 1997), "Java Man" (Delson et al, 2000; Broadfield et al, 2000), etc. — see figure 8), and probably reached Europe as well (Ascenzi et al, 1996; Oms et al, 2000; Rightmire, 1995; Clarke, 2000; Roebroeks, 2001), though the evidence is not totally clear (Tattersall, 1997; Ascenzi et al, 2000). As far as we know they did not reach the New World[49], but they did manage to colonize islands

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[48] There are unconfirmed reports of fragmentary finds in Asia that may be attributable to *Homo habilis*, but so far nothing substantial.

[49] But see Turtledove (1988) for some entertaining speculations.

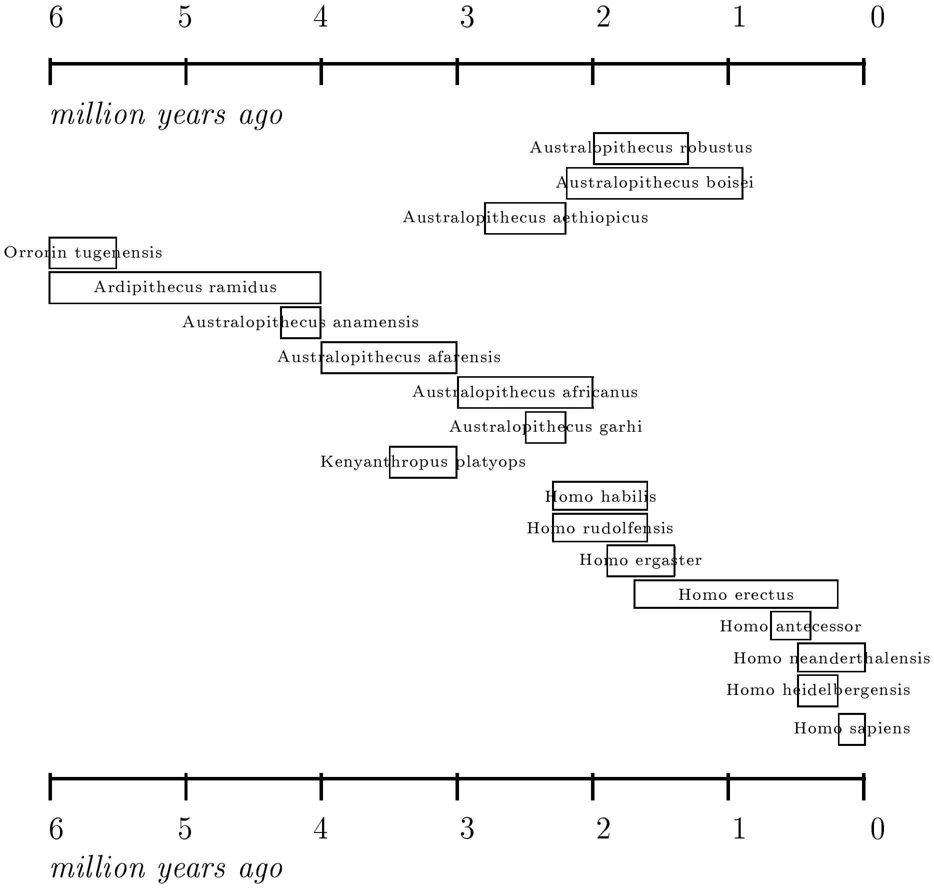
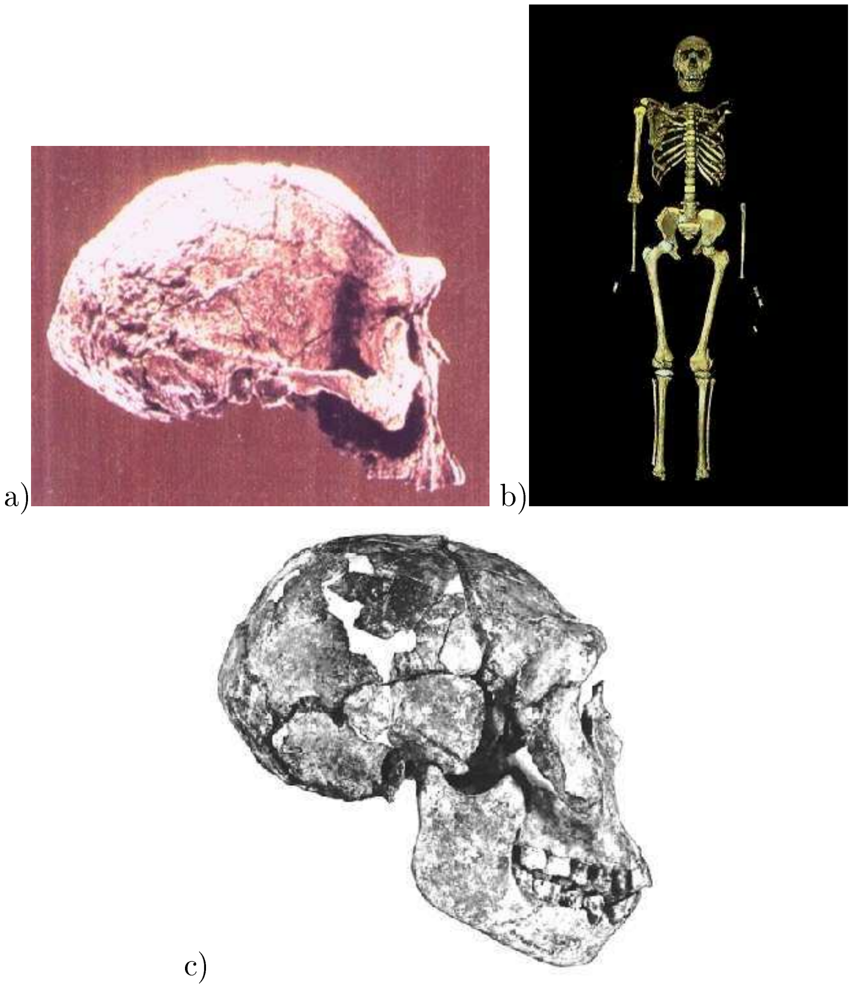


Figure 6: Overview of the approximate times at which the various hominid species existed.



(Foley, 1997)

Figure 7: Fossils of *Homo ergaster* (sometimes labeled as *Homo erectus*). a) KNM-ER 3733 b),c) Different views of KNM-WT 15000, “Turkana Boy”.

(Foley, 1997)

Figure 8: *Homo erectus* — "Peking man".

in what is now Indonesia, that were unreachable without boats (Morwood et al, 1998).

The material culture of *Homo erectus* included a well-defined set of standardized stone tools, known as the Acheulean industry, which represents a significant step forward from the crude tools of earlier humans (Oldowan industry). These are used by *erectus* everywhere except[50] possibly Western Europe, where Oldowan tools have been found (Carbonell et al, 1999; Roebroeks, 2001). It is possible that *Homo erectus* used fire, since traces of fire, interpreted as ancient hearths, have been found in caves where they lived, but the evidence has recently been increasingly questioned (Balter, 1995; Wuetrich, 1998; Wu, 1999).

The last *Homo erectus* may have persisted in Asia until quite recent times, possibly as late as 25,000 years ago, well after the arrival of modern *Homo sapiens* (Gibbons, 1996b; Swisher et al, 1996, but see also Grün & Thorne (1997)).

In conclusion, the period from 2 million years ago up to 0.5 million years ago marks the transition from bipedal apes, with no remarkable cognitive abilities, to people with brains near the modern human norm, and with the cognitive skills to develop a material culture effective enough to enable their spread across half the world.

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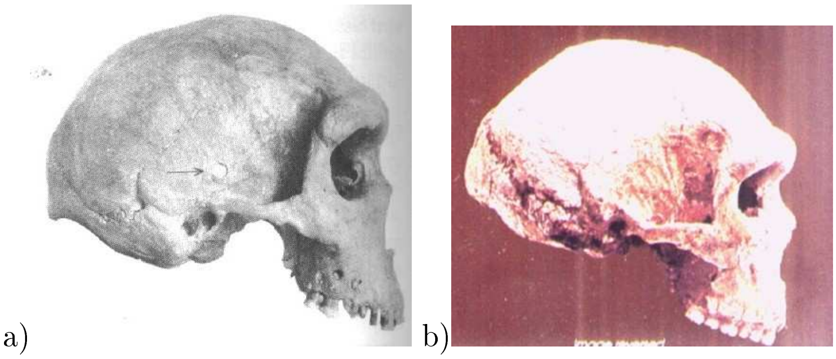
[50] It was formerly believed that this toolset was lacking also in East Asia (Tattersall, 1997; Ciochon & Larick, 2000), but Acheulean tools have recently been found in China (Yamei et al, 2000).



a) b)

(Foley, 1997)

Figure 9: Fossils of intermediate forms between *Homo erectus* and *sapiens*, that may be attributed to *Homo heidelbergensis*. a) "Rhodesia Man", skull found in what is now Zimbabwe b) Skull found in Petralona, Greece.

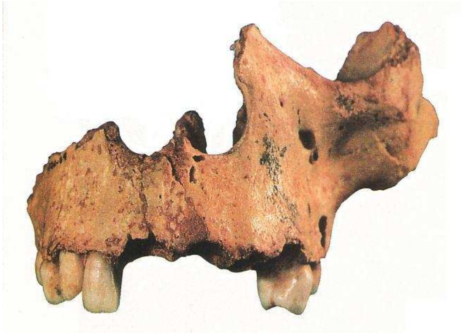
3.3.3 Ourselves and other humans

This brings us, finally, to the origin of our own species, *Homo sapiens*. But again, just like with the habilines, the fossil situation is messy and complex, with many different fossils displaying different mixtures of *erectus* and *sapiens* characters. It is likely that there were at least two separate branches on the family tree during the last 500,000 years, one leading to us and one leading to Neanderthals (figure 11). But it is unclear how isolated these branches were from each other.

This entire assembly of *erectus-sapiens* transitional fossils (figure 9) is sometimes labeled as *Homo sapiens*, in which case the phrase "archaic *sapiens*" is used for the more *erectus*-like ones and "anatomically modern *sapiens*" is used to specify the late fossils that are indistinguishable from us living humans. Likewise, some people regard Neanderthals as just a subspecies: *Homo sapiens neanderthalensis* (Foley, 1997). Others prefer to split this group into several species. *Homo heidelbergensis* has gained a fair amount of acceptance in recent years as a label for the clear *erectus-sapiens* intermediates, as discussed in Rightmire (1995; 1996), whereas McBrearty & Brooks (2000) favour the name *Homo helmei* for the African intermediates. But the naming of some recent fragmentary Spanish finds (figure 10) as a separate species, *Homo antecessor* (Bermudez de Castro et al, 1997; Bermudez de Castro et al, 1999; Arsuaga et al, 1999; Falguères et al, 1999; Carretero et al, 1999; Lorenzo et al, 1999), has met with considerable skepticism (Gibbons, 1997b; Delson, 1997).

The issue of how many species there were in the *erectus-sapiens* interface is intimately entwined with a major debate concerning the origin of *Homo sapiens*, that has been ongoing for some decades: the fight between the two hypotheses (Treisman, 1995):

- *Out of Africa:* We evolved from a small subpopulation of *Homo erectus*



(Foley, 1997)

Figure 10: *Homo antecessor*, part of a face.

in Africa, and spread from there all over the world, replacing the resident *erectus* and *neanderthalensis* populations without significant intermixing. (Stringer & McKie, 1996)

- *Multiregional evolution:* The different races of modern humans evolved separately from different local populations of earlier humans: Asians evolved from "Peking Man", Europeans from Neanderthals, Africans from African *erectus*, and so on. (Wolpoff et al, 1984; Trinkaus & Shipman, 1993; Wolpoff & Caspari, 1996; Hawks et al, 2000)

The debate is now approaching a consensus, in favour of the Out-of-Africa hypothesis, largely based on the recent arrival of massive amounts of molecular evidence, as well as on difficulties with the multiregional hypothesis — separate evolution would generally lead to separate species, whereas modern *Homo sapiens* is most definitely one single, genetically rather homogeneous species[51] (Barbujani et al, 1997; Gibbons, 1995a; Hickson & Cann, 1997).

The molecular data strongly support a fairly recent common origin for all extant humans, somewhere in the vicinity of 200 000 years ago (Ayala & Escalante, 1996; Wood, 1997a; Bergström et al, 1998). The so-called "Mitochondrial Eve"[52] (Cann et al, 1987; Saville et al, 1998; Cavalli-Sforza, 1998), the putative common ancestress of all women, was at the forefront of this molecular wave, but she has since been joined by a corresponding "Y-chromosome Adam"[53] (Fu et al, 1996;

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[51] The standard biological criterion for regarding two individuals as belonging to the same species is based on their ability to produce offspring together. By this criterion, *Homo sapiens* is definitely a single species, as conquered people on all continents have found out the hard way.

[52] Mitochondria are small bodies inside each cell, which carry their own DNA, and which are inherited from mother to daughter exclusively (or nearly so (Ankel-Simons & Cummins, 1997; Awadalla et al, 1999, but see also Kivisild et al (2000))). This makes it possible to trace descent through the female line. See the review of Stoneking & Soodyall (1996) for more details.

[53] The Y-chromosome is inherited exclusively from father to son, so it traces the male line, in the same way that mitochondria trace the female line.

Dorit et al, 1995; Pääbo, 1995), as well as by data from non-sex-linked genes (Fischman, 1996), and from X-chromosomes (Disotell, 1999). All this supporting evidence makes the fact that problems (Gibbons, 1998a) have been found with the original Eve studies (Cann et al, 1987) rather uninteresting; the total case for a recent common origin[54] for all humans is highly compelling.

The case for placing this recent common origin in Africa, rather than elsewhere, rests on three types of evidence:

- *Fossils.* The oldest modern human fossils (Tattersall, 1997; Pickford & Senut, 1998, but see also Wolpoff & Caspari (1996)), are found in Africa.
- *Archaeology.* The oldest archaeological traces of modern human behaviour, with more complex tools and ornaments, are found in Africa as well (Brooks et al, 1995; Gibbons, 1995b), and appear to arise gradually there (McBrearty & Brooks, 2000).
- *Genes* (Templeton, 1997). When constructing our family tree from the present-day distribution of genes, it appears that non-African populations share an even more recent common ancestor with each other, than Africans do. This implies that the human family tree is rooted in Africa (Reich & Goldstein, 1998). This has been checked with various types of genes:
  - Mitochondria: (Cann et al, 1987; Stoneking & Soodyall, 1996; Saville et al, 1998; Cavalli-Sforza, 1998; Parks, 1999; Disotell, 1999; Maca-Meyer et al, 2001), but see also Adcock et al (2001) and Relethford (2001).
  - Three different kinds of small repeated DNA pieces: (Batzer et al, 1994; Goldstein et al, 1995; Tishkoff et al, 1996), but see also Pritchard & Feldman (1996)).
  - Y chromosomes: (Gibbons, 2001; Ke et al, 2001; Thomson et al, 2000), but see also Brookfield (2000).
  - X chromosomes: (Disotell, 1999), but see also Harris & Hey (1999).

  as well as with more general methods (Ruvolo, 1996). Population genetic data also indicate that Africa had a larger population throughout the relevant period (Relethford & Jorde, 1999), and that non-African people may have passed through a bottleneck with very small population (Alonso & Armour, 2001; Rogers, 2001).

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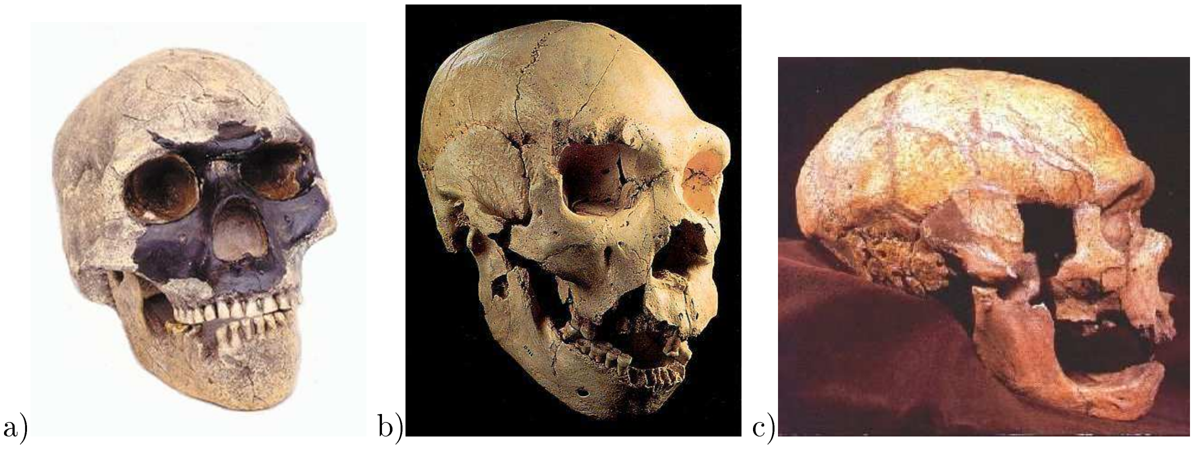
[54] But the Adam-and-Eve talk should not be taken too literally, as has been done by some Biblical literalists (and some journalists) — the results by no means imply that only a single pair of humans existed at any particular time, and the time frame is nowhere near the Biblical one, There is, however, a fair bit of evidence for a tight population bottleneck in our not-too-distant past, perhaps 100,000 years ago (Ambrose, 1998; Gibbons, 1995a; Zietkiewicz et al, 1998; Gagneux et al, 1999a; Takahata & Satta, 1997), when humans apparently came perilously close to extinction (but see also Ayala et al (1994) and Hey & Harris (1999)). Chimps, on the other hand, haven't gone through any bottleneck, and retain high genetic diversity (Kaessmann et al, 1999).



(Foley, 1997)

Figure 11: Fossils of *Homo neanderthalensis*. a) The original Neanderthal from the Neander valley b) Atapuerca 5, from the same site as *Homo antecessor* c) The old man from La Chapelle aux Saints.

- *Morphology.* The modern people who most closely resemble our ancestors in anatomical details live in Africa (Irish, 1998; Stringer et al, 1997).

A recent common origin for *Homo sapiens* is further supported by the recent recovery of DNA[55] from two different Neanderthal fossils (Kahn & Gibbons, 1997; Ward & Stringer, 1997; Krings et al, 1999; Höss, 2000; Ovchinnikov et al, 2000), showing that Neanderthals had diverged from *Homo sapiens* somewhere around half a million years ago, and were not more closely related to modern Europeans than to other modern humans, as the multiregional hypothesis would predict. But multiregionalism supporters, like Wolpoff (1998), are not entirely convinced. And there is also a recent report of a fossil find of a Neanderthal-sapiens hybrid child (Duarte et al, 1999)[56], which would argue for a closer relationship between the two[57].

Apart from this possible hybrid, Neanderthals appear to have had a rather

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[55] The Neanderthal DNA discussed above is the oldest confirmed fossil hominid DNA. There was, however, a recent news report, still unconfirmed, of 1.8 million years old DNA recovered, presumably from *Homo ergaster* (Smillie, 2001). If true, this would be a major sensation.

[56] This article led to emotional outbursts that are remarkable even by the standards of paleoanthropology (Holden, 1999); see Tattersall & Schwartz (1999) and particularly the response of Trinkaus & Zilhao (1999). On a not totally unrelated note, this find was also regarded as of sufficient general interest to be spread by a major news service (Hatton, 1999), which is quite rare for any scientific result.

[57] On the other hand, the last surviving Neanderthals appear "pure", with no admixture of *sapiens* genes (Hublin et al, 1996), and the earliest *sapiens* in Europe more resemble Africans than Neanderthals, as observed in body proportions by Holliday (1997; 1999) and in general morphology by Tyrrell & Chamberlain (1998).

stable existence in Europe and western Asia, coexisting with *Homo sapiens* for quite some time in the Middle East, but eventually being driven to extinction. The last Neanderthal finds are from southwestern Europe, about 30,000 years ago (Hublin et al, 1996), which also may have been the area in which they evolved, as rather clear *erectus*-Neanderthal transitional fossils have been found in Europe (Arsuaga et al, 1997; Dean et al, 1998). For most of their existence, the Neanderthals used the so-called Mousterian set of stone tools, but the very last Neanderthal populations showed some technological and cultural progress, with more complex and diverse tools, as well as personal ornaments (Hublin et al, 1996; Simek & Smith, 1997). This progress may have been influenced by the encroaching *sapiens* hordes, with which these Neanderthals must have been in contact for some time, though others argue in favour of independent invention (Bahn, 1998).

The exact cause of the demise of the Neanderthals remains uncertain, though interaction with *Homo sapiens* is high on the list. But this interaction may have been anything from out-and-out genocide to simple competition for food. There is some evidence of the Neanderthals having led a much more strenuous life than contemporary *sapiens* (Gibbons, 1996a), which may indicate their being less efficient food-gatherers. But the cause of the difference in efficiency, if any (Sorensen & Leonard, 2001), is far from clear. Everything from the domestication of dogs (Sejnowski, 1999; Morell, 1997; Vila et al, 1997) to the origin of language (Maddox, 1998) has been invoked, assuming in both cases that the Neanderthals lacked dogs or words, which is far from obvious. Any straightforward physical takeover is unlikely, since the Neanderthals were larger and stronger than we are (Gibbons, 1997a; Holliday, 1997; Kappelman, 1997; Ruff et al, 1997). There is some evidence that modern humans had a more varied diet than the mainly meat-eating Neanderthals (Richards et al, 2001), and also evidence from hand anatomy indicating that Neanderthals and modern humans used their tools differently, a difference that can be attributed to modern humans, but not Neanderthals, hafting their tools (Niewoehner, 2001). On the other hand, Briggs (2002) reports finds of what is interpreted as glue associated with Neanderthals, possibly used for gluing hafts to tools.

What is quite clear from the archaeological record is that the arrival of modern humans was accompanied by a marked increase in cultural diversity and inventiveness. The oldest traces of such a “modern” culture are from Africa (Brooks et al, 1995; Gibbons, 1995b) (thus lending more support to the “Out of Africa” scenario).

The extent to which Neanderthals had a human mind and human culture remains controversial. Their brain is, if anything, larger than ours, but differently proportioned with smaller frontal lobes and larger occipital lobes. There is some evidence of ceremonial burial of (and presumably by) Neanderthals (Trinkaus & Shipman, 1993), which would imply a human level of awareness of self and others, but the evidence is still open to other interpretations (Gargett, 1999), and there is also evidence of Neanderthal cannibalism[58] (Defleur et al, 1999; Culotta, 1999b). Neanderthals also cared for their elderly and crippled members, as fossils have been found of Neanderthals with healed injuries and chronic diseases, who must have lived for years unable to fend for themselves (Trinkaus & Shipman, 1993; Onion, 2001). Fragments of what may have been musical instruments have also been found associated with Neanderthals[59] (Zhang et al, 1999).

After the demise of the Neanderthals (and the possibly simultaneous disappearance of Asian *erectus* (Swisher et al, 1996)), the only humans left on Earth was a homogeneous population of modern *Homo sapiens*, which was fruitful and multiplied and rapidly spread to all continents except Antarctica. By 10,000 BC, essentially all inhabitable land was the territory of some hunter-gatherer tribe or another. Since their first appearance in Africa, modern humans have remained morphologically unchanged, apart from the minor superficial details that we use to tell apart people from different continents. The uniform language capacities of all human populations today prove that all adaptations for language, biological and otherwise, must have been in place at the very latest by the time modern humans parted company on their way to different continents some 60,000 years ago or more.

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[58] Cannibalism is also indicated for *Homo antecessor* (Fernández-Jalvo et al, 1999a), and for that matter *Homo sapiens* (Marlar et al, 2000).

[59] While the Neanderthals may have been the oldest musicians, Lineweaver (in press) would place the oldest *music* some 13 billion years before their time, echoes of which are still detectable today.

4 On the anatomical and neurological prerequisites for language

The use of language is possible only for beings possessing a number of specific capabilities. Spoken language requires the physical ability both to produce and to perceive complex strings of sounds, making great demands on the performance of the vocal and hearing organs, discussed in section 4.1 and 4.2. Other possible modalities of language, such as sign language, make corresponding demands within their own domains, e.g. manual dexterity and visual acuity. The emphasis here will be on speech both because it is our dominant modality today, and because there is considerable evidence that our vocal organs are specifically adapted for speech. Sign language will be discussed further on page 85. The greatest language-specific demands are, however, those placed on the processing capacity of the brain, regardless of the modality used. A substantial fraction of the human brain is used in language processing, though there is no consensus on to what extent language is processed in physically separate, dedicated modules, nor any consensus on to what extent our language processing machinery is genetically determined. Neurological evidence addressing these issues is reviewed in section 4.3

4.1 Sound production

All mammals, with rare exceptions, are capable of producing a variety of sounds, and many of them use sounds for communicative purposes (Hauser, 1997). But human language, at least in the forms spoken by people today, requires a highly sophisticated vocal apparatus, capable of rapid sequences of precisely modulated sounds (Deacon, 1997), that are out of reach of most other mammals, specifically including our closest relatives (Savage-Rumbaugh et al, 1993a). There are three main factors contributing to this deficit in non-human primates:

- *The shape and flexibility of the vocal tract.* In humans, the larynx has descended further down the throat, compared with its position in other primates[60], increasing the space available for articulation. Furthermore, the supralaryngeal tract in humans is bent almost 90 degrees, unlike the fairly straight tube of most other mammals, broadening the spectrum of articulatory possibilities (Lieberman & McCarthy, 1999; Aiello, 1998). Figure 12 compares the vocal tract of a human and a chimpanzee.

  Humans also possess a more mobile and flexible tongue.

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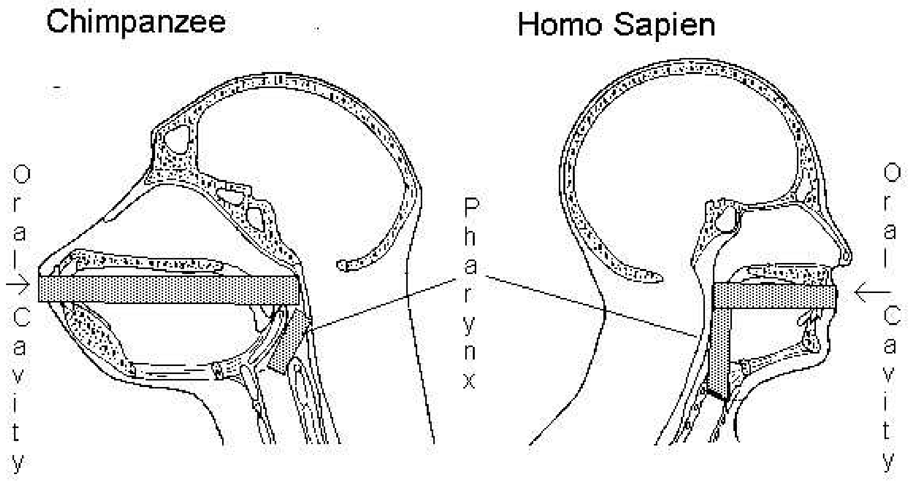
[60] In this particular case, ontogeny does recapitulate phylogeny, as human babies are born with the larynx in the ape position (Lieberman & McCarthy, 1999), which is better suited for breast-feeding. The larynx then descends as the baby graduates from breast-feeding to talking, gradually from age 3 months to 3 years or so (Fitch, 2000).



(Dwyer, 1999)

Figure 12: The vocal tract of a chimpanzee (left) and a human (right). The superimposed bars indicate the major segments of the supralaryngeal tract.

Apes can produce approximations of several human vowels, but not all, and have severe difficulties with consonants, particularly stops, largely due to the anatomical impossibility of their achieving rapid velopharyngeal closure (closing off the connection between nose and mouth), without which air isn't forced towards the constrictions that we use to make consonants (Savage-Rumbaugh & Lewin, 1994).

There have been some controversies concerning at what point in human evolution did the descent of the larynx take place. It has been argued that it did not take place until the advent of *Homo sapiens*, and that Neanderthals retained an apelike vocal tract (Lieberman & Crelin, 1971), but others would place it earlier (Falk, 1975; Le May, 1975), possibly as early as *Homo ergaster* (Aiello, 1998). The position that the Neanderthal vocal tract differed substantially from ours still has its defenders (Schwartz & Tattersall, 1996; Laitman et al, 1996, but see Franciscus (1999)), but appears hardly tenable after the discovery of a Neanderthal hyoid[61] bone (Arensburg et al, 1989). This bone was very similar to a *sapiens* hyoid, leading to the conclusion that Neanderthals had a human vocal tract (Houghton, 1993) and were anatomically capable of human speech (Arensburg et al, 1990; Arensburg & Tillier, 1991)[62]. This conclusion will be strengthened if recent

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[61] A bone which sits in the floor of the mouth, providing attachment for muscles moving the tongue and larynx (Aiello & Dean, 1990), thus playing a crucial role for speech.

[62] Also Philip Lieberman (of Lieberman & Crelin (1971), the seminal paper arguing for Neanderthal muteness) appears to have changed his mind, at least partially, according to Holden (1998). (Note that Lieberman & Crelin (1971) and Lieberman & McCarthy (1999), both cited in this section, are two different Liebermans.)

(August 2001) rumours are true, that a skull of *Homo antecessor* has been found which also displays a human vocal tract.

The bending of the supralaryngeal tract introduces some changes in the cranial base, hints of which can be seen already in *Homo ergaster* (Tattersall, 1998), though Fitch (2000) cautions against drawing far-reaching conclusions. The cranial base is affected by our increased brain size, by the change to bipedal posture, and by the shrinking of our jaws (Spoor, 2000), all of which will confound any effect from speech adaptations.

It would appear then that the human vocal tract has an ancient history, dating back at least to our common ancestor with Neanderthals, perhaps half a million years ago. This common ancestor would be *Homo erectus* or a close relative, thus extending the age of the human vocal tract for the full span of *erectus*, a million years (Holden, 1998) or a bit more. Reeves et al (1996) argue for a larynx move around two million years ago, among the first *Homo*, not primarily for speech, but as an adaptation to a drier habitat, and Pearl (2000) places it even earlier, as a byproduct of the transition to bipedalism. Its later utility for speech can in these cases be regarded as an exaptation.

Another proposed reason for the descent of the larynx is sexual selection favoring a deeper voice in males (Randerson, 2001). This is a plausible explanation for the additional descent taking place in males at puberty, but hardly for the whole process.

A puzzling aspect of larynx evolution in humans is the loss of the laryngeal air sacs that all our relatives have. The sacs almost certainly play a role in the vocal communication of apes, but little is known of the details. Nevertheless, the loss of a vocal adaptation in such a vocal species as ours is odd (Fitch, 2000).

The human vocal tract in its current form is exquisitely adapted for speech, at considerable evolutionary expense (Pinker & Bloom, 1990; Spangle & Menzel, 1991; Pinker, 1995; Fitch, 2000). This makes it somewhat problematic to argue for its origin as a rather marginal improvement for some other purpose, or just a byproduct of some other adaptation. If the modifications of the vocal tract did evolve for the purpose of facilitating speech, as appears highly likely, this implies that our ancestors had some form of spoken language before they had a human vocal tract — evolution does not plan ahead!

- *The neural wiring of the vocal apparatus.* Humans have direct conscious control of their vocal chords from the cortex, whereas apes have access only through indirect means, that cannot be easily modulated voluntarily, similar to human laughter and other non-voluntary sounds. This limits the range of sounds that apes and monkeys can produce to minor variations around largely innate templates. With extensive training, some progress can be made, but cross-fostering experiments between different primate species (ape-human and monkey-monkey) have been near-total failures — even monkeys cross-fostered with another monkey species whose vocalizations ought to be within reach, failed (Fitch, 2000). The easy vocal learning and vocal imitation of humans appears to be unique among primates.

The standard mammal neural wiring of the vocal chords includes tight connections between the procedures for swallowing and breathing, that need to be precisely synchronized. This system has apparently been re-wired in humans, in evolutionarily recent times (as everybody who has choked on a piece of food knows, some debugging remains to be done) (Deacon, 1997). The situation in other primates is, however, not entirely clearcut, and may be interpreted as intermediate between the human and the standard mammalian condition (Mueller, 1996). Humans also have significantly more motor neurons going down the spine to the thorax (presumably for breathing control), which may well be an adaptation for speech[63] (MacLarnon & Hewitt, 1999). This would be visible in well-preserved fossils, but as recently as *Homo ergaster* it is absent (Walker & Shipman, 1996), as it is in australopithecines. Neanderthals, on the other hand, are similar to modern humans in this respect (MacLarnon & Hewitt, 1999), indicating that the enhanced breathing control evolved sometime between 1.6 and 0.5 million years ago. If language were the driving force behind this evolutionary step, then *Homo erectus* must have possessed language in some form.

This enhanced breathing control has also been linked to bipedal walking, as effective quadrupedal walking requires close coordination of breathing pattern and stride. The independent breathing control necessary for speech wasn't possible until we were walking upright (Melichar, 1999).

A similar case of nerve canal enlargement is the hypoglossal canal, which is a conduit for the nerves controlling the tongue. The hypoglossal canal is significantly larger in humans than in most other apes, again presumably because of the finer control of tongue movements necessary for speech. Concerning the fossil situation here, Kay et al (1998) and DeGusta et al (1999) are in direct contradiction. Kay et al (1998) state that australopithecines have ape-sized hypoglossal canals, and later *Homo* have modern ones, consistent with what is found for vocal tract shape, whereas DeGusta et al (1999) claim that human-sized hypoglossal canals are found both in some australopithecines and in various nonhuman primates, making any conclusions concerning speech effectively impossible.

Concerning neural control of articulation, MacNeilage (1997) proposes a

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[63] It has been suggested by Verhaegen (1998), a proponent of the Aquatic Ape Theory (Morgan, 1982, but see also Langdon (1997)) that the breathing control is instead an aquatic adaptation, later co-opted as an exaptation for language. But MacLarnon & Hewitt (1999) reject both this and other alternative explanations for the nerve canal enlargement.

detailed theory of its evolution, invoking the rhytmic jaw motions of chewing and sucking (still visible in infant babbling) as exaptations.

- *Control of rapid sequencing of motor actions.* Humans have the ability to produce rapid complex sequences of actions, an ability which is obviously vital to speech[64], but which is also used for e.g. accurate throwing (Calvin, 1993). The action sequences performed by humans are too rapid for sensory feedback, so the sequences must be pre-planned, and executed with split-second timing. Other animals also use rapid action sequences, but these are generally shorter and more stereotyped than what humans are capable of (Ott et al, 1994).

  The timing precision requirements, both in speech and in throwing, is a matter of milliseconds. For example, throwing a ball and hitting a 20 cm target 8 meters away, which most people are capable of, requires the ball to be released within a time window on the order of 2-3 milliseconds, with the various muscle actions involved coordinated at a similar level of precision (Chowdhary & Challis, 1999). It takes around 100 times longer for the brain to receive and act upon any return signals from the throwing arm, so the throw has to be entirely pre-planned. A further complication is that individual neurons in the brain do not have that kind of timing accuracy — the intrinsic timing jitter in neuron firing is on the order of 10 ms. Higher precision can be achieved by averaging the signals from multiple neurons, which is both mathematically and neurologically straightforward, but the number of required neurons grows exponentially with the precision requirements (Calvin, 1993).

  In comparison with human beings, monkeys perform miserably in throwing tasks — they need to be ten times closer to the target to achieve comparable accuracy (Westergaard et al, 2000, cited in Watson (2001)).

  Some speech features, such as voice onset time, also need to be produced with a timing accuracy much better than any conceivable feedback loop time (Ladefoged, 1971; Cho & Ladefoged, 1999). Before we receive any feedback on our speech production, we are several phonemes further ahead, so the feedback comes much too late to do any good. Nevertheless, we manage to produce streams of dozens of phonemes, each of which requires several separate motor actions (tongue, lips, vocal chords, lungs, ...) to be coordinated to within 10 ms or so[65].

  Likewise, the decoding of speech must work at similar speeds, detecting features in incoming sounds with millisecond precision, and going through all the multiple steps in the decoding of a full sentence in a time not sig-

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[64] Donald (1997) appears to disagree, but offers no real arguments.

[65] Other aspects of language are remarkably rapid as well. For example, in an elegant experiment Turennout et al (1998) demonstrate that it takes only 40 ms from the lexical retrieval of a word until its phonetics is generated.

nificantly longer than the time it takes to say the sentence. This requires a different kind of rapid-sequence handler, the origins of which is unclear.

There are multiple proposals for the brain location handling this rapid sequencing of both speech and other actions[66]. Broca's area (Broca, 1861, further discussed in section 4.3.2) is one candidate (Passingham, 1981; Wilkins & Wakefield, 1995), which may provide an alternative explanation for the nonfluent speech of Broca's aphasia. In further support, Calvin (1993) cites cases of patients with aphasia, and Joanisse & Seidenberg (1998) cases of children with specific language impairment, who also had trouble with motor sequences in general (but without general paralysis; the actions could be performed one by one, but not in rapid sequence). Calvin argues that a large chunk of the "language cortex" on the left side of the brain is actually a general "sequence handler", which handles language but also other sequencing tasks[67]. Hickok et al (1998a) disagree, citing evidence from sign-language aphasia, but Corina (1999) identifies gaps in Hickok et al's arguments, and labels their conclusion *"premature"* (p 234).

But other parts of the brain may also be involved; Richards & Chiarello (1997) propose a right-hemisphere role in higher-level action planning, and Desmond & Fiez (1998) cite evidence of the actual timing circuits being located in the cerebellum. This proposed role for the cerebellum is supported by both lesion and functional imaging studies reported in Ackermann & Hertrich (2000), but Mauk et al (2000) interprets the cerebellum as the seat of more generalized temporally specific learning. Lesions of the cerebellum commonly cause minor impairments of a variety of language components, something which Fabbro et al (2000) interprets as *"cerebellar lesions [...] may be related to altered language control processes (such as the control of the temporal and sequential organization [...]) rather than to impairment of specific modules of the language system [...]."* (p 185-186)

The evolution of a sequencing module may, as argued by Calvin (1993), have been a crucial step in human evolution[68]. It may originally have been an adaptation for improved throwing or other motor sequences, driven by straightforward natural selection for better hunting skills, something which may be supported by the persistent sex differences in throwing accuracy among modern humans (Watson, 2001). But once established, for whatever reason, such a sequencing module would be a vital exaptation for language, making the eventual evolution of speech much easier (Wilkins & Wakefield,

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[66] But the claim of Lorig (1999) that odor perception is one of these actions, that taxes the sequencing processor heavily enough to interfere with language processing, strikes me as rather unlikely.

[67] A pertinent experiment would be to compare the throwing accuracy of patients with different types of aphasia, but to my knowledge this has not been done, though Richards & Chiarello (1997) do refer to deficits in motor action planning among aphasia patients.

[68] A related scenario is that of McNeil (1996), where her central concept of "narrativity" means something very close to the sequencing of Calvin (1993).

> 1995; Calvin, 1993). Concerning the timing of its evolution, the first unequivocal throwing weapons in the archeological record are about 400,000 years old (Thieme, 1997), but, as Calvin (1993) notes, Acheulean "hand" axes, a million years older, would make excellent throwing weapons as well.

The evidence concerning the evolution of humanlike speech capabilities is not conclusive; we do not know for sure when it evolved, though it may well have been evolutionarily recent, certainly sometime during the past two million years or so. Some type of speech must have been present in our last common ancestor with Neanderthals, 500,000 years ago or so, though fully human speech with all our articulatory capacity need not be older than 100,000 years.

But this does not necessarily mean that language as such evolved at the same recent time. Language does not strictly require the full human set of speech sounds, but could well make do with a smaller number of phonemes, emitted by a simpler and more primitive vocal apparatus. In fact, no modern language uses the full capacity of our speech organs — there are languages that use as few as 11 sounds out of the hundreds that we are capable of producing (Vaneechoutte & Skoyles, 1998). It is thus not difficult to imagine proto-speech (MacNeilage, 1994), that could be spoken with a proto-human larynx with a much smaller repertoire of sounds. And the vocal apparatus of apes and monkeys does appear capable of producing a non-negligible number of phonemes that are usable for communication (if subtle to human ears), with a richer structure than has often been believed (Rendall et al, 1999; Fischer, 1998). This structure includes features like fundamental frequency declination (Hauser & Fowler, 1992), which has sometimes been claimed as a human language universal, as well as others (Maurus et al, 1988).

It is also conceivable that language first evolved in some other modality than oral speech. This possibility is further discussed on page 85.

But once our ancestors did possess speech, in any form, they would have been under a fair bit of selective pressure[69] for improving the vocal apparatus (Donald, 1997). This is the plausible time (whenever it was) for the descent of the larynx. There is also some evidence for the co-evolution of the shape of the vocal tract, its motor control system, and the human vowel system (Honda & Kusakawa, 1997), further strengthening the case for speech driving the evolution of the vocal apparatus.

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[69] Wray (1998) postulates an early phase of language evolution, without grammar. I would call this a one-word stage (see p 121), but Wray (1998) prefers to talk about holistic unanalyzed phrases. A system with a large number of wordlike units but no grammar may well, as argued by Wray (1998) and also from a different perspective by Nowak and associates (1999; 2000), place even heavier demands on phonetic differentiation than modern speech. This would strengthen the selective pressure towards articulatory richness and a complex vocal tract during early speech evolution.

4.2 Sound perception

The auditory apparatus as such is essentially identical in humans and other primates[70], and very similar in all mammals. Measured auditory abilities of humans and other apes do not differ significantly (Spoor & Zonneveld, 1998). The processing of sounds in the brain also appears similar, as described in detail by Kaas & Hackett (2000), at least up to the point where the processing becomes linguistic in a narrower sense, when human processing of language sounds shows a pattern of neural activation different from that of other sounds (Mueller, 1996).

The evolution of the mammalian ear is described in many textbooks, such as Cowen (1995), and also in e.g. Rowe (1996), with Manley (2000) covering the history of the inner ear in more detail. Clack (1998) covers the earliest history of our ears. The advantages of the mammalian ear, compared with its predecessors, consists mainly in a wider frequency range, extended towards higher frequencies (Meng & Fox, 1995; Manley, 2000).

It would appear then that the hearing of most mammals ought to be sufficient for speech perception, as is demonstrated by our everyday experience of e.g. dogs and horses responding to voice commands. As for the finer details of phonetic analysis, this does not appear to be a uniquely human skill either (Zoloth & Green, 1979). Monkeys are quite able to discriminate human phonemes (Sinnott, 1989; Sinnott & Adams, 1987; Sinnott & Kreiter, 1991), as are even guinea pigs (McGee et al, 1996) and some birds (Mueller, 1996). As noted by Savage-Rumbaugh et al (1993a), this is counterevidence against the fairly popular view that humans have a unique "phonetics module" that is needed to decode our phonemes.

Both monkeys (Rendall et al, 1996) and other mammals, such as elephants (Poole, 1999), dolphins[71] (Sayigh et al, 1998), seals (Insley, 2000) and hyaenas (Holekamp et al, 1999), have sufficient aural discrimination to recognize individual voices of conspecifics (and have the social intelligence needed to use this information). Likewise, the time resolution necessary for speech perception (around 25 ms) is present in mammals in general, and appears to be the basis even for such an apparently language-specific feature as the human categorical perception of voice onset time (Mueller, 1996; Simos et al, 1997). Categorical perception of entire calls is observed in the processing of vocalizations among several species of apes (Hauser, 2000), though the results of Fischer et al (2001) are less clearcut. Monkeys also show categorical perception of human phonemes, with perceptual boundaries close to where humans have them (Kuhl, 2000). The general auditory processing in primates is reviewed in Kaas et al (1999), and the processing of vocal communication in Wang (2000).

It is well established that humans, even pre-verbal infants, are very good at

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[70] For an image of some minor changes during primate evolution, see Kay et al (1997, fig 5).

[71] In the case of dolphins, they react to a kind of "signature whistle", different for each individual, and functioning very much like a name (Tyack, 2000; Janik, 2000).

perceiving speech, and segmenting it into language-relevant units (Kuhl, 2000; Saffran et al, 2001; Jusczyk, 1999)[72], a capability which has been invoked as an innate language specialization, notably by Chomsky (1957, cited in Kuhl (2000)). However, the sound-pattern analysis abilities that infants use for this purpose have been found to be usable also for the analysis of non-speech sounds, such as music (Saffran et al, 2001), which indicates that the abilities are not language-specific. The experiments establishing speech-analysis capabilities in infants have also been replicated in monkeys, who performed at the same level as the human infants (Hauser et al, 2001), from which it can be concluded that this segmentation capability has not evolved for the purpose of speech perception. Similarly, Ramus et al (2000) have found that monkeys and human infants are both good at discriminating between different unfamiliar human languages, when played forwards but not when played backwards.

One may thus conclude that human hearing in general, as well as phonetic discrimination and segmentation in particular, has not evolved especially for speech perception, but was available as an exaptation among our ancestors. This makes more sense than the converse, as it is evolutionarily more reasonable that the "choice" of phonetic distinctions to be used in communication was guided by the pre-existing discriminatory capacity of our hearing system, rather than having our hearing evolve in order to perceive speech. Some fine-tuning may have taken place to optimize speech perception (Pinker & Bloom, 1990; Moore, 2000) but the overall system is basically unchanged from our ancestors.

4.3 Brain anatomy, modularity, and lateralization

Our brain is our most complex organ, by far, and it is also the seat of the most important language adaptations. Unfortunately, our knowledge of this complex organ is far from complete, and is not really sufficient to determine how the brain handles language, other than at a gross anatomical level[73]. The study of brain function has nevertheless made great strides forward in the past decade or so, due to new non-invasive techniques, such as PET, MEG, ERP, and MRI, making possible imaging of the functioning brain (Horwitz et al, 1999; Lounasmaa et al, 1996; Osterhout et al, 1997). A review and synthesis of what is known about the evolution of our brain can be found in Allman (1999).

Brain evolution starts very early indeed in our history, in Precambrian times. The common ancestor of all bilaterian[74] animals most likely possessed some-

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[72] Newborn infants can even do this in their sleep, learning to discriminate sounds while fast asleep (Cheour et al, 2002). In adults, learning of any kind during sleep has been notoriously difficult to establish.

[73] There is only one animal whose brain anatomy is known in adequate detail to determine its exact function, and that is the nematode *Caenorhabditis elegans*. We can follow its growth, cell by cell (De Pomerai, 1990) and have mapped every single neuron in its nervous system, including the brain (Bargmann, 1998). The linguistic talents of this nematode are, however, modest, so it is of no great relevance in this context.

thing that might be called a brain (Nielsen, 1999), though a true brain, clearly homologous with ours, is a vertebrate characteristic (Pendleton et al, 1993; Shimeld & Holland, 2000).

One of the few consistent trends in evolution is towards larger and more complex brains, a trend that can be related to the argument of Ng (1996), that increasing complexity in nature favors the evolution of what Ng (1996) calls "rational species" (p 303) with larger brains — but the presence of rational species increases the complexity of the environment for other organisms, creating a complexity⇔brain feedback loop.

Even so, this trend towards larger brains is really clear only within the vertebrate lineage. Fish have fairly small and simple brains, but significant modification took place with each major evolutionary step, starting when the first fishes acquired legs and went ashore (Ahlberg et al, 1996; Coates, 1998). Evolutionary brain growth has taken place both through enlargement of already existing structures, and through the addition of new structures on top of the old ones. People sometimes refer to the "reptilian" part of our brain — this expression is quite literally true, since that part of the brain does correspond to structures that we have in common with reptiles. On top of the reptilian structures, mammals and birds have independently evolved an additional layer, with considerably larger processing capacity. The bird brain is basically an expanded reptile brain, anatomically quite different from the mammalian brain, but functionally comparable, at least up to a point. Figure 14 shows the relation between brain size and body size for different vertebrate classes. The distinction between fish and reptiles on one hand, and birds and mammals on the other, is evident. Primates cluster along the upper edge of the mammalian distribution, with humans together with dolphins as outliers well above the others.

The mammalian top layer is known as the neocortex. It evolved during the reptile-mammal transition 200 million years ago, in parallel with the ear changes mentioned in the previous section (Rowe, 1996; Karten, 1997; Kaas & Reiner, 1999). It is not just an additional layer of brain tissue, but adds a novel organizational principle (Nishikawa, 1997; Karten, 1997), opening the way for increasing complexity and processing power. The details of its origins are not quite clear, with at least two competing hypotheses (Kaas & Reiner, 1999; Nishikawa, 1997), but embryological studies with molecular techniques are approaching an answer (Karten, 1997; Deacon, 1997).

The basic brain structure of all different mammals is similar, with mainly quantitative differences (Nishikawa, 1997); figure 13 shows a few examples of different mammalian brains. The human brain is not notably different from others, apart from being much larger than the brain of a normal mammal of the same body size — but, as can be seen in figure 13, dolphin brains are comparable

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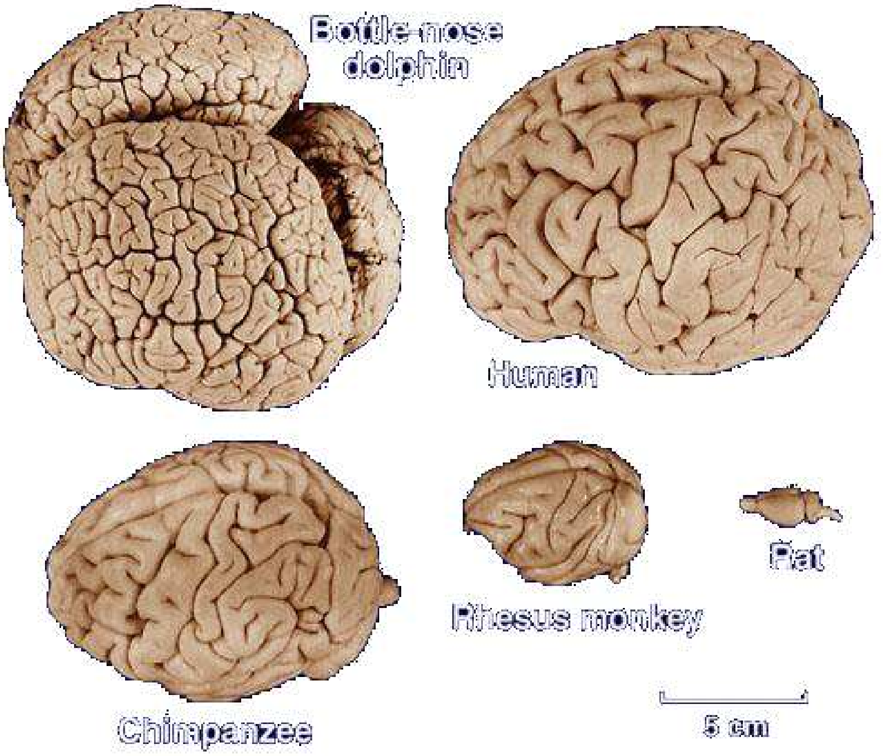
[74] Bilaterians are those animals that are bilaterally symmetric (or nearly so; see section 4.3.1). This includes pretty much everything that we see as animals in our everyday world, from flatworms to fruit flies, the only prominent exceptions being jellyfish and their relatives.



(http://serendip.brynmawr.edu/bb/brainevolution/brainevol1.html)

Figure 13: Brains of dolphin, human, ape, monkey and rat, all shown at the same scale.

to ours, in a similar-sized body. Much of the differences in brain size between different mammals can be attributed to body-size allometry[75]. But not all of the differences; primates in general, and humans in particular, have much larger brains than allometry would predict (Deacon, 1997; Martin, 1998).

The size differences are, however, not evenly distributed throughout the brain. The neocortex, and particularly the prefrontal lobes, have traditionally been regarded as a human specialization, even larger than would be predicted from a general enlargement, and constituting a larger fraction of the brain in humans than among other primates (Rilling & Insel, 1999). Recent studies of ape brains have, however, failed to confirm this, and instead appear to show that all the main parts of the human brain have increased in tandem (Nishikawa, 1997; Semendeferi et al, 1997; Semendeferi & Damasio, 2000; Clark et al, 2001). On the other hand, both Barton & Harvey (2000) and Clark et al (2001) find a neocortex enlargement

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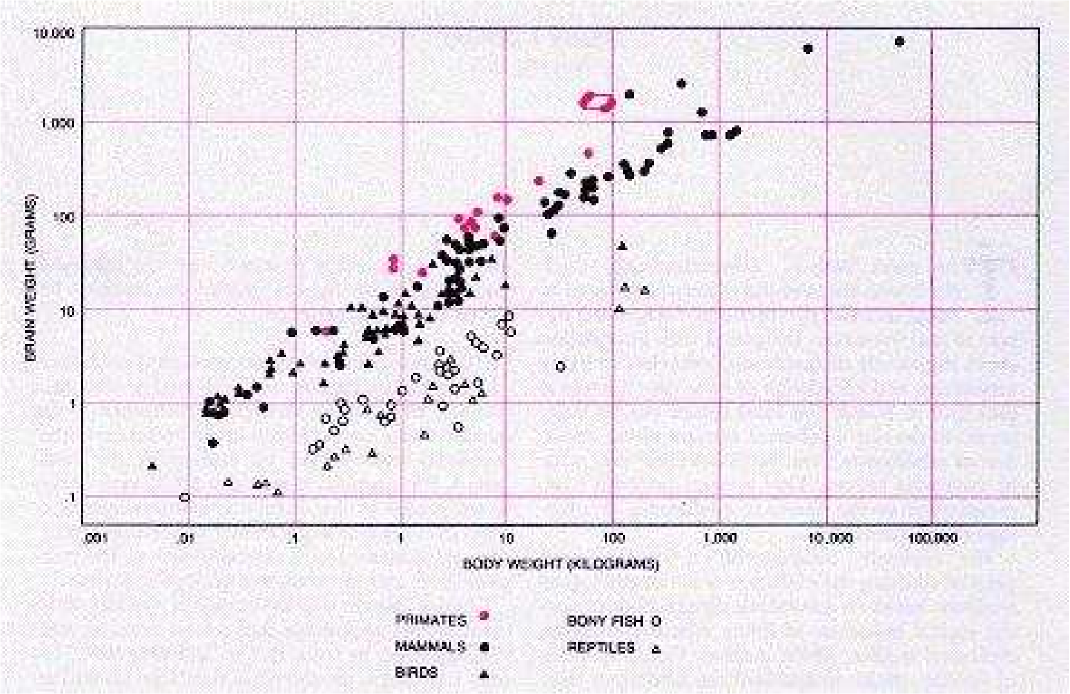
[75] “Allometry” is about the correlations between the sizes of different body parts, or between some part and the whole. “How much larger brain (or heart or whatever) does twice as big an animal have? Twice as large, or more, or perhaps less?” The answer to that question is a matter of allometry (Rifkin, 1995; Deacon, 1997).



(Jerison, 1976)

Figure 14: Brain size plotted against body size for about 200 species of vertebrates, with different symbols for different classes, as shown above. The four connected dots in the middle of the upper part of the figure delineate the range of variation in brain and body size in modern humans.

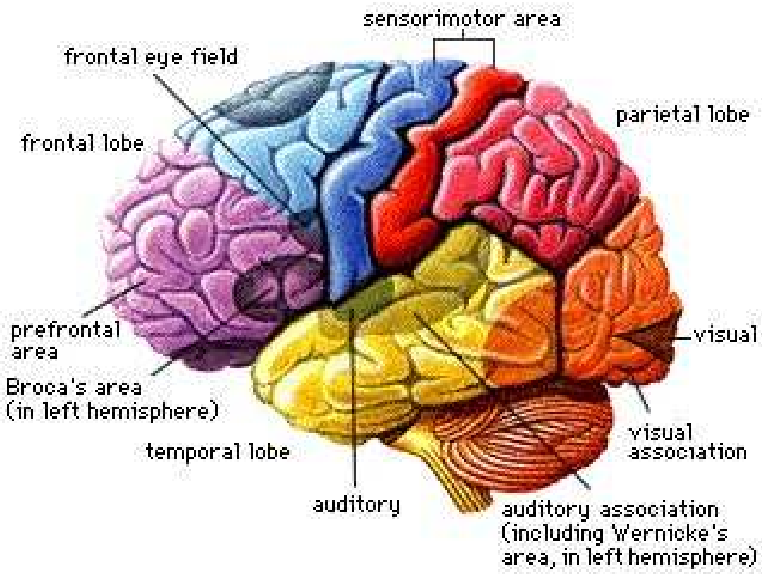


Figure 15: The different lobes of the human brain.

instead when comparing primates with insectivores.

Embryologically, this additional brain tissue in humans is largely controlled by the pattern and timing of fetal brain growth versus body growth, with expression patterns of homeobox genes playing a central role (Deacon, 1997; Karten, 1997). In mammals in general, the brain grows rapidly during early fetal development, and slows down later. In humans (and to some extent other primates) the rapid-growth phase is prolonged, into early childhood in the case of humans, leading to a larger brain-to-body size ratio, a growth pattern sometimes labeled as neoteny (McKinney, 1998). If it is a straightforward matter of prolonging growth, the expected result would indeed be the straight allometric increase of all parts, as observed by Semendeferi & Damasio (2000) and others (but see also Kaas & Collins (2001)). This developmental logic is supported by the allometric and embryological comparisons reported by Finlay et al (2001).

On top of the size differences, it has also been discovered recently that humans and apes share a unique new type of neurons, not found in other mammals. These spindle-shaped projection neurons are located in the anterior cingulate cortex. In humans, these cells are highly susceptible to Alzheimer and other degenerative diseases, hinting at a role in the higher cognitive functions hardest hit by these diseases (Nimchinsky et al, 1999).

The reasons why larger relative brain size[76] evolved in primates are not totally

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[76] When I talk about "relative brain size", or "brain-to-body size ratio", I should properly use the more appropriate but mathematically messier concept of "encephalization quotient" (EQ). The EQ (no relation of the "emotional intelligence" of recent fame) is an attempt to take

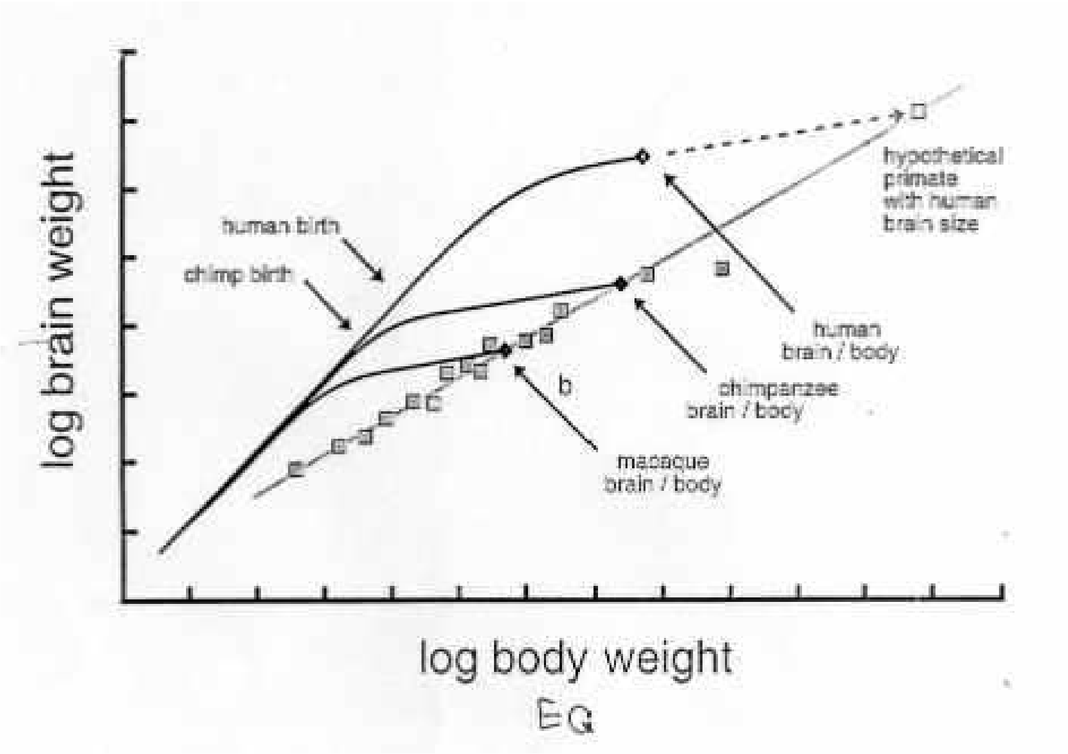

Figure 16: The ontogenetic development of brain size and body size in humans and other primates. The filled squares along a straight line show the adult state of various non-human primates. The trajectories ending with a diamond show the ontogenetic growth pattern of humans, chimpanzees and macaque monkeys. Note how the steep part of the trajectory ends at birth for the other apes, but continues for humans, giving adult humans a brain size far above that corresponding to their body size.

obvious. A larger brain presumably implies improved cognition[77], which in most contexts would be an advantage, but this advantage is at least partially offset by the brain being a metabolically very expensive organ to maintain (Nilsson, 1999). Any hypothesis of brain evolution needs to explain both why primates have grown larger brains, and why most other mammals haven't. Three types of hypotheses have been proposed (Rifkin, 1995; Martin, 1998):

- *Energy limited.* The brain grew until it used up all the surplus energy. Fruit-eating primates presumably had more "spare" energy than e.g. grass-eating ruminants. A variant of this hypothesis is the "maternal energy hypothesis" (Martin, 1998), in which the energy supply from the mother to the growing fetus is the limiting factor.
- *Environementally driven.*
  - *Diet driven.* A fruit eater needs more brain power in order to keep track of when and where ripe fruit is available, and the picking of fruit is more complex than grazing or browsing, It is, however, not obvious that fruit is harder to keep track of and catch than the prey of carnivores is. Carnivores do have fairly large brains as well, larger than most herbivores, but not as large as primates. Furthermore, far from all primates are frugivores; the group also includes e.g. gorillas, leaf-eating but still pretty smart[78].
  - *Navigation driven.* This is related to the cognitive demands of fruit eating above, but focuses in one version specifically on the demands on spatial cognition and mental map making, and in another version on the cognitive demands associated with arboreal life — climbing trees safely is not trivial for a heavy ape (Byrne, 2000).
  - *Tool driven.* The suggestion that the evolution of human intelligence was "tool driven" also belongs in this category; see section 5.2.2 for more on this issue.
- *Socially driven.* Most primates live in complex social groups, where relations with (and manipulation of) conspecifics play a major role. Unlike most social mammals, where a rather straightforward dominance hierarchy is the rule, politics and coalition-building are important for a primate's success,

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into account how brain size normally varies with body size, and measure how large a brain an animal has compared with other animals of the same size.

[77] The correlation between brain size and cognition (or intelligence) is not well established within *Homo sapiens* (Schoenemann et al, 2000), but is obvious when comparing between different species (Savage-Rumbaugh et al, 1993b). Some measure of brain complexity may be relevant here, but such measures that exist, e.g. Tononi et al (1994), are far from being operationally useful in this context.

[78] Patterson & Cohn (1990) report that they have administered a variety of standard IQ tests to a gorilla in their care. She is said to have achieved test scores ranging between 70 and 95, well within the human range.

> driving the evolution of what has been called “Machiavellian intelligence” (Byrne & Whiten, 1988, cited in Tomasello (2000b)). And humans live in larger and more complex societies than other primates, so this selective force would be unusually strong for us (Flinn, 1997). This can indeed lead to a runaway “arms race” of brain power, but begs the question of where the social complexity came from in the first place. An interesting parallel is the evolution of similarly large brains in dolphins and related whales, who have comparable social complexity (Connor et al, 1998). Dunbar (1996) has found a strong correlation in primates, not between group size and brain size as such, but between group size and neocortex fraction of the brain, which is not inconsistent with the Machiavellian hypothesis, as the neocortex is the part of the brain that has increased the most in size among primates, and particularly humans. It can also be noted that McComb et al (2001) have demonstrated that among elephants (who also have sizeable brains), social intelligence and knowledge directly translates into Darwinian fitness.

As for the additional brain growth that has taken place in the human lineage, the reasons for this are intertwined with the reasons for language evolution, which will be addressed in section 5.2. Arguments for a causal link between language and brain growth have been proposed in both direction, either with the needs of language driving the brain enlargement, or with the enlarged brain a vital exaptation for language. Deacon (1997) for example regards the growth of the prefrontal lobes as instrumental in the evolution of human symbolic abilities, which of course are vital for language.

Any arguments concerning this brain growth must, however, take into account the allometric pattern of increase (Finlay et al, 2001), which makes it difficult to argue that a new function for any particular part of the brain was the driving force behind its increased size. Specifically, the large size of the human neocortex, particularly the prefrontal lobes, noted by Deacon (1997) and others, may simply be explained by its gaining most by the prolonged neurogenesis period, just by virtue of being the last part to grow during fetal development — a selective advantage gained from growth of just about any part of the brain, would have given a large neocortex as a byproduct, a spandrel. It is possible that selection acted directly on the neocortex, but neocortex size *per se* is not conclusive — selection for neoteny and/or general brain growth would cause a disproportionate allometric increase in neocortex size. But regardless of which part of the brain is significant here, any postulated selective advantages of our large brains have to be enormous, in order to offset both the high metabolic cost (Nilsson, 1999) — we need something like 25% more food just for our brain — and the high costs associated with large-brained childbirth (Byrne, 2000).

4.3.1 Lateralization

One notable aspect of language processing in the brain is its lateralization. It was noted at least as early as the 19th century, by Broca (1861) and others, that language is mainly handled by the left hemisphere of the brain (Radick, 2000). Damage on the left side of the head commonly led to aphasia, whereas right-sided damage had little effect on language[79].

There is some disagreement on how absolute this left-sided language specialization is, and what effect it has on our general cognitive faculties. Lately, some evidence has surfaced for a right-hemisphere role in some aspects of language, notably prosody, but also phonology (Simos et al, 1997) and word learning (Sabbagh, 1999) and others (Bonvillian et al, 1997; Locke, 1997; Richards & Chiarello, 1997). Syntax, however, does appear to be the near-exclusive domain of the left hemisphere (Grodzinsky, 2000), even though Vigliocco (2000) presents neuroimaging studies where the right hemisphere is activated in syntax processing. And language is not totally absent (though it is severely impaired) even in patients whose left hemisphere has been completely removed (Code, 1997). If the left hemisphere is damaged very early in life, normal language development can follow, but handled largely by the right hemisphere (Müller et al, 1998), showing that the laterality of language is not strictly hardwired, but is handled with considerable plasticity (Mueller, 1996). Nevertheless, the left hemisphere does dominate language perception and production, in the vast majority of people.

The brain is by no means unique in its lateral specialization. Various other organs in the body have a distinct left-right asymmetry, and the asymmetry is initiated very early in fetal development (Izpisua Belmonte, 1999), by molecular (Ramsdell & Yost, 1998; Levin & Mercola, 1998) and genetic (Isaac et al, 1997; Pinker, 1994) mechanisms that are beginning to be understood. Left-right asymmetry also has an ancient evolutionary history (Bisazza et al, 1998), and has evolved several times in different groups of animals (Palmer, 1996).

Likewise, speech is far from the only brain activity that is laterally localized. The vast majority of humans preferentially use one hand rather than the other for precision work, and for most of us this is the right hand (and thus the left hemisphere of the brain, since it's cross-connected). This asymmetric pattern of behaviour can be observed very early in fetal development (Hepper et al, 1998). Natsopoulos et al (1998) argue for a connection between handedness and language lateralization, based on evidence for weaker language development in left-handed children, but this conclusion is disputed by Annett (1998). This issue is further discussed by Halpern (1996).

Human hand preferences have an ancient history, as the oldest stone tools

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[79] The right hemisphere has other functions, such as spatial and synthetic, "holistic" (as opposed to analytic) thinking (Walsh, 2000). The latter aspect has led to a large New-Age-flavored literature surrounding right-hemispheric cognition, of dubious scientific value.

show tell-tale asymmetries revealing that they were knapped by right-handed tool makers (Westergaard & Suomi, 1996; Wilkins & Wakefield, 1995). Similar behavioral asymmetries can be found among whales (Clapham et al, 1995), monkeys (Westergaard & Suomi, 1996), orangutans (Rogers & Kaplan, 1996), and chimpanzees (Hopkins & Bard, 1993; Morris et al, 1993). Corresponding anatomical asymmetries have been identified in rhesus monkeys (Falk et al, 1986) and chimpanzees (Gannon et al, 1998), as well as in fossil hominid skulls, at least as far back as *Homo habilis* (Wilkins & Wakefield, 1995). According to Westergaard et al (1998b), there is an apparent connection between handedness and bipedal posture, as observed in extant primates, which may have implications for the evolution of handedness in humans.

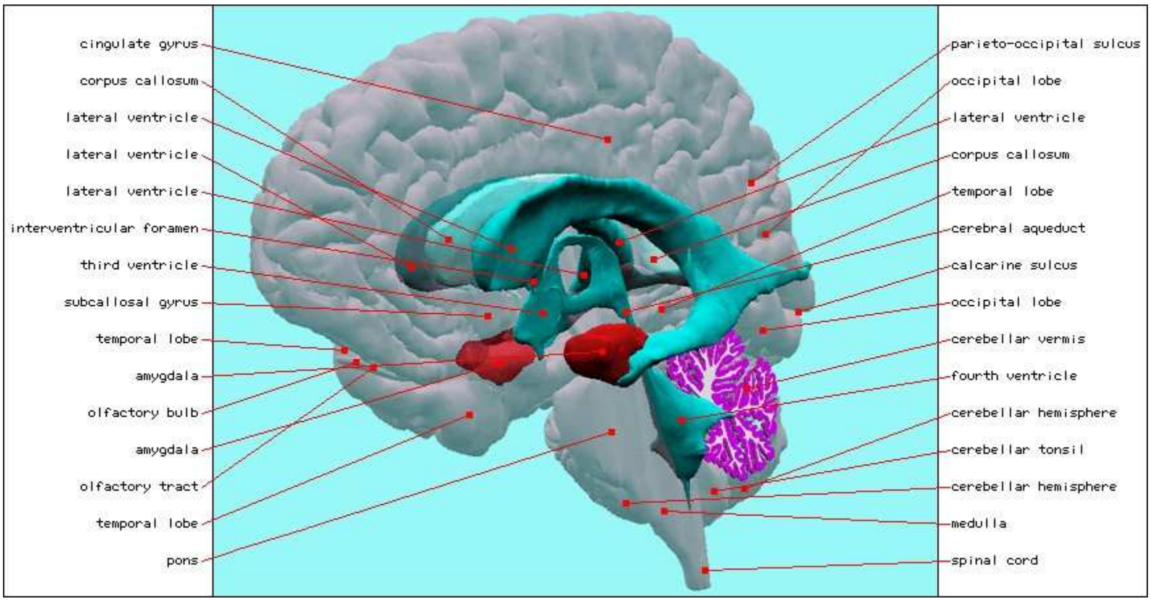
During the acquisition of sign language, there is a marked preference for using the right hand for signing. This might be partially explained by the general preference for using the right hand for tasks requiring precision, but Bonvillian et al (1997) found that right-hand dominance was even stronger for signing than for non-language-related tasks.

Concerning the asymmetry of speech processing, it is interesting to note that many other animals also process species-specific communications preferentially on one side of the brain (Bisazza et al, 1998). Songbirds do (Cynx et al, 1992; Mueller, 1996), though they are so phylogenetically distant from us that this can hardly be relevant. That the same kind of asymmetry is found in monkeys (Hauser et al, 1998; Locke, 1997; Hauser & Andersson, 1994; Bisazza et al, 1998; Ghazanfar & Hauser, 1999) is more interesting, and even more so the signs of language-related lateralization in chimpanzees, both anatomical (Gannon et al, 1998; Neergaard, 1998) and behavioral (Hopkins & Leavens, 1998; Hopkins et al, 1991), though the evidence here is ambiguous (Hopkins et al, 1992; Hopkins & Morris, 1989). Particularly interesting is the observation (Neergaard, 1998) that bonobos use almost exclusively their right hands for gesturing.

4.3.2 Modularity

Paul Broca is famous in the history of neurolinguistics not only for discovering the laterality of language processing mentioned above, but also for pinpointing a specific part of the brain, now known as Broca's area, where injuries would impair language. Wernicke and others found more such apparently language-specific brain pieces, which led to the conjecture that language (and for that matter other brain functions as well) is handled by dedicated brain modules, so that each section of the brain has a specific purpose. For low-level input and output functions, the modularity is well established; there is ample evidence that e.g. hearing is handled by one dedicated part of the brain, and vision by another dedicated part. What remains controversial is the modularity of higher-level functions like language.

This anatomical modularity is closely related to, but distinct from, the func-



(http://mail.biocfarm.unibo.it/aunsnc/3dobjl2b.html)

Figure 17: Various interior parts of the human brain.

tional modularity hypothesis of language organization, in which the language faculty (as well as the rest of the mind) is composed of several autonomous computational modules. Modularity in this sense is a hypothesis developed by Fodor (1983, cited in Sandler (1993) and Levy (1996)). Chomsky, e.g. (1988), has supported a related modularity hypothesis, but this is less evident in his most recent works (Uriagereka, 1999; Stemmer, 1999).

Language is not the only aspect of brain function for which modularity is proposed — Duchaine et al (2001) argue for a system with separate innate brain modules for everything from sex to semantics.

A functional module may, but need not, correspond to a distinct piece of the brain, an anatomical module. Chomsky emphasizes the logic with little interest in the hardware. Fodor is commonly interpreted as equating functional and anatomical modularity, but according to Coltheart (1999), Fodor explicitly acknowledges the possibility of modules being distributed, or arising in an equipotential brain.

The scope of the proposed modules is not well-defined. The language faculty as a whole is sometimes regarded as a single module, but there is also much talk of smaller submodules that are supposed to handle specific components of language, such as syntax or phonology. Levy (1996) introduces such a distinction between "Big Modularity" and "small modularity", and compares the empirical evidence for different-sized modules.

The hypothesized "Language Acquisition Device" of children would be a Big Module in this sense. It should be noted that it is *not* self-evident (though often taken for granted) that this would be the same module(s) as adults use for normal language processing. The sensory and processing demands in acquisition, are quite different from those in routine use of a known language (Bates, 1993). Furthermore, there is some evidence from lesion studies that language acquisition is affected by a pattern of lesions quite distinct from the lesions of the left temporal area that typically causes adult aphasia (Plunkett, 1997). Notably right-hemisphere damage in children, unlike adults, may severely affect language acquisition (Selnes, 2000; Curtiss et al, 2001), and Sabbagh (1999) proceeds to propose a specific right-hemisphere role in acquisition. There is evidence of such dissociation also in Williams syndrome; see p 72 below.

The hypothesized modularity of language is relevant in the context of language evolution, because an autonomous, encapsulated, monolithic language module must have an evolutionary history that is quite different from (and more difficult to trace than) that of a language faculty based on a combination of pre-existing general cognitive systems.

It is sometimes erroneously assumed that modularity and innateness are necessary postulates for any evolutionary explanation of any cognitive system, including language. But, as shown by Cummins & Cummins (1999), much weaker postulates are sufficient for evolutionary explanations to be tenable. Either a modular or a distributed language faculty can work in this context, and innateness is required only in the weaker form of predispositions and developmental biases and canalization.

Furthermore, as argued by Karmiloff-Smith (1994), modules need not be innate and genetically pre-programmed. She proposes instead a gradual process of modularization as the infant mind develops.

Empirical evidence that is relevant to the issue of language modularity includes:

- *Normal child development.* What correlations are there between language acquisiton and other cognitive development?

  According to Bates (1993), such correlations have been observed between major steps in language acquisition, and the acquisition of various non-linguistic behaviours, mostly related to communicative and social skills; see table 2.

  There are some intriguing similarities between the language and non-language columns in the table, suggestive of a common underlying mechanism. This would argue against any language acquisition device being strictly language-exclusive.

  Also, as noted by Levy & Kave (1999), *"normal language development is seen as a major predictor of neurological intactness in children"* (p 115). This would hardly be the case if language acquisition were totally separate.

Age	*Language*	*Non-language*
8-10 mo	Word comprehension	Communicative gestures and routines, causal analysis, tool use
12-13 mo	Naming	Gestures symbolizing an action or object
16-20 mo	Multi-word utterances	Multi-action sequencing and planning
20-30 mo	Grammar	Scripts in playing

Table 2: Ontogenetic stages in linguistic and non-linguistic cognitive and social development.

- *Developmental defects and delays in children.* Are there any defects that exclusively affect language, or are language acquisition problems always accompanied by non-language deficits? Conversely, are there defects that affect general cognition, but leaves language unscathed? Are there different defects that affect different subcomponents of language? Are any of these defects caused by any identifiable "language genes"?

  "Specific language impairment" (SLI) is a label used for children with significant discrepancies between their linguistic and non-linguistic development, without any obvious reason such as hearing problems (Levy & Kave, 1999). It is, however, a rather vague diagnosis for a heterogeneous group of children, and it is not well established that SLI is a single well-defined disorder (Bishop, 1994). Instead, there may well exist several different disorders of language, as listed in Joanisse & Seidenberg (1998) or van der Lely & Stollwerck (1997), with different causes. Furthermore, a significant fraction of children with an SLI diagnosis do turn out to have general cognitive problems, which only happened to be most apparent in the language sector (Bishop, 1994). Several specific non-language problems commonly associated with SLI are also known (Joanisse & Seidenberg, 1998), notably an impairment of timing and rhytmic ability (Alcock et al, 2000), that might be interpreted in the context of the sequencing hypothesis of Calvin (1993) discussed on page 55.

  Grammatical SLI appears to be the best established variety leka99,vast96,vast97, and a considerable amount of work (reviewed by Levy & Kave (1999)) has been done concerning the precise deficits of grammatical-SLI-children, mostly in terms of the absence of specific structural grammatical principles (such as Binding and coreference as proposed by van der Lely & Stollwerck (1997)). On the other hand, Tomblin & Pandich (1999, but see also responses by van der Lely (1999) and Marcus (1999a)) argue that the children with grammatical SLI just populate the extreme tails of the normal distribution of language abilities. And explanations for "grammatical" SLI that are based on processing deficits rather than grammar *per se* may remain tenable (Joanisse & Seidenberg, 1998; Levy & Kave, 1999), though Gopnik & Goad (1997) rule out low general IQ as well as auditory and articulatory processing deficits as explanations. And SLI is rarely if ever characterized by a total absence of grammar, as would be the case if a grammar module were totally non-functional — rather, the SLI children are aware that syntactical rules exist, and apply many of them correctly, but miss a few. If SLI means that a module is knocked out, it must be a very small and highly specific module. It appears premature to conclude, as van der Lely & Stollwerck (1997) do that *"[t]he data provide additional evidence for* **an** *[my emphasis] innate syntactic module..."* (p 283).

There exists a fair amount of evidence for grammatical SLI having a genetic cause (van der Lely & Stollwerck, 1996), including twin studies (Palmour, 1997; Gopnik, 1997) as well as numerous family studies (Gopnik & Goad, 1997; Palmour, 1997). On the other hand, pre- and perinatal problems (which commonly cause general neurological problems, with associated language deficits) are not a significant cause of SLI (Bishop, 1997). But Locke (1997) cautions against concluding from SLI data that a "grammar gene" exists.

Gardner (1991) argues for the existence of a language gene on chromosome 15, but he bases his argument on syndromes that produce a wide variety of behavioral anomalies, of which language deficit is one. Thus, his finds are not compelling evidence of language-*specific* genes.

Interestingly enough, Palmour (1997) observed a specific anatomical abnormality in the brain of many SLI patients, in the perisylvian fissure (in the vicinity of the traditional "language areas" of the brain).

In the opposite direction, there are several syndromes that cause severe general retardation but with little effect on language, such as the Cocktail Party Syndrome, the Savants[80] (Levy & Kave, 1999), Spina Bifida, and Williams Syndrome (Pinker, 1995).

Williams Syndrome, a genetic disorder where a contiguous sequence of genes along a chromosome has been deleted (Meng et al, 1998) with consequent malformations in numerous places, notably the posterior cortex, has attracted particular attention, because the dissociation between linguistic and other skills appeared clear (Deacon, 1997). But recent investigations have revealed some subtle language deficits also in Williams-patients whose language is superficially normal (Karmiloff-Smith et al, 1998). Clahsen & Almazan (1998) interpret the pattern of language deficit in Williams-patients as stemming from difficulties with lexical access, with an intact syntactic-computational system, in contrast with the opposite pattern in SLI patients[81]. Deacon (1997) on the other hand sees the lexicon *per se* in Williams-patients as intact, but with impaired extralinguistic association patterns. Deacon (1997) goes on to conclude that the non-symbolic processing machinery is what is impaired in Williams Syndrome, leaving

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[80] But note that many Savants also have symptoms of autism, which does have associated language deficits (Frith, 1997).

[81] This is suggestively similar to the opposite loss patterns in agrammatic and anomic aphasia.

symbolic processing intact, leading to the observed dissociation between language (dominated by symbolic processing) and non-linguistic cognition (heavily hit by the degradation of non-symbolic processing). Taken at face value, Deacon's interpretation of Williams syndrome would imply that symbolic and non-symbolic processing have modules of their own, genetically specified, (or they could hardly be selectively affected by a genetic disorder), but that language is not separated from other symbolic processing. Paterson et al (1999) find that, while Williams patients do well enough on linguistic tests in adulthood, their language acquisition is significantly delayed, indicating a dissociation between the brain machinery used for acquisition and for mature language processing. Paterson et al (1999) also reports that the Williams patients, oddly enough, display the opposite pattern for mathematics, with good acquisition but poor performance in adulthood. To the extent that mathematics is a matter of symbolic processing, this would argue against the dissociation proposed by Deacon (1997).

- *Brain lesions in adults.* Same questions as for the developmental problems: do any brain lesions damage nothing but language?

  Broca's aphasia is the classic example of a brain lesion that mainly damages language. There are many other kinds of aphasia, but Broca's is noteworthy in that grammar is severely impaired, but other cognitive functions are largely spared — unlike most other aphasics, Broca patients retain their previous IQ (Grodzinsky, 2000). And Broca's aphasia is closely associated with damage to Broca's area in the brain, which could be taken as evidence of Broca's area being a grammar module. But more detailed studies show that the situation is more complex (Deacon, 1997; Mueller, 1996). The pattern of grammar loss in Broca's aphasia (or agrammatic aphasia in general) does not lend itself to any straightforward explanation in terms of a disabled grammar module, which ought to affect all modes of language equally. Instead, there is a pattern of partial aphasia in all possible dimensions, with grammar lost for one aspect but not another, different for different patients (Mueller, 1996):

    - Production vs. reception
    - Oral vs. written
    - Oral vs. sign language
    - Different languages (for bilinguals)

  Furthermore, parts of the syntactic loss can be compensated using heuristic strategies[82], partially restoring comprehension, in patterns that may mask

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[82] A heuristic strategy is basically a matter of applying a combination of semantic knowledge and normal (non-language) intelligence to sentence analysis.

the pattern of the original aphasia. Training can restore language performance in some but not all aphasia patients (Weinreich et al, 2001).

There is also some evidence of specific non-language abilities residing in Broca's area. Sequencing was discussed on page 56, and may be implicated in the motor control deficit observed in in some patients (Vigliocco, 2000). Iacoboni et al (1999) report activation of Broca's area, as well as its homolog in monkeys, in imitation tasks. Another interesting discovery is that damage to Broca's area impairs the ability to handle non-verbal hierarchical structures (Greenfield, 1993, cited in Savage-Rumbaugh & Lewin (1994)) — highly significant in view of the hierarchical nature of grammar. If Broca's area contained a general hierarchy handler, this would explain much of Broca's aphasia. Non-language deficits are not commonly reported for Broca patients — but Schweiger & Brown (2000) may have a point in that *"[t]he apparent uniqueness and dissociability of language from other skills, and specifically grammatical deficits, reported in the aphasia literature, reflect the narrow focus of researchers rather than the scope of symptoms presented by the patients."* (p 214).

Just as for the SLI children, there are two classes of hypotheses concerning the deficits of agrammatics (Levy & Kave, 1999; Crain et al, 2001):

- Structural deficits, where some specific principle of grammar is disabled. The "Trace Deletion hypothesis" is a typical example, in which the trace that is left after movement (in a transformational-grammar framwork) is lost, so that the patient cannot reconstruct the pre-movement position (and thus theta-role) of a moved noun phrase. Further structural hypotheses are reviewed in Levy & Kave (1999), Berwick (1997), and Grodzinsky (2000).
- Processing deficits, where syntactic knowledge as such is unharmed, but where computational or working-memory resources are diminished, so that processing limitations are exceeded even in fairly short sentences (just like it is quite possible to construct a sentence with fifty nested embedded clauses which is perfectly grammatical but which cannot be parsed by any normal person without paper and pencil, because of processing limitations). Miera & Cuetos (1998) test one processing hypothesis, by measuring the working memory of agrammatics, comparing it with that of anomics and normal controls. They find that both groups of aphasics have poorer memory than controls, but also that the performance of agrammatics is not significantly affected by sentence length, from which they conclude that a working-memory deficit is not sufficient to explain agrammatism. Both Hartsuiker et al (1999) and Crain et al (2001) on the other hand do find evidence of a shortage of processing resources in Broca's aphasia. Processing hypotheses thus remain tenable (Levy & Kave, 1999), though the normal nonverbal intelligence of Broca-patients argues against any significant

general computational deficits.

The conclusion of Levy & Kave (1999) is that we have insufficient evidence to choose between structural and processing hypotheses. Structural hypotheses have an inherent theoretical elegance, appealing to many linguists, but that in itself is no guarantee of truth[83] — the messier, but possibly more psychologically realistic, processing hypotheses cannot be discounted. Beretta et al (2001) present empirical comparison of a processing hypothesis with several structural hypotheses[84], claiming to find solid evidence against the structural hypotheses.

Here again, no clear case either for or against the modularity of language can be made. I have only discussed agrammatism, but the other varieties of aphasia do not change this non-conclusion. There is, for example, some evidence of bilinguals with selective aphasia in one of their languages (Gomez-Tortosa et al, 1996; Daroff, 1998), but this remains controversial[85] (Paradis, 1996). But even if it were true that different languages occupy different modules, this would tell us little about the central language modules for syntax and grammar, which, according to the Universal Grammar hypothesis, the two languages would have in common.

An interesting recent result is that of Caramazza et al (2000), where it is shown that consonant and vowel production can be affected separately in aphasia, indicating that they are processed by distinct neural mechanisms. Another is that reported in Pinker (1997) concerning selective aphasias affecting either regular or irregular verbs. Both of these support the existence of small and highly specific modules. But the complex patterns of deficits exhibited by most aphasia patients, commonly affecting what linguistic theory regards as separate components (Blumstein & Milberg, 2000) does not indicate any simple modular structure. The issue of Big Modules remains unsettled.

- *Brain activity.* Do brain scans show any areas of the brain that are used for language processing and nothing else? Does everybody use the same brain areas for language? How about other language modalities?

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[83] As a physicist, I am struck by the parallel with the issue of theoretical elegance within physics. It is a historical fact that physical theories that have the same kind of inherent theoretical elegance, have indeed turned out to be true much more often than might reasonably be expected. Does this tell us something fundamental about the universe — or about our sense of elegance? In any case, the success of elegant theories has been so striking that elegance has become a major heuristic criterion in recent theoretical physics. In linguistics, a similar quest for elegance is quite explicit in Chomsky (1995), according to the review of Uriagereka (1999).

[84] Note that Beretta et al (2001) use the label "structural" for what I call "processing", and "linear" for what I call "structural". This discrepancy is due to their labeling hypotheses after what capacities remain, and I naming hypotheses after what is damaged.

[85] It may be noted that MRI scans of bilinguals show that in early bilinguals, the two languages share the same brain structures, but not in late bilinguals (Kim et al, 1997).

The development of non-invasive high-resolution techniques for studying the activites of living conscious brains has led to a flood of data. Unfortunately, it is not trivial to interpret this data, as it is very difficult to ascertain that a brain is doing one thing and one thing only — no matter how hard you concentrate on the experimental task, extraneous thoughts will be flitting through your mind every now and then, adding noise to the scan results. Experiments are necessarily comparative, measuring the difference in brain activity between the task of interest and some control task.

Despite these difficulties, some interesting results have been obtained. To begin with, the auditory cortex contains an area specifically sensitive to human voices (Belin et al, 2000), which is the first step towards decoding speech.

Lounasmaa et al (1996) present results from picture naming exercises, where a clear temporal progression could be seen from the visual cortex at the back of the head, towards more frontal areas, ending up in Broca's area which was activated when the actual naming took place (passive viewing of pictures without naming them caused very little Broca activity). It can be noted that Lounasmaa et al (1996) observed only a modest difference between the left and right hemisphere, in contrast both with other studies of word generation such as Klein et al (1995), and with the general evidence of language lateralization reviewed in section 4.3.1. In a similar exercise (Caramazza, 1996b) it was found that the semantic system used for recognizing picture or word stimuli appears to be distributed through large areas of the left hemisphere. On the other hand, Thompson-Schill et al (1997) report that a number of experiments have identified a certain piece of the brain (the left inferior frontal gyrus (IFG)) as consistently activated in semantic tasks, but Thompson-Schill et al (1997) go on to argue that the IFG is not a semantics module, but instead a selection module, activated when choosing between semantic alternatives. On the other hand, Klein et al (1995) find IFG activation also in purely phonological rhyming tasks. Price (1998) and Klein et al (1995) have also found brain activation in additional areas in a variety of semantic tasks.

Lexical knowledge can with some modest degree of confidence be pinpointed to the left temporal lobe of the brain, apparently with different semantic categories of words stored separately at some level, with one small piece of brain handling animal names, another small piece of brain handling words for tools, and so on (Damasio et al, 1996). This is also indicated by the existence of similarly selective aphasia (Caramazza, 1996a). However, Martin & Chao (2001) present evidence that the neural organization of semantic knowledge is more complex and distributed in the brain.

Neuroimaging studies of syntax processing have been rare, but are now accumulating at a rapid rate[86]. Syntax encoding in speech production is

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[86] When I first wrote this section, in 1999, no such studies were available, and this paragraph

> located by Indefrey et al (2001) to an area adjacent to "classical" Broca, the Rolandic operculum. In a study of syntax parsing, Embick et al (2000), find that sentences with syntax errors (with spelling errors used as control) specifically activates Broca's area. Vigliocco (2000) reviews several studies, most of which point towards the vicinity of Broca's area in syntax tasks, and slightly forward of Broca for semantic tasks. These results strengthen the case for Broca as a syntax module, though the non-linguistic deficits in Broca's aphasia mentioned on p 74 raises the question of whether such a module is really language-specific.

In conclusion, there is ample evidence for the existence of small specific modules, but it is difficult to pinpoint the exact purpose of any given module. On the other hand, there is little sign of any big monolithic modules encapsulating any major brain function, apart from low-level sensory processing. Specifically, language appears to be handled by a large number of separate subsystems, spread out over a significant fraction of the brain (Blumstein & Milberg, 2000). Some of the systems may be language-specific but others may not — not all aspects of language need to be handled in the same manner (Bloom & Markson, 2001) — and it is difficult to find compelling evidence either way. Corina (1999) appears correct in his assessment: *"All higher cognitive systems (i.e. language, [...] etc.) exhibit a range of domain-specific and domain-general processes."* (p 231). It is also difficult to find a clear correspondence between the functional subsystems identified in the brain, and the logical components of the language faculty identified in linguistic theory.

Another problem for the concept of innate modules is the fact that the brain displays considerable plasticity in development. The same part of the brain can be recruited for totally different purposes depending on what sensory input the growing brain receives at a sensitive age (Wong, 1995). Experimental re-routing of the optical nerve to the auditory cortex, results in the auditory cortex being transformed into visual cortex, and the signals coming to it being perceived as vision and not sound (Merzenich, 1999; Swindale, 2000). The molecular-level mechanisms behind one such case of input-driven neural wiring is reviewed by Fox (1999).

In embryology, there is good evidence for large-scale innate patterning of the brain (Ragsdale & Grove, 2001; Bishop et al, 2000), but little sign of the fine structure needed for more specific modules — active recruitment of neurons for different tasks during a critical period of plasticity appears more plausible, given what we know about neural patterning in the brain (Berardi et al, 2000; Knudsen et al, 2000).

Furthermore, it is obvious that a large fraction of our cognitive capacity is *not* located in encapsulated genetically determined task-specific modules — such genetically determined modules can only have evolved for tasks that were relevant

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looked quite different.

for fitness in the EEA[87] where we evolved, but today we have no problem recruiting cognitive capacity in our brains to tasks like solving differential equations or analyzing quark-antiquark annihilation processes, tasks that brain modules cannot possibly have evolved for. This demonstrates a cognitive versatility that is a strong argument against having any large fraction of the brain devoted to encapsulated "Big Modules", and an argument for the possibility of task-switching even for those smaller modules that we most likely do have: *"Exaptation of intelligence does appear routine for at least modern humans, and it seems safer to leave the issue of modularity to empirical enquiry (...) rather than assuming that cognitive mechanisms are immune from recruitment to other functions."* (Byrne, 2000, p556)

4.3.3 Brain and language in other species, fossil and extant

Detailed information on the history of human brain anatomy is difficult to extract from fossils; what is available is largely limited to the gross size and shape of the inside of the skull, giving a rough estimate of the size of the brain. At best, endocasts[88], and impressions from brain features on the inside of the skull, give some insights to the surface anatomy of the brain (Rilling & Insel, 1999; Brandt, 1993). Sometimes the blood supply to the brain can also be deduced from the size of blood-vessel conduits through the skulls of fossils (Braga & Boesch, 1997), but few firm conclusions can be drawn from this.

The overall size of the brain does not show any significant increase until fairly late in human evolution. Australopithecines have brains comparable in size to those of chimpanzees or gorillas. Australopithecines, at least the gracile varieties, were, however, quite small creatures (around 30 kg), smaller than modern chimpanzees, and much smaller than gorillas, which implies a larger brain-to-body-size ratio (Kappelman, 1996). On the other hand, there is little indication of any humanlike features on australopithecine endocasts according to Brandt (1993), whereas Culotta (1999a) quotes Dean Falk as claiming the presence of a humanlike brain shape in *A africanus* (but not in robust australopithecines).

There have also been some recent controversies surrounding australopithecine brain sizes, primarily involving one recently found *A africanus* skull (Conroy et al, 1998), but calling into question a variety of other australopithecine skull measurements as well (Falk, 1998; Conroy et al, 1998; Lockwood & Kimbel, 1999; Holloway, 1999). The outcome is still uncertain, but there appears no reason to believe that the conclusion of Kappelman (1996) referred to above will change.

The brain status of the habilines is unclear, for several reasons. Only a few skulls are sufficiently undamaged to permit a reasonable estimate of cranial ca-

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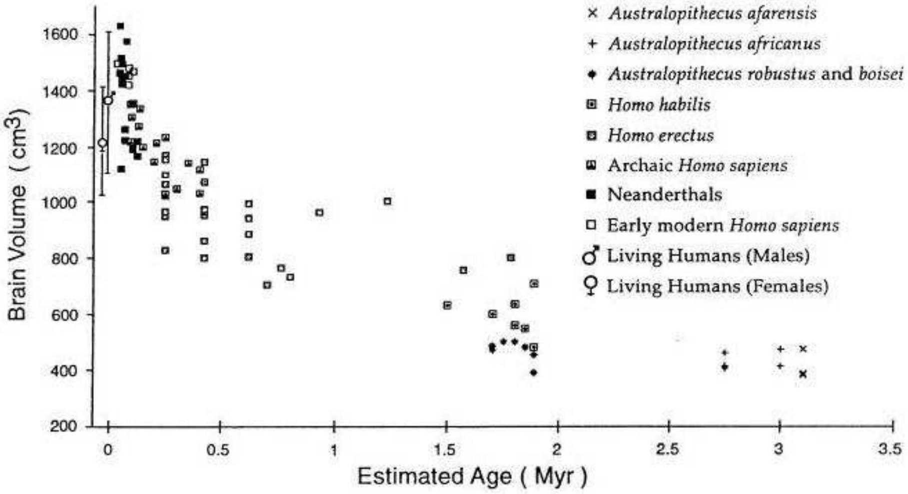
[87] EEA = Environment of Evolutionary Adaptedness; see page 95.

[88] An endocast is a "petrified brain", either a natural copy of the brain formed when the braincase is filled with sediment after the brain itself has rotted away, or an artifical mold of the interior shape of the skull. The most famous proto-human endocast belongs to the australopithecine "Taung baby" (Dart, 1925) shown in figure 3 on page 35.



(Foley, 1997)

Figure 18: Brain sizes of various fossil and extant hominids, plotted against the time when they lived. As comparison, it may be noted that the brains of modern apes range between 300 and 500 cm^3.

pacity, and they are widely different from each other, spanning the full range from australopithecines to more clearly human *erectus* specimens (Kappelman, 1996). Likewise, available endocasts indicate that some specimens have a very apelike brain surface, whereas others have a more human-like pattern (Brandt, 1993). This spread of data may well be connected with the taxonomic uncertainty surrounding this group.

Homo erectus presents a clearer picture, with brain capacities just below the modern human range. The gradual increase in brain size throughout the *erectus* period is clearly seen in figure 18. The transitional forms between *erectus* and modern humans are, as expected, intermediate in brain size. Neanderthals actually have larger brains than we do, but with a larger body size as well, their brain-to-body size ratio is not significantly different from ours.

Concerning signs of specific language adaptations in the brain, the only ones that may conceivably be detectable in fossils are an increase in lateral asymmetry, and increased size of those brain modules, if any, that are dedicated to linguistic processing.

Outside of *Homo sapiens*, Wernicke's area can be anatomically identified also in chimpanzees (Gannon et al, 1998), though Marshall (2000) cautions against over-interpreting this discovery. Broca's area is seen in both chimpanzees and gorillas (Cantalupo & Hopkins, 2001). Likewise, some fossil skulls, notably that of *Homo ergaster*, have a bulge in the right position to accommodate an enlarged Broca's area (Walker & Shipman, 1996; Holloway, 1983). Some enlargement of these parietal areas can be observed also in australopithecines (Holloway, 1983).

But since we have little or no data on their use in chimps and ancient hominids, and since it is not well established that they have no non-linguistic function even in modern humans, the significance of their presence in our relatives is unclear.

Some lesion studies have been performed on monkeys. One notable result is that damage to Broca's area does not affect their vocalizations, nor their gestures, implying that the human use of Broca's area for language processing is a later development, and that speech is not a direct descendant of monkey vocalizations. Instead, part of Broca's area in monkeys control chewing and other mouth motions, according to MacNeilage (1997), who invokes this functional change in support of his hypothesis of speech evolving from chewing motions (see section 5.3.1). Other monkey homologs of human language areas are used for facial muscles and auditory processing, which may also be useful exaptations for language evolution (Nowak, 2000b).

5 The Evolution of Human Language

The previous sections have all dealt with various background material needed in order to understand the evolution of language. In this section, the focus is on the main issue itself — why and how and when did our ancestors evolve the human language capacity? There are two main issues in explaining the evolution of any feature (Byrne, 2000):

- *Historical*: at what time, and at what point in the family tree, did different aspects of language appear?
- *Causative*: what were the selective advantages that drove the evolution of language, and what evolutionary precursors did it evolve from?

The main focus here will be on the causative issue, with historical data used mainly to constrain causative hypotheses.

It is clear from the previous sections that there is much that we simply do not know about the human capacity for language, certainly concerning its history, but also concerning the details of its implementation in modern humans. It is far from well established exactly how and where the human brain processes language, and the links between linguistic theory and neurological observables are tenuous at best. This means that firm conclusions will be difficult to achieve.

A reasonable starting point in the analysis of the evolution of language, is the last common ancestor of us and the chimpanzees. Presumably this ancestor had roughly the same capabilities and exaptations that modern chimpanzees do, so what needs to be explained here is how we went from chimpanzee-like[89] to human-like linguistic abilities, in less than ten millions years.

This removes quite a few areas from consideration, notably the entire sensory system — as shown in section 4, the senses of an ape are perfectly adequate for language already. Likewise, the apparent capacity for at least proto-symbolic thought in chimpanzees (Savage-Rumbaugh et al, 1978; Savage-Rumbaugh et al, 1980; Deacon, 1997; Savage-Rumbaugh & Lewin, 1994) shows that the earliest steps towards symbolic thought can be dissociated from the origin of human language. The same can be said of mind and self-awareness, traces of which can be also be found in chimpanzees (Lin et al, 1992; Kitchen et al, 1996; Povinelli et al, 1997) and a few other animals, as reviewed in Johansson (2001).

At the opposite extreme, those unique human features that are exquisitely adapted for language, notably our vocal tract, cannot be invoked as explanations for the evolution of language either — language must have been in use *before*

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[89] The linguistic abilities of chimpanzees are not negligible, as shown in Savage-Rumbaugh & Lewin (1994) or Johansson (2001), but we are concerned here only with the capabilities that humans have but chimps lack, notably the universal acquisition of and habitual use of a rich and complex language.

natural selection had any reason to adapt the vocal tract for it. So the vocal tract can be disregarded as well, at least in the early stages of language evolution.

When discussing language evolution, the prerequisites for evolutionary processes (listed on p 9) must be kept in mind. An important point here is that heritable variation in language abilities is necessary, otherwise there is nothing for natural selection to select. To the extent that language is innate, this heritable variation must be genetic. As was shown in section 4.3.2 in the context of SLI, the evidence supporting the existence of "language genes" is moderately compelling, but not overwhelming. One might invoke also the non-negligible heritability of verbal IQ, but it is unclear both to what extent verbal IQ is independent of other cognitive abilities (Alarcón et al, 1999), and to what extent verbal IQ actually measures language abilities in the sense relevant here. Pinker & Bloom (1990) adds some more data and anecdotal evidence supporting variability in our syntactic abilities, but they also point out that, while feeding on variation, natural selection also eliminates variation — if only the most able individuals breed, and their offspring inherit their abilities, the spread in ability will decrease with each subsequent generation, unless new variation is added in the form of mutations. It is conceivable that early hominids did vary in language abilities, even though little such variability may remain today.

A more serious problem for the issue of genetic variability is the argument, usually based in the Chomskian paradigm, that our language capacity is a monolithic universal grammar module (Chomsky, 1982), a unified whole in which variation is logically impossible. But there are several ways around this problem:

- Even if grammar, as an abstract entity, may be monolithic, its implementation in our brain may be more or less efficient — possibly all people have the same innate universal grammar, but some can acquire and process language faster and easier than others. That shows us an evolutionary path from an initial state where the same grammar was handled in a slow and muddled way by whatever cognitive and heuristic abilities were available, through more and more efficient neural circuits, towards the modern human brain with which we effortlessly acquire language at an early age.

- It is not self-evident that grammar actually is monolithic, with no imaginable partial proto-grammar. We'll return to this point in section 5.3.4 below.

- Complex, tightly coupled, superficially monolithic systems are not rare in biology. But the fact that a system is inextricably monolithic today does not necessarily imply that it has always been so. There are several possible types of evolutionary paths into tightly coupled complexity (Thornhill & Ussery, 2000), and there is no reason to believe that none of them is applicable to language. The fact that for Chomsky *"...it is not easy even to imagine a course of selection* [towards language] ..." (1988, p 167) is not a strong counterargument. Pinker (2000) has a better case when he states

> that *"the game theorists have demonstrated the* **evolvability** *of the most striking features of language..."* (p 442, emphasis added).

In conclusion, the evolvability of our apparently monolithic grammar is far from excluded (Pinker, 1994; Jackendoff, 1999b).

5.1 Dimensions of language evolution hypotheses

There are several dimensions along which to classify hypotheses about how we acquired our language capacity. Among the more important ones are:

- *Adaptation vs. spandrel*
- *Early vs. late*
- *Gradual vs. sudden*
- *Speech first vs. gestures first*
- *Innate and genetically determined vs. learned and culturally determined*

The dimensions should not be interpreted as either-or dichotomies, but as continua along which different hypotheses can be located at different points. The different dimensions are not totally disconnected from each other either. Hypotheses with early language tend to be gradual and adaptationist as well, and vice versa. And late sudden hypotheses tend to postulate that speech came first, rather than signs.

The available evidence from the preceding sections constrains these five dimensions in various ways:

5.1.1 Adaptation vs. spandrel.

Evolution is a strong force for shaping our bodies and minds. But this does not mean that every single feature has been shaped by natural selection to perfection. Many aspects of our bodies may simply be accidental byproducts (spandrels) or leftovers (vestigial), with no particular adaptive function in themselves (Gould & Lewontin, 1979; Gould, 1997). Male nipples are a case in point — female nipples are obviously adaptive, but it is likely that males have nipples, not because they are of any use, but simply because both male and female embryos follow the same developmental program, and it's embryologically simpler to give nipples to both of them than to just one (Gould, 1992).

Is language an adaptation, shaped by natural selection, or can it be just a spandrel, an accidental byproduct of human cognitive evolution? Pinker & Bloom (1990) argue strongly in favor of language as an adaptation, based on both its complexity and its obvious usefulness: *"Evolutionary theory offers clear criteria* *for when a trait should be attributed to natural selection: complex design for some function, and the absence of alternative processes capable of explaining such complexity. Human language meets this criterion:...”* (p 1, online edition). The argument is further elaborated by Pinker (1994; 1998a).

Gould (1997) and Bickerton (1995), on the other hand, seriously consider the possibility of language being a spandrel. Chomsky (1988) can also be interpreted this way — he certainly argues that our mathematical ability is a spandrel (p 168f), but he is less explicit about language; the closest he comes is *“It surely cannot be assumed that every trait is specifically selected. In the case of such systems as language or wings, it is not easy even to imagine a course of selection that might have given rise to them.”* (p 167). Neither of them, however, offers any strong counters to the complexity argument of Pinker & Bloom (1990) above. I find the case for language as an adaptation, at least in its full modern form, compelling. This by no means excludes the possibility that language co-opted numerous other systems, either spandrels or exaptations, but the final refinement of the human language capacity into the exquisitely fine-tuned system we have today, must have been an adaptive process.

This conclusion does not, however, tell us to what extent this adaptation is a matter of biological evolution, and how much of it is cultural or memetic evolution. That issue will be address in section 5.1.5 below.

5.1.2 Early vs. late.

Did our language capacity evolve long ago, in the early stages of hominid evolution, or was language evolution a late development, taking place in anatomically modern *Homo sapiens*? “Early” would mean one or two million years ago, whereas “late” would be within the past 100,000 years or so. As noted in the previous sections, the time frame of language evolution is not strongly constrained by either fossils or anatomy. Language cannot be younger than 60,000 years or so (p 50), but it can be much older. Exactly how much older depends on the language capacity of apes — but even without ape language, human language could have evolved at any time after our common ancestor with chimpanzees, 5 million years ago or more (p 32). Neither “early” nor “late” hypotheses can be excluded on paleontological grounds alone. However, this conclusion needs to be amended when the evolution of our speech organs is taken into account — see section 5.1.4 below.

5.1.3 Gradual vs. sudden.

Did we acquire our language capacity in one single step, without intermediate forms, or did we go through a long sequence of successive proto-language stages? To begin with here, there is perennial confusion over the word “sudden” as used in deep historical and geological contexts. An event that took, say, 10,000 years would appear very gradual to the participants — but would appear instantaneous in the fossil record to paleontologists working a million years later, and would be labeled as "sudden" by them. Many evolutionary transitions belong in this category of events that are paleontogically sudden but on human timescales gradual. However, most proponents of gradual evolution of language intend the process to be geologically slow, and most proponents of sudden evolution are talking about a single jump from ape-like to human-like language abilities, so this problem is not severe when it comes to differentiating between hypotheses in this context.

The sudden single-step evolution of something as complex as the human language capacity is biologically highly problematic. If we have an innate dedicated "language organ" and a universal grammar that is genetically specified in some detail, then "sudden" hypotheses are totally untenable without divine intervention, *contra* Chomsky (1988) and Bickerton (1995). The only context in which "sudden" hypotheses are not totally ridiculous is if most of the bodily and cognitive features that we use for language evolved for some other purpose, and were available as exaptations, with only some minor additional change needed to put all the pieces together as a workable language organ, and even then some intermediate stages of proto-language would appear necessary to render the hypothesis evolutionarily plausible.

5.1.4 Speech first vs. gestures first.

Did language first evolve in the spoken modality dominant today, or was another modality, presumably gestures, used in the early stages?

Darwin (1872) felt quite certain about the origin of language:

> *I cannot doubt that language owes its origin to the imitation and modification, aided by signs and gestures, of various natural sounds, the voices of other animals, and man's own distinctive cries.*
>
> (Darwin, 1872, p 56)

Unfortunately, this is one of the rare cases where Darwin's intuition led him partially astray — there is good reason to doubt the homology of animal calls and human speech. This means that it is not self-evident that language started with sounds, precursors to the speech modality. The "signs and gestures" that Darwin invoke as aids may conceivably have been the main modality of early language instead.

Language *per se* is basically modality-independent, as long as the modality used supports a sufficiently rich structure. In modern society, a large fraction of all language use is written rather than spoken. If anything, the written modality supports more complex language than the spoken. Other alternative modalities can easily be imagined, and quite a few have been used, both in ape language experiments[90] (Johansson, 2001) and in the teaching of severely retarded non-speaking children (Savage-Rumbaugh & Lewin, 1994).

Written language is of course derived from spoken in evolutionarily recent times, and so it is not highly relevant to the origin of our language capacity. But another alternative modality, sign language, is more interesting in this context. Sign language, just like spoken or written language, is a *bona fide* language (Sandler, 1993; van der Hulst & Mills, 1996), with all the functionality of any other modality.

That the first human language was a sign language, fully or partially based on gestures, is a possibility conjectured by Darwin (1871, cited in Radick (2000)), popularized by Auel (1980) and Reeves et al (1996) and discussed more seriously by Corballis (1992), Mueller (1996), Armstrong et al (1995, cited in King (1996)), Rizzolatti & Arbib (1998) and Miklosi (1999), among many others.

Sign language displays the same features as spoken language, not only in its mature form, but also in its development and in its neurological organization. Deaf children of signing parents "babble" in sign language during their early development (Petitto & Marentette, 1991; Berent, 1996), and their further development goes through basically the same stages as hearing children (Locke, 1997). The formation of pidgins and creoles have been observed among deaf people (Goldin-Meadow & Mylander, 1998; Goldin-Meadow, 1999). Brain lesion studies, as reviewed by Hickok et al (1996; 1998a; 2001), show a pattern of sign language aphasia among the congenitally deaf that resembles speech aphasia among hearing patients in the correlations between deficit patterns and affected brain areas. Likewise neuroimaging experiments (Neville et al, 1998; Hickok et al, 1998b) see similarities between speaking and signing[91]. There are also minor differences between speech and signing in the brain, but it is unclear how much of this is simply attributable to the different sensory and motor areas involved.

Even among people using spoken language, gesturing is firmly wedded to language use (Goldin-Meadow, 1999) — your hands are likely to be moving even when you are talking on the telephone, and even congenitally blind people (who can hardly have acquired the habit by observing others) gesture while speaking, also when addressing a blind listener (Iverson & Goldin-Meadow, 1998). Normal hearing children acquire the use of symbolic gestures in parallel with speech acquisition (Acredolo & Goodwyn, 1988), and there is some evidence that gesturing actually precedes speech in acquisition (Goodwyn & Acredolo, 1993; Goldin-Meadow, 1999). At the very least, gesture is as important as speech in early child communication, before the advent of syntax in the two-word stage

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[90] An interesting case is when the two chimps Sherman and Austin apparently invented a new modality on their own, spontaneously, when deprived of their usual computerized system (Savage-Rumbaugh & Lewin, 1994).

[91] Including the surprising observation that brain areas normally used for auditory processing are involved in sign processing in congenitally deaf individuals (Nishimura et al, 1999; Hickok et al, 1998b). Petitto et al (2000) make the same observation, and conclude that the brain areas traditionally believed to handle auditory speech processing are in fact more general modality-independent language modules. An alternative explanation could be that these brain areas are indeed auditory in hearing people, but lie fallow in deaf people and are recruited for sign processing.

(Iverson et al, 1999).

And the manual dexterity required for gesturing, is present in many primates, including our closest relatives, so it is reasonable to assume that it has been present for a long time among our ancestors, tens of millions of years at least. Apes also have the cortical control of their hands needed for sign language (while lacking the corresponding vocal control, as discussed on p 53) (Corballis, 1999).

Mimesis (or mimetics — not to be confused with memetics[92] (Wilkins, 1998b)) concerns the art of miming or, as Donald (1997) puts it, *"us[ing] the whole body as a representational device"* (p 4, online edition) or *"...as a communication device..."* (p 6), which both Donald (1997) and MacNeilage (1994) regard as a vital first step in the evolution of language. It is not an unreasonable suggestion that miming, imitating, and pretending can be regarded as proto-symbolic activites that may be related to the origin of language, particularly if language started in a gesturing modality, for which miming abilities are plausible exaptations — modern sign languages still have considerable mimetic components (Newport, 1982).

Zlatev (2001a) identifies a mimetic stage in human ontogeny, at which preverbal children acquire awareness of self and others, and take the first steps on the road towards social communicative competence, using miming and gestures for communication. This stage, and the self-consciousness and social interactions that it entails, *"appears to be the only way to acquire true meaningful language."*, according to Zlatev (2001a, p 179).

The hypothesis of Rizzolatti & Arbib (1998), that the roots of language can be traced to the so-called "mirror neurons", has some parallels with mimetics, but has a neural rather than a behavioral basis. "Mirror neurons" make up a neural system that is activated both by performing a certain action, and by observing the same action performed by others. This is very likely part of the neural basis of imitative learning, with the mirror neurons performing a high-level synthesis role in the network of neural connection reviewed by Schaal (1999). Rizzolatti & Arbib (1998) hypothesize that the mirror neurons also led to a system of gestural communication, with iconic gestures mimicking the action that's the topic of communication. The gestural system would have included both manual and oro-facial gestures, with speech growing out of the oro-facial gesturing system. It is interesting to note that the mirror system in monkeys is located in their equivalent of Broca's area (Schaal, 1999). However, even though we share the mirror system with monkeys and apes, there are qualitative differences between the imitative learning of humans and other primates (Call & Tomasello, 1995; Tomasello et al, 1993; Nagell et al, 1993) — but interestingly enough, enculturated apes who have grown up with humans show human-like imitative learning (Tomasello et al, 1993).

But if language did first evolve in a gesturing modality, why did we switch to speech? This question can only be answered speculatively, but there are two

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[92] Though Gabora (1998) apparently does wish to conflate mimetics with memetics.

obvious advantages of speech over gestures:

- There is no need to see each other, an advantage in the dark, or in heavy vegetation.
- The hands are not needed for communication, making it possible to work or carry things while communicating. (Carstairs-McCarthy, 1996)

Sign language has corresponding advantages in very noisy environments, or when stealth is an issue, situations in which people even today communicate with gestures. One can well imagine a gradual transition from gesturing to speech, with intermediate stages similar to those depicted in Auel (1980), in which sign language is augmented by a few sounds.

Bradbury & Vehrencamp (2000) review the economic viability of communication systems, setting a lower limit for the accuracy of signal coding, below which it is not worthwhile for receivers of signals to pay any attention to their content. In this model, it makes sense for communication systems to start out by using as signals such behavior that potential receivers have already evolved to pay attention to for other reasons. Much animal communication can readily be interpreted within such a framework. It is unclear, but would be relevant to investigate, whether hominoid vocalizations or gestures are better from this perspective.

An alternative possibility is that gestures and speech were used in parallel in the beginning, while the production and reception of both modalities were still in their infancy. According to Rowe (1999), such multicomponent signaling improves detectability and discriminability beyond that possible with either component alone.

If gestures came first, then this implies early language, since anatomical speech adaptations turn up in fossils well before the postulated time frame for late language.

Alternatively, if speech came first, then we have two possibilities:

- Early speech, gradually evolving in articulation, starting with the sounds that also apes can produce, with selection pressure from speech driving the anatomical reconstruction of the speech organs. This kind of coevolution of speech organs and language is evolutionarily plausible.
- Late speech — but this is problematic for the same reasons as late signing; language must be in place before obvious anatomical language adaptations.

In either case, language evolution must be well underway before the anatomical speech adaptations can be selected for. And since some of these adaptations go all the way back to *Homo erectus*, a million years ago (see p 53), this effectively rules out late language.

5.1.5 Innate and genetically determined vs. learned and culturally determined

Reviewing the full debate of whether language is innate in humans, and if so, what this means, is beyond the scope of this essay. On one level, innateness in the limited sense that Chomsky alluded to when he said *"I have no idea what the phrase* [innateness hypothesis] *is supposed to mean and correspondingly have never advocated any such hypothesis — beyond the truism that there is some language-relevant distinction, ... , between my granddaughter and her pet kitten (...)."* (Chomsky, quoted in Stemmer (1999)) is hardly controversial — it is self-evident that humans have innate, genetically determined abilities that kittens don't.

What is controversial, however, is to what extent those innate abilities are specifically linguistic, and to what extent they constitute a genetically hardwired "universal grammar". Chomsky, e.g. (1965), as well as other linguists working within the Chomskian paradigm, e.g. Pinker (1995), commonly make stronger claims about innateness than Chomsky's kitten quote above. But the debate is often unnecessarily polarized — it is not a matter of total genetic determinism on one side, and total *tabula rasa* conditioning on the other, despite the rhetoric of both sides (Seidenberg & MacDonald, 1999; Jackendoff, 1999a).

The claims of "strong innateness" rest on two main pillars:

- The universality of certain language features (Chomsky, 1988). Particularly compelling is the emergence of the same universal features in the independent origin of creoles (Bickerton, 1995, but see also Owens (1990)).
- The poverty of the stimulus (Chomsky, 1965; Chomsky, 1986; Laurence & Margolis, in press) — the impossibility of language acquisition without having the central concepts of language available *a priori*, in an innate language acquisition device (LAD) (Chomsky, 1965; Wanner & Gleitman, 1982).

Arguments against innateness take several different forms. Laurence & Margolis (in press) review (and dismiss) a variety of philosophical objections; I choose instead to focus mainly on empirical issues, particularly from outside linguistics proper:

- The poverty of the genes. We simply don't have enough genes to specify in detail all the complex neural connections in a putative language organ (Mueller, 1996) — no more than 30,000 or so have to account for the entire human body and brain (Pääbo, 2001; Claverie, 2001). This problem is exacerbated by the fact that we share the vast majority of those genes with the other apes, so that everything uniquely human must be handled by the tiny number of non-shared genes.

- Brain development is highly plastic, and dependent upon the sensory impressions received at an early age (Wong, 1995; Mueller, 1996). Those systems that are understood in more detail (like vision) are *not* genetically hardwired in the detailed sense that an innate grammar would need to be. Instead, only the rough outlines are laid down genetically — the optical nerve is led to the occipital lobe of the brain under genetic control — and the detailed neural connections are then gradually formed and pruned, in response to the sensory data received during a critical period. By surgically re-routing the optical nerve in the fetus, a vision module can be formed elsewhere in the brain instead (Merzenich, 1999).

- The impossibility of language acquisition is not self-evident[93]. To begin with, this argument is based on particular assumptions about what is actually acquired in language acquisition. *"The notion of what constitutes important evidence for learning a particular structure is not theory-neutral."* argue Seidenberg & MacDonald (1999, p 575), who make a distinction between the abstract "competence grammar" that is central to the Chomskian approach, and the more pragmatic learning for functional communication that they see as the primary goal of language acquisition. This undercuts the "poverty of the stimulus" argument in that *"... many of the classic arguments rest on the assumption that the child's task is grammar identification, and these arguments simply no longer apply if the task is instead acquiring the performance system underlying comprehension and production."* (Seidenberg & MacDonald, 1999, p 574).

  But even within the Chomskian paradigm, the issue is not so clearcut. E.g. the lack of negative evidence in the learner's input is frequently cited

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[93] In an interesting twist of logic, Bever (1982) reverses the logic of the impossibility argument. The standard syllogism of the impossibility argument can be stated as follows:

1. **Language has property P_i**
2. **P_i cannot be learned by any known theory of learning**
3. **Therefore P_i is innate**

But what about this syllogism:

1. **Language has property P_i**
2. **P_i cannot be transmitted by any known genetic mechanism**
3. **Therefore P_i is learned**

(Adapted from Bever (1982), p 432)

It is not self-evident that one syllogism is more valid than the other. Bever (1982) proceeds from this point into an odd Platonic essentialist view of language; I prefer to regard this as a challenge to premise 2 of both syllogisms. Premise 2 of the first syllogism is related to the classical 'Poverty of the stimulus' argument, but contains also more general learnability arguments, whereas premise 2 of the second syllogism is the 'Poverty of the genes' argument above. The empirical matter of which poverty argument is more nearly valid is not settled.

as evidence against learnability (Marcus, 1993; Marcus, 1999b; Pinker, 1995), but Saxton (1997) and Strapp (1999) provide examples of negative input that children may use. Furthermore, comprehension comes before production in language acquisition (Bates, 1993) — and there is no shortage of negative feedback for miscomprehension (Savage-Rumbaugh, 1990; Savage-Rumbaugh et al, 1993a). Pinker (1995) even provides an example of a child who, being mute, acquired full comprehension of grammar with no production whatsoever.

And the speech that language learners hear is rather different from normal adult discourse. Surprisingly young children can exploit linguistic and non-linguistic cues as an aid in speech perception and language acquisition (Shady & Gerken, 1999). As is well known, those adults who interact with language acquirers enrich their speech in such cues, sometimes to the point of nongrammaticality (Chafetz et al, 1992), creating what is known as "motherese"[94] (Elliot, 1981; Pinker, 1995) or "parentese" (Chafetz et al, 1992) when directed towards children, and "teacher talk"[95] (Håkansson, 1987) when directed towards adult learners. Even phonetic contrasts are enhanced (Kuhl et al, 1997), making phonemes easier to distinguish. The gestures that accompany speech are likewise modified into a "gestural motherese" that may function to reinforce or disambiguate speech (Iverson et al, 1999). There are, however, examples of cultures where speech to children does not appear to be adapted like this, without obvious ill effects on language acquisition (Pinker, 1995).

- There is no shortage of alternative theories of language acquisition, that do not postulate an innate language acquisition device, though not all of them have a firm basis in modern linguistics. Some examples:
  - Empiricist theories
    - Connectionism, reviewed by Rispoli (1999), with attached discussion and comments, pro and con: (Chater & Redington, 1999; Ellis, 1999; Feldman, 1999; MacWhinney, 1999; Maratsos, 1999; Gobet, 1999; Hahn, 1999; Valian, 1999; Plunkett et al, 1999).
    - Probalistic and distributional approaches (Redington & Chater, 1997; Plunkett, 1997).
  - Cognitivist theories
    - Schemas, of several types (Arbib & Hill, 1988; Mandler, 1994).
    - Functionalist approaches (Bates & MacWhinney, 1982).
    - Language emergent from cognition (Gomez & Manning, 1997).
  - Social-cognitive interactionist theories

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[94] A usage which I, being a father, consider sexist.

[95] Why not "teacherese" ?

    - Socio-perceptual language emergence (Zukow, 1990).
    - Cultural acquisition of language (Harkness, 1990).
    - Ecological language acquisition (Dent, 1990a; Dent, 1990b).
  - Neo-nativist theories
    - Chomsky
    - Optimality (Prince & Smolensky, 1997; Tesar, 1998, but see Fodor (1997)).

  Optimality and connectionism have the attractive feature that they are amenable to direct computer simulations of language acquisition, and appear to work, at least for the "toy languages" that are computationally tractable (Prince & Smolensky, 1997; Parisi, 1997). Furthermore, both optimality and connectionism are eminently compatible with Chomsky's (1982) Government & Binding grammar (Uriagereka, 1999), and only take issue with Chomsky's language acquisition model. Smolensky (1999) presents a formal grammar within a connectionist framework.

- The ape language experiments, to the extent that their results are accepted (e.g. Savage-Rumbaugh & Lewin (1994) present some very impressive results), argue against the necessity of innate language-specific abilities.

  Why would apes, who do not, as far as we can tell, acquire language in the wild, possess a *language* acquisition device, dormant for millions of years until human scientists came along? Parallel evolution of a complex device that isn't used is evolutionarily ridiculous. More reasonable is the hypothesis that the common ancestor of humans, chimps, and bonobos already possessed those components of the device that we have in common. This implies one of the following three possibilities:

  - Chimps and bonobos do use and acquire language in the wild, with a language acquisition device that's a shared inheritance from our common ancestor. This cannot be totally excluded, but there is no real evidence in favor of it either. Of course, if this possibility is correct, then the whole controversy over ape language acquisition is moot.
  - This common ancestor already had language, which was then subsequently lost in the chimp/bonobo lineage, with some vestiges of the language acquisition device retained. But why would they lose something so obviously useful?
  - The "language" acquisition device isn't language-specific, but is a more general learning device, used by the common ancestor, and still by the chimps, for some purpose other than language.

  As long as we have no evidence of language acquisition among apes in the wild, the third possibility appears most likely.

The innateness issue is, as far as I can tell from the arguments and available evidence, far from settled. There is a disturbing tendency for the debate to be split along disciplinary lines, with mainly linguists on the innateness side, and mainly cognitive scientists on the other, which indicates a lack of adequate communication between the fields. There is merit in the arguments of both sides. On one hand, the arguments for underlying universals in the structure of human languages are compelling — but on the other hand the successes, however modest, of the explicitly computational models, optimality and connectionism, indicate that the supposed impossibility of language acquisition without a Chomskian language-specific language acquisition device may not be as absolute as claimed (even though at least optimality postulates other innate features). Furthermore, the "poverty of the genes" argument conclusively shows that strong claims of a complex and fully genetically determined innate grammar are untenable. Possibly the model discussed in Svensson (1993), with a few innate fundamentals at the bottom, but with social interactions playing the main role for acquisition, can be a reasonable compromise model, consistent with the evidence from both sides?

The impact of the innateness issue on language evolution is actually rather modest, if subtle. Nobody doubts innateness in Chomsky's kitten sense (see p 89), which implies that *some* language-relevant genetic changes must have taken place along the human lineage, since the last common ancestor we shared with kittens (which was a primitive mammal sometime in the Cretaceous, about 100 million years ago (Murphy et al, 2001)). Many, but not all, of those changes can be located to the last five million years, after we and the the other apes parted company in the family tree — there is certainly a difference in language abilities, not only between young Miss Chomsky and her kitten, but also between the gorilla Koko (Patterson & Cohn, 1990) and her[96] kitten.

Innateness does have an impact on the issue of gradual vs. sudden language evolution, as mentioned above. Innate complex features cannot evolve suddenly with any reasonable probability — intermediate steps are necessary. Even with the rather modest degree of innateness that is empirically well-established, a gradual transition is more biologically plausible, *contra* Chomsky (1988).

Nevertheless, even though an innate grammar may not be *necessary* for language acquisition, this does not prove that humans don't have one anyway, since an innate grammar would certainly facilitate language acquisition, even without being strictly necessary. The Baldwin effect, described on page 20, implies that if language has been a central part of human behavior for a sufficiently long time, an innate predisposition to acquire language (which may or may not mean an innate grammar) is an expected result.

There are innateness debates (though less acrimonious) in other areas of human cognition as well, with a long list of proposed cognitive universals that goes back to the geometrical axioms of Euclid, and Kant's category of synthetic *a priori* knowledge (Kant, 1781). It is argued in this context by Shepard (2001), Schwartz

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[96] Yes, the gorilla Koko also had a pet kitten (Patterson & Linden, 1981).

(2001), as well as Konrad Lorenz (cited in Beer (1996)), that knowledge that for us is perceived as *a priori* self-evident, is actually evolutionary adaptations of our cognition to the world around us[97], so that Kant's synthetic *a priori* knowledge is really evolutionarily *a posteriori*[98]. This is a possibility also for language universals.

On the non-genetic side of the issue, we need to consider the different levels of language-related evolution, discussed on page 20. Very little empirical data is available concerning the cultural or memetic evolution of language, but it would still be an error to discount such processes and focus exclusively on the biological evolution of a hypothetical innate language acquisition device. Even though little is known, it would be highly surprising if language, regarded as a memetic-type entity, did not change over evolutionary time. As discussed in section 2.5.1, selection for both improved learnability and communication can be expected to occur. In parallel with this memetic evolution, there will be Baldwinian evolution towards an innate language acquisition device — but memetic evolution is a much faster process, so the result is likely to be biased towards languages that are easy to learn, rather than towards learners who are innately good at learning languages (Bull et al, 2000).

In conclusion, it may well be that the final resolution of the innateness debate will be a compromise, with coevolution of language memes and acquisition genes (Kirby, 1996). It is certainly not a simple black-or-white dichotomy.

5.2 What drove the evolution of language?

Evolution of complex and specialized features does not occur without being driven by some selective pressure — some evolutionary advantage accruing to those who possess the feature. And it is self-evident that language is such a complex and specialized feature (Pinker & Bloom, 1990). But what was the crucial advantage conferred by language, that drove its evolution? One may think that the advantages of having a language are obvious — but that would instead raise the question of why only humans have acquired it, why not a lot of other animals as well, if it is so useful? There must be something unique in *human* history, that made language particularly advantageous for our ancestors, but not for the other apes. This has close parellels with hypotheses concerning why our brains are so much larger, discussed on p 65. The different levels of evolution, as well as the features and limitations of evolutionary processes, reviewed in section 2, should also be kept in mind.

Another important aspect is the context in which language evolved. Before the

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[97] It is interesting to note in this context that one of the traditional *a priori* truths, Euclid's parallelity axiom, has been found to be empirically false, though an excellent approximation in our everyday world (Einstein, 1915; Dyson et al, 1920).

[98] Chomsky, oddly enough, argues *against* this form of innateness, stating that *"We cannot appeal to this* deus ex machina *to explain the convergence of our ideas and the truth about the world. Rather, it is largely a lucky accident..."* (1988, p 158).

advent of agriculture (which certainly postdates language), modern humans lived as hunter-gatherers, in modest-sized tribes, presumably with a lifestyle and social structure not vastly different from that of the few remaining present-day hunter-gatherers. The chimpanzee lifestyle can reasonably be called hunter-gatherer as well. Thus it appears not unreasonable to assume that language evolved in a hunter-gatherer context, in tribes with a social structure somewhere in between that of chimps and modern hunter-gatherers. This is the "Environment of Evolutionary Adaptedness" (EEA), the Stone Age environment for which evolution has shaped us — the time since we abandoned the hunter-gatherer lifestyle is much too short for any substantial evolutionary changes (Daly & Wilson, 1999; Nesse & Williams, 1994; Byrne, 2000). Reasonable hypotheses of language evolution must postulate that language carried some crucial advantage for people in such an EEA society — advantages that language confers only in modern societies are irrelevant.

Numerous hypotheses have been proposed as answers to these questions about human language evolution, a selection of which will be evaluated here. In order to provide some structure and overview, the hypotheses will be classified under several categories, though the boundaries between the categories are sometimes fluid. Many authors propose multicomponent hypotheses, rendering them a mention under several categories.

5.2.1 Hunting.

An obvious starting point is to postulate that language evolved for the purpose of communication, and that the main selective advantage gained by improved communication was enhanced coordination of group activities. Prominent among the group activities discussed in this context is hunting, which has played a central role in many scenarios for human evolution (Landau, 1991; Sagan, 1977), but more general resource acquisition activities can be included here as well (Cziko, 1995). Apart from communication during hunts, the hunting argument has also been connected with the teaching argument of section 5.2.4 below: *"The "quality education" needed to become an expert Pleistocene hunter could not do without a complex form of information transmittal interaction in which the transcendence of the* here and now, *[...] played a key role."* (Roebroeks, 2001, p 451).

There are, however, several problems with the notion that hunter coordination was a major driving force in language evolution.

- Most hunter-gatherers for whom we have data don't get nearly as much food from hunting as from gathering — hunting simply isn't important enough for their subsistence, to be a major force in their evolution. Exceptions are the Inuit, who live in an Arctic environment with little to gather, and very likely the Neanderthals of Ice Age Europe, for similar reasons. Isotopic evidence from Neanderthal fossils indicates that meat from large herbivores was a major part of their diet, which implies that hunting was an economically vital activity (Richards et al, 2000; Bocherens et al, 2001). But living in a glacial environment is a very late development in human history, well after *H sapiens* and Neanderthals had gone their separate ways, so an Arctic origin of language does not appear plausible.

- Modern humans do not use all that much language during a hunt — it is a rather silent activity.
- Non-human social carnivores manage to coordinate their hunts without using language. This includes wolves and lions, but also chimpanzees, who do hunt on occasion (Mitani & Watts, 1999; Plummer & Stanford, 2000; Mitani & Watts, 2001; Stanford, 1998). Chimpanzee hunts take place in modest-sized groups (almost exclusively male)[99], and give the impression of being collectively planned and coordinated in advance. The communication systems that chimps have in the wild are to all appearances perfectly adequate for hunting purposes, as evidenced by a hunting success rate in excess of 50% (Mitani & Watts, 2001), which compares favorably with human hunting prowess.

Gathering may well be more plausible than hunting as an explanation for language, since gathering in modern human hunter-gatherers relies on an encyclopedic knowledge of thousands of edible plants and other items, the communication and discussion of which may well be highly advantageous (Pinker & Bloom, 1990).

However, as noted earlier, a plausible hypothesis of language evolution should explain not only why our ancestors did evolve language, but also why the chimp ancestors didn't. And in the case of gathering it is far from obvious that there is any notable difference between the two. Concerning hunting, chimpanzees do hunt, as mentioned above, but they don't do it very often; meat is regarded by them as a rare delicacy, but it does not contribute significantly to their subsistence.

It is a matter of some controversy when hunting became economically important for our hominid ancestors. There is evidence for meat-eating and meat-processing quite early in the fossil record — isotopic hints of a dietary shift are found in 3-million-year-old *Australopithecus africanus* (Sponheimer & Lee-Thorp, 1999), and bones with cut marks from stone tools first occur around 2.5 million years ago (Semaw, 2000) and become common from about 2 million years ago (Brantingham, 1998; Dominguez-Rodrigo, 1997; Capaldo, 1997; Fernández-Jalvo et al, 1999b), in the context of *Homo habilis*. However, it is not obvious to what extent animals were actively hunted, and to what extent meat was scavenged from

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[99] Chimpanzees do not hunt out of economic necessity — hunting is *less* common when fruit is scarce. Instead, the evidence indicates that the main function of chimpanzee hunting is male bonding and coalition building (Mitani & Watts, 2001; Stanford, 1998). It is not entirely obvious how this differs from hunting among humans, particularly in modern Western countries.

carcasses killed by carnivores. Scavenging is argued on ecological grounds (Brantingham, 1998), whereas cut marks are used both to support hunting (Dominguez-Rodrigo, 1997) and scavenging (Capaldo, 1997). It may be relevant to note here that chimpanzees actively hunt, but never scavenge (Plummer & Stanford, 2000). The issue of hunting versus scavenging is argued even in the case of Neanderthals and early modern humans, but more recent evidence clearly supports hunting in these cases (Marean, 1998; Milo, 1998; Richards et al, 2000; Bocherens et al, 2001). As a matter of fact, it appears that Neanderthals hunted *more* than modern humans, who had a broader diet (Richards et al, 2001), which under the hunting hypothesis would imply that Neanderthals, who according to Balter et al (2001) obtained 97% of their sustenance from meat, had even more reason to evolve speech than we did.

Regardless of whether the meat was hunted or scavenged, there is evidence for a major dietary shift in early hominids, somewhere between 3 and 2 million years ago, from a diet similar to that of chimpanzees, to one including significant amounts of meat from larger animals. It is intriguing that the timeframe coincides with the emergence of the genus *Homo* and the first stone tools, as well as the start of human brain growth. New communicative needs associated with this new lifestyle are not ruled out. But communication about scavenging is at least as likely as communication about hunting.

5.2.2 Tool making

Tool use and tool making is not entirely limited to humans. The *making* of tools is reported only for chimpanzees and bonobos (pygmy chimps) (Boesch & Boesch, 1990) (who even make stone tools (McNeil, 1996; Savage-Rumbaugh & Lewin, 1994)), but numerous species have been found to *use* tools, including all the great apes (Sugiyama, 1994; Nakamichi, 1998) and some monkeys (van Schaik et al, 1999; Westergaard et al, 1998a), as well as numerous others, from spiders to naked mole rats (Shuster & Sherman, 1998). That chimpanzees use tools has been known at least since Darwin's time (Savage & Wyman, 1844, cited in Whiten & McGrew (2001)), but the uniqueness of human tool use was nevertheless still argued for another century. Still, tools do appear to have played a major role in human evolution, as reviewed by e.g. Schick & Toth (1993), and are frequently invoked as one of the factors that drove the evolution of hominid brains and intelligence, a hypothesis supported by the complexity found in the brain activity of modern humans during stone-tool manufacture (Stout et al, 2000). A few authors, such as Gibson (1990, cited in King (1996)), have invoked tool making as a driving force also behind the evolution of language. As for the driving forces behind tool-use evolution itself, see the review of van Schaik et al (1999).

The oldest stone tools are about 2.5 million years old (Semaw et al, 1997), and bone tools of comparable age have been found as well (Backwell & d'Errico, 2001; Shipman, 2001). It is not known whether less durable tools, like wooden sticks, were also used by early hominids, as they are by chimpanzees, since such

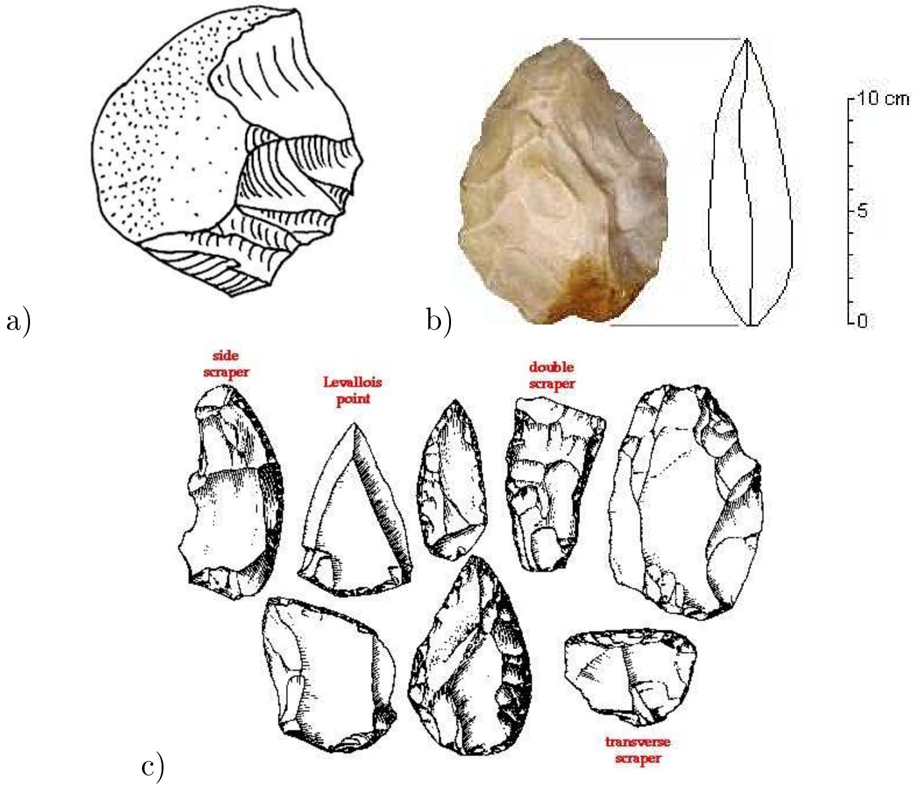

Figure 19: Tools from different cultures. a) Oldowan, commonly associated with habilines (http://www.amonline.net.au/human_evolution/images/oldowan.gif) b) Acheulean, commonly associated with *Homo erectus* (http://anthro.palomar.edu/-homo/images/Acheulean_hand_ax.gif) c) Mousterian, commonly associated with Neanderthals (http://www.hf.uio.no/iakk/roger/lithic/MOUST/mousterian.html)

tools are not preserved; the diversity of tools in the fossil record is likely to be underestimated. For the first million years or so, a simple stone tool kit, called Oldowan, was used, without significant change through time (Semaw, 2000) (the various tool kits discussed in this section are shown in figure 19). The Oldowan industry is mainly associated with *Homo habilis* (Kimbel et al, 1996), though tool-using robust australopithecines remains a possibility, according to Susman (1994; 1998). Interestingly enough, the australopithecines who went through the dietary shift towards meat mentioned in section 5.2.1 above had, according to Teaford & Ungar (2000), teeth that are totally unsuitable for tearing and cutting meat, which suggests that they had other meat-cutting implements at their disposal.

After the Oldowan, and coincident with the arrival of *Homo erectus*, the Acheulean tool kit, with more advanced and consistently shaped hand-axes, became widespread instead. The significance of this change is, however, controversial (McPherron, 2000), though Aiello (1998) attributes it to the same cognitive breakthrough that he postulates as the first step in the evolution of language.

For another million years, throughout the lifespan of *Homo erectus*, the Acheulean tools underwent little change. Even more remarkable, the rate of technological diffusion was so slow that Oldowan tools were still used in Europe as late as less than a million years ago, even though they had been obsolete in Africa for almost a million years by then (Roebroeks, 2001).

The Mousterian tools associated with Neanderthals were likewise fairly uniform in time, from half a million years ago onwards, though some technological progress has been observed through time at Neanderthal sites that were occupied during many millennia (Simek & Smith, 1997; Otte et al, 1998), as well as adoption of presumed *Homo sapiens* inventions by late Neanderthals (Hublin et al, 1996).

And then *Homo sapiens* came along, and with us a clear acceleration of the pace of technological and cultural innovation, an acceleration that is still with us today. Here we have the main role of tools in the debate about language evolution — the sudden increase in creativity is interpreted by many, e.g. Mellars (1998), Diamond (1991), or Donald (1997), as evidence that we had suddenly acquired language.

However, the appearance of a sudden dramatic “cultural revolution” around 40,000 years ago, has turned out to be an illusion caused by the predominance of European sites in the documented archeological record, and possibly the Eurocentrism of archeologists. *Homo sapiens* did indeed invade Europe rather suddenly about 40,000 years ago, bringing along an advanced toolkit — but that toolkit had been developed gradually in Africa over the course of more than 200,000 years (McBrearty & Brooks, 2000). There was no sudden revolution, and thus no need for a sudden cognitive leap (as in sudden language acquisition) to explain the revolution.

5.2.3 Sexual selection.

The core of natural selection is reproductive success — no matter how successful you are by other measures, if you do not reproduce you're an evolutionary failure. Sexual selection, the selection of certain features because they directly influence the mating success of their bearers, therefore plays a prominent role in evolutionary theory (Darwin, 1871), accounting for innumerable features, from peacock tails to birdsong to horns (Emlen, 2001). If one observes (or participates in) the mating rituals of *Homo sapiens* today, it is obvious that language plays a non-negligible role. The possibility that this may have been true also for early hominids is considered by many authors, e.g. Cziko (1995). In this scenario, the selective advantage that drove language evolution may simply have been that the better speakers were preferred as mates, and so got more offspring. A variation on the same theme is the hypothesis of sexual conflict as a driving force (Aiello, 1998), as is the observation that verbal skills can be translated into political power, which in turn enhances reproductive success (Pinker & Bloom, 1990) — as Henry Kissinger reputedly expressed it: *"Power is the strongest aphrodisiac"*. This "political hypothesis" is further discussed on p 105 below.

But, as for the gathering hypothesis in section 5.2.1 above, it is not sufficient that it is plausible that the fitness of language is based on sexual selection — we also need to explain why chimps and other apes did *not* evolve language if it's so great for your sex life. Human sex life is certainly very complex, with our officially monogamous but actually semi-polygamous system[100] (Diamond, 1991), with multiple mating strategies available for both men and women (Gangestad & Simpson, 2000), with the strategies at least partially having a biological basis, under hormonal control (Thornhill & Gangestad, 1999). Such a complex system would enhance the adaptive value of language. But it is not obvious that the other apes have simpler mating systems:

- Gibbons (1998b), who were long thought to have a purely monogamous system, similar to the official human one, have turned out to have an actual system very close to the actual human one instead (Brockelman et al, 1998; Gibbons, 1998b).
- Gorillas were likewise believed to have a fairly simple system, based on the physical dominance of a single large male, who monopolized a harem of females. But also in this case, careful observations have shown that the actual system is more complex, with "illicit" matings with other males than the harem owner very common (Robbins, 1999).
- Bonobos are probably the most sexually active of all the apes, including us, and use sex for a multitude of purposes apart from reproduction — sex for friendship, reconciliation, or even pure recreation, is ubiquitous, in all conceivable combinations of gender and number (Savage-Rumbaugh & Lewin, 1994). They are also famous for having the same taste as humans in sexual positions, with the missionary position and other face-to-face positions being the most common, unlike most other mammals, including the other apes, where the male enters the female from behind.
- Common chimpanzees may have the most complex system of all, with both males and females choosing between several different mating strategies (Goodall, 1971; de Waal, 1998; Gagneux et al, 1999b). A female chimp may some of the time engage in promiscuous mating within the group, at other times seek out partners in other groups for a quick discreet mating in the forest, or form temporary monogamous relationships with a preferred male. Males may either try for political power in the group, thereby gaining

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[100] Genetic screening of human infants, done on more-or-less random samples for *other* reasons than to determine paternity, regularly turn up on the order of 10% children, even within superficially monogamous families, who were not fathered by the "official" father (Salter, 1996; Marlowe, 2000).

preferred access to females, or try to mate on the sly with willing females, either in his own group or from another.

Empirical data on the prevalence and success of different strategies are not readily obtained, and the data on patterns of paternity within chimpanzee communities are contradictory (Vigilant et al, 2001).

- Orangutans are solitary and arboreal, and difficult to study in the wild. I have not found any detailed studies of their sex life, other than Nadler (1977), who describes orangutan sex in captivity, but the context is quite unnatural, and unlikely to be informative. According to Schwartz (1987), they are mainly monogamous, but the evidence for this is modest.

There is no strong reason to believe that language is more advantageous in the human mating system than in any of the others. Particularly the gibbon system is quite similar to ours, including similar levels of paternal care, something which the other apes don't engage in. Furthermore, there is some evidence that the mating system of humans has changed during the past few million years. One fossilizable mating-system indicator is male-female dimorphism — in monogamous species, males and females are very similar, whereas in polygynous species males are commonly larger and more robust. Gorillas, with their enormous and fearsome males and tiny females, have a typical polygynous system, whereas gibbon males and females, with their quasi-monogamous system, are hard to tell apart. Humans and chimps have similar levels of dimorphism, which might have been interpreted as a sign of continuity in mating systems since the last common ancestor — but some australopithecines have a male/female size ratio comparable to gorillas, indicating a strongly polygynous system (Ward et al, 2001).

In other apes, the canines are commonly used for intraspecific displays and conflicts between males, and unsurprisingly males of polygynous species typically have very large canines. In humans, canines are not used for this purpose, and are correspondingly modest in both sexes — but it is intriguing and puzzling to note that this trend towards smaller and non-dimorphic canines was begun among the highly bodysize-dimorphic australopithecines, where the opposite trend would be naïvely expected.

But sexual selection has the odd property that features can be selected for even though they are *dis*advantageous by any objective criterion, if they attract the opposite sex. The tail of a peacock male is of absolutely no practical use, and is actually detrimental to his survival — but since peacock females prefer to mate with males with large tails, a large-tailed male will have higher reproductive success, despite dying young himself when his large tail makes him too slow to escape a predator. Why a certain feature attracts females may well start out completely at random — if both the feature in males and the preference in females are inheritable, runaway sexual selection can result.

Quite a few features in humans may well have a similar origin, notably the ones that we find attractive in the opposite sex. For example, there is no obvious *practical* reason why human females should have several times larger breasts than chimp females — chimps manage to produce just as much milk. The evolution of large breasts in humans may instead be adequately explained by the human (but not chimp) male reaction to big breasts.

It is conceivable that language was sexually selected in this random fashion, but the obvious utility of language for various purposes points towards an adaptive explanation instead — sexually selected features are commonly either useless or harmful (Emlen, 2001).

5.2.4 Child care and teaching.

Primate babies in general mature slowly, and need parental care for an extended period, often several years. During these years, the juvenile primates not only grow up physically, but also learn about their environment. Behaviors that have to be learnt include practical issues like food gathering, but the main thrust is towards learning to function in their social environment (Joffe, 1997).

This extended childhood period has been carried to an extreme in *Homo sapiens*, who take fifteen years or more to reach physical maturity, and sometimes even longer to become socially adult. At the same time, human infants are born immature and helpless compared to other primate babies, and require intensive parental care during the first years, severely restricting the caregiver's activities. The immature babies appear to be the result of a compromise in fetal development — in other primates, the gestation period follows a simple relation, but when that relation is applied to humans it predicts a gestation period twice as long as our customary nine months. So human babies are systematically born many months premature, naturally quite helpless. The reason for this prematurity ought to be obvious to every woman — imagine trying to give birth to a one-year-old child, weighing ten kg or more! Given the rate of brain (and head) growth of the human fetus, after nine months the baby's head size reaches the diameter of the birth canal through the pelvis, and it had better get out before it's too late. Increasing the diameter of the birth canal is not an option, since a wider pelvis would lead to inefficient bipedal running (Byrne, 2000). Our early immature birth is thus a necessary consequence of our large brain. Elman (1993) proposes that the immature birth may be adaptive in itself, but I do not find his arguments compelling.

The extended juvenile period in humans, as in other primates, is largely spent on getting an education. But human societies, even hunter-gatherer tribes, are much more complex than ape societies (see section 5.2.5 below), and so presumably require more time to understand. Active teaching of children, by parents and others, is ubiquitous among humans, and there are many anecdotal reports of deliberate teaching among apes as well (King, 1996; Savage-Rumbaugh & Lewin, 1994; Byrne, 2000) though no solid experimental evidence (Tomasello, 2000b).

Teaching is a process that would obviously benefit from having a language, and King (1996) proposes this as a driving force behind language evolution. This is a plausible suggestion, but I think it should be seen in the wider context of our social complexity, as discussed below.

5.2.5 Social relations in groups and tribes.

Humans are social animals[101], as are chimps and gorillas and most other primates, living in groups with complex social relationships; O'Neil (2001) provides a brief overview of primate social structures. But humans differ from the other apes in that human social groups are much larger and more complex than chimp or gorilla groups, with correspondingly heavier demands on our ability to handle social relationships. Whiten (2000) also argues that *"we [humans] are more* deeply *social than any other species on earth in our cognitive makeup.* (p 477). These increased social demands are very likely the cause of our increased brain size and intelligence, according to the hypothesis of "Machiavellian intelligence" (see p 66).

Group size in animals is affected by many different factors:

- *Predation.* On one hand, there is safety in numbers, both for mutual defense against predators, and simply because when a predator attacks a large group, the probability of any given animal being eaten is small. On the other hand, large groups are conspicuous and may well attract more predators than a small discreet group. The optimal group size depends on predator characteristics. In the case of hominoids, the group defense argument appears most pertinent, favoring large groups (Aiello, 1998; Dunbar, 1996; Lewin, 1993).

- *Inter-group competition* (Isbell & Young, 1996; Zemel & Lubin, 1995). In many social animals, including both humans (Malmberg, 1980) and other hominoids, groups maintain territories and defend them against other groups of conspecifics. Large groups have obvious advantages in such conflicts, which may well translate into more territory per member in larger groups, again favoring large groups for our ancestors.

- *Intra-group competition for resources.* In a group, the members are close together during feeding, and are likely to be each other's worst competitors for food and other resources, decreasing food availability particularly for low-status members of large groups, as well as increased travelling for the whole group in order to gather enough food for all — the latter is invoked by Isbell & Young (1996) as an argument for the evolution of bipedalism.

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[101] A single example of a non-social human tribe, the Ik, is reported in the anthropological literature (Turnbull, 1978). However, the Ik are described as being able to communicate with visiting anthropologists, so presumably they had language, as well as some notion of human contact, so one may wonder how complete their supposed non-sociality were.

At an extreme, a very large group may strain the carrying capacity of the local environment (Caporael, 1996). On the other hand, if food occurs in rare but rich patches (e.g. fruit trees in the jungle, or large carcasses to scavenge on the savannah), the larger number of food seekers in a large group increases the chance of finding a food patch in which everybody can feed well (Zemel & Lubin, 1995; Lewin, 1993). Chimpanzee group size (which is quite variable in the wild) is to a considerable extent affected by local food availability (Matsumoto-Oda & Hosaka, 1998).

- *Mating opportunities.* In a large group, more individuals of the opposite sex will be available — but more competitors of your own sex as well. The net effect will be strongly dependent on your status in the group. Given the generally larger variance in reproductive success for males than for females, particularly in non-monogamous species, the effects of competition for mates can be expected to be more pronounced for males than for females. It is indeed not rare among mammals for groups to contain more females than males, with the balance of the males living alone. Whether small or large groups were advantageous for the sex life of our ancestors depends largely on the outcome of the next point below.

- *Intra-group aggression and politics.* Given the fierce competition for food and mates in large groups, conflicts between group members are likely to become more common the larger the group — but open aggression is costly, both in time and energy spent, and in risk for injuries and death. All parties would gain if all conflicts could be resolved peacefully. However, if all other group members retreat from aggression, a single aggressor can invade and dominate the group, to the detriment of everybody else. Even though all individuals would gain by peace, in a peaceful group each individual can gain by aggression — this paradox is known as "The prisoner's dilemma" (Koeslag, 1997). This dilemma has been the subject of considerable research for some years, seeking the roots of the cooperative and altruistic behavior that we do observe in many groups, and seeking to explain the comparative rarity of open aggression, despite its apparent benefits to the aggressor.

  The solution to the dilemma lies in the evolution of social intelligence, starting with the recognition of other individuals, remembering past interactions with each individual, and differentiation of behavior towards other individuals depending on their past behavior. But in a large group, this taxes the brain power of most animals, limiting either the group size or the complexity of the social system (Dunbar, 1993).

  A static status hierarchy is a common solution with limited cognitive demands — but the complexity rises fast if the status hierarchy isn't static, and if status relations aren't transitive. And if you're not at the top, a static hierarchy isn't to your advantage, so it pays to keep track of the actual power of all those around you, and figure out the right moment for a bid for higher status — but this raises the cognitive stakes again.

> What really leads to a cognitive arms race is when the simple hierarchy based on one-on-one dominance relationships is abandoned, and the possiblity of status based on friendships and coalitions and negotiations is considered. In this case, you have to keep track of not only your own position in the hierarchy, but also the social networks[102] of everybody in the group — who is friendly with whom, who might consider an alliance with whom, what happens if you attack individual A, when B, C, and D are also present — B might side with you, since you did him a good turn last week, but that might cause C and D to gang up on him, in which case ...
>
> The possibilities are endless, and grow exponentially with increasing group size. Here we have the basis for the hypothesis of "Machiavellian intelligence" mentioned earlier. Considering that both humans and chimps spend a major fraction of their time and cognitive abilities pondering intra-group relations, and considering that humans do it in much larger and more complex groups than chimpanzees, the hypothesis appears highly plausible — we hardly need such an enormous brain to outwit Nature, but we might well need it to outwit our fellow humans (Pinker, 1994), in order to win the game that we might call "social chess" (Andrews, 2001).

In the context of our early ancestors, it would appear that larger groups were desirable for several reasons. But a system of highly complex intra-group political machinations had evolved already before our common ancestor with the other apes, as both we and the chimpanzees are living with such systems (de Waal, 1998), which would limit the maximum group size to something an early hominoid could handle mentally. Chimpanzees can keep track of and be competent participants in the politics in a group with a few dozen members — but they would likely be lost if they formed a typical human-sized tribe with well over a hundred members (Dunbar, 1996).

This political argument strongly suggests a socio-political hypothesis for the evolution of language — because politics, also in the ape version, is very much about communication. Agreements, formation of alliances, trading of favors, coalition building, all aspects of politics place heavy demands on the communication between the parties involved. A better communicator is a better politician, and a better politician can gain higher status in the group, and reap the associated reproductive benefits for his communicator genes and memes — and spread them in the tribe.

Dunbar (1993; 1996) adds another twist to the socio-political hypothesis. Social and political relations are based on friendship, and friendship requires

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[102] In the simplest case, social networks are based on blood relationships, so that kin form permanent alliances. This is fairly common among e.g. baboons (Strum, 1989) and various other mammals. Kin networks are permanent, making them easy to keep track of, limiting the cognitive demands, but also limiting the political possibilities. DNA testing on chimpanzees have shown that their politics is not limited in this way — coalitions of non-relatives are common (Goldberg & Wrangham, 1997). They are not unknown among baboons either (Byrne, 2000).

maintenance — in order to become and remain friends with people, you have to spend time bonding with them. Among monkeys and apes, this bonding largely takes the form of mutual grooming — but grooming takes time (Byrne, 2000), and apes commonly spend a substantial fraction of their time grooming each other, time during which they cannot pursue either food or sex. The time needed for grooming is essentially constant per individual groomed, so the total time an ape spent grooming would grow linearly with group size. Already for the small groups of apes, grooming is eating up significant amounts of time — if that time is extrapolated to common human group sizes, the time required is around twelve hours per day, most of our waking hours, leaving precious little time for other activities. But not spending the time required for social maintenance leads to instability in the group. It follows that grooming is untenable as social lubricant in complex groups much larger than those of chimpanzees.

In order to maintain friendships in very large groups, a more time-effective method is needed. Dunbar (1993; 1996) proposes that language evolved for this purpose, as a tool for "verbal grooming". He notes that a large fraction of all human speech consists of friendly gossip, which serves both to bond those who gossip together, and to exchange valuable social information about others. In other words, gossip fulfills the function of grooming, with an information bonus added. Furthermore, gossip is much more time-effective than grooming, both because other chores can be done in parallel, and because it doesn't have to be performed one-on-one like grooming — a group of ten people can gossip together simultaneously, and get bonded in a small fraction of the time it would take them all to groom each other in all pair combinations. As we all know from experience, it is perfectly possible for a human to keep up with the gossip in a fair-sized group, without having to spend twelve hours a day at it.

Further support for the social hypothesis comes from the various experiments attempting to teach language to non-humans, reviewed in Johansson (2001). The only species having any kind of success in these experiments, apes, dolphins and parrots, are highly social with complex group relations. Additionally, teaching experiments are significantly more successful if they take place in a social setting (Pepperberg, 2001; Savage-Rumbaugh & Lewin, 1994).

Aiello (1998) extends the socio-political hypothesis in another direction, arguing not only that social complexity drove the need for language, but also that social intelligence provided the cognitive structure for language: *"There are similarities in reasoning processes or procedures between primate social intelligence and the computational basis of language processing including both the semantic aspects of language and syntax..."* (p 29). It is argued that we store social events as scripts that provide the procedural basis for syntax. We shall return to this possibility in section 5.3.4.

All in all, the basic socio-political hypothesis appears highly plausible as a basis for the selective advantage of language. The verbal grooming hypothesis of Dunbar (1996) is worth considering as well.

5.2.6 Miscellaneous ideas.

In this category, hypotheses are included that are far from the mainstream, and have few supporters. The list below could have been much longer than it is, but I have excluded obvious crackpots.

- **Children at play** is proposed as the main environment of early language evolution by Foster (1991), with language not used for communicative purposes, but instead in mimicry and random repetitive playing. Foster, however, clearly illustrates the point of my reversed quote from page 6: *we cannot leave the discussion of language evolution to those linguists who have yet to understand the concerns of modern evolutionary theory*; she is one of those linguists, displaying serious misunderstandings of (and a negative attitude towards) evolutionary biology.

- **Music** is the theme of Vaneechoutte & Skoyles (1998), according to whom *"[s]ong ... underlies both the evolutionary origin of human language and its development during early childhood."* (p 2), with the early stages analogous to birdsong, and selected for similar reasons. Their hypothesis is unorthodox, but is presented in a well-researched and carefully argued paper. Some role for singing and rhytmic music in early language evolution cannot be excluded, but I do not find plausible their dismissal of language evolving as an adaptive communication system — the role of music, if any, is very unlikely to be as dominant as Vaneechoutte & Skoyles (1998) propose.

  Verhaegen (1998) also links music to language origins, but in the context of the Aquatic Ape theory (Morgan, 1982), which does not add to its credibility (Langdon, 1997).

- **Art** has been invoked in two opposite roles here. Davidson & Noble (1993, cited in Savage-Rumbaugh & Lewin (1994)) cast it in a positive causative role, driving language evolution. Even more odd, Bowles (1998) presents an argument that inverts both the causal direction and the connection between language and art, asking whether it was the *absence* of language that drove the evolution of art. The empirical basis for this hypothesis is, however, modest, apparently limited to a single autistic child (presumably lacking language), who draws images that resemble cave art.

5.2.7 Why us and not the other apes?

Several of the ideas discussed above are plausible driving forces behind language evolution. But general plausibility is not sufficient — as has been pointed out repeatedly, a serious theory of language evolution must also account for the apparent absence of language in the other apes. Many of the factors that might have driven human language evolution, could equally plausibly have driven chimpanzee language evolution — except that in reality there must have been insufficient selective pressure towards language in chimpanzees, since they didn't evolve any language.

The split between the human and chimp lineages is commonly attributed to the progressively drier climate in Africa in the relevant time frame (Cane & Molnar, 2001), causing deforestation and the spread of savannah biotopes (Lewin, 1993; Isbell & Young, 1996). The general idea is that chimp and gorilla ancestors stayed in the remaining forests, retaining something close to the ancestral lifestyle, whereas human ancestors got stuck on the newly formed savannah, or in isolated patches of forest. The oldest hominid fossils are associated with woodland fauna (Haile-Selassie, 2001; Leakey et al, 2001; WoldeGabriel et al, 2001), but later ones lived in more open terrain (Sponheimer & Lee-Thorp, 1999; Vogel, 1999).

This new open-terrain lifestyle is the major ecological difference between our ancestors and chimp ancestors, and it appears highly likely that whatever factors drove language evolution in humans but not in chimps, are associated with this lifestyle. Larger group size, likely driven both by the more intense predation pressure on the savannah, and by the patchier food distribution, is an obvious factor to consider. It is commonly found, when comparing forest-dwelling arboreal and savannah-dwelling terrestrial relatives, that the terrestrials live in larger groups (Lewin, 1993). Given a larger group size, the socio-political complications that follow would generate a strong selective pressure towards improved social cognition and communication, as discussed above. The sexual aspects, increased teaching needs, and the dietary shift towards more hunting and/or scavenging, would all reinforce this trend, but it appears likely that the social pressures dominate. This is a reasonably plausible scenario that could lead to the evolution of language in the human lineage but not in chimps.

5.3 Proto-language

The preponderance of the evidence reviewed so far points towards language as an adaptation, shaped by Darwinian selection in a process of interacting biological, cultural, and memetic evolution. But *"natura non facit saltum"* — nature does not make sudden jumps, specifically not in evolution, which implies that language evolved in a gradual process, through several intermediate steps. The issue in this section is what those intermediate stages may have looked like.

There are several aspects of language for which intermediate stages are required. We need both proto-syntax, proto-semantics, proto-speech, and possibly proto-gestures (if sign language came first). Furthermore, the interdependence between these components needs to be clarified, as a basis for discussing their possible order of appearance, as well as their viability at every stage as a communication system. Throughout the entire process, a Darwinian perspective needs to be kept in mind — is every step actually an improvement in the Darwinian sense, conferring a selective advantage on the individual taking that step?

This section has much in common with Jackendoff (1999b), though this is mainly due to convergent evolution — we have arrived at similar conclusions from similar data.

5.3.1 Proto-speech

Only the mechanics of speech production and perception will be covered here, not its semantic and syntactic contents, which will be treated in sections 5.3.3 and 5.3.4 below. The evolution of the production and perception of speech sounds has already been dealt with in some detail in section 4, the main results of which are reviewed here.

Speech perception is the easiest part, since chimpanzee perception is already adequate, as demonstrated by their comprehension of human speech in blind tests at the same level as a human two-year-old (Savage-Rumbaugh et al, 1993a). No proto-perception stage is needed.

Speech production is more difficult, since the vocal apparatus of our cousins (and presumably our ancestors) is inadequate to produce the full range of speech sounds. Furthermore, the neural control of vocalizations in apes is not well suited for speech production. With great efforts, chimps can produce sounds that vaguely resembles the vowel patterns of context-appropriate words — one gets the impression from the description in Savage-Rumbaugh & Lewin (1994) that their chimpanzee student Kanzi is trying very hard to reproduce the human word that he's heard for the item that he's just successfully produced the sign for. As already mentioned, Kanzi has demonstrated that he understands English well enough (Savage-Rumbaugh et al, 1993a), but his production is severely handicapped.

Still, the sound repertoire of chimps is far from negligible — if only they had adequate neural control, so that they could combine freely the sounds that they do produce, they'd have a set of phonemes adequate for a simple language.

MacNeilage (1994; 1997) has developed a hypothesis for the origin of the first speech sounds, which is concerned with the evolution of neural control of jaw movements. He combines evidence from ontogeny (infant babbling) with evidence from universal sound patterns in human languages, to propose a set of simple syllables as the core of the *ursprache*. The exact set has evolved over time, from MacNeilage (1994) to MacNeilage & Davis (2000). In the latter, it consists of three CV syllables (coronal+front, labial+central, dorsal+back), and one CVC combination (labial-vowel-coronal).

As is easily verified, the three CV syllables correspond to the same simple up-down jaw motions with the tongue fixed in three different places[103]. These are

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[103] Modern humans (or at least I) normally produce repeated coronal-front (te-te-te) and dorsal-back (go-go-go) syllables by moving the tongue rather than the jaws — but holding the tongue fixed and moving the jaw works perfectly fine as well, producing recognizably the same phonemes.

indeed arguably the articulatorily simplest possible syllables. These syllables are also very common, and occur in both infant babbling and the world's languages at frequencies well above those expected from the frequency of their component sounds, and also form a large fraction of Ruhlen's (1994) proposed proto-world vocabulary (MacNeilage & Davis, 2000). The findings of MacNeilage & Davis (2000) are further discussed in Locke (2000).

The neural control of jaw motions was available as an exaptation, well before the evolution of language, since we need that control for chewing and biting, and chimps use it also for lip-smacking sounds, so the step from a biting or lip-smacking motion to babbling does not appear large, involving mainly a steady airflow from the lungs and the maintenance of a steady tongue position with respect to the lower jaw.

The hypothesis of MacNeilage & Davis (2000) appears to be one plausible model for the origin of proto-speech. And once speech got started, with these syllables or otherwise, it would be a matter of straightforward Darwinian selection to improve the vocal tract and neural control, in order to produce a richer variety of crisp and easily-understood phonemes. A rich repertoire of sounds is particularly valuable at this early stage, before the invention of combinatorial phonology, as each concept needs a sound of its own.

As for combinatorial phonology, the stringing together of syllables into longer words, Nowak and associates (Nowak & Krakauer, 1999; Plotkin & Nowak, 2000) have shown that this is advantageous as soon as the number of concepts exceeds a certain threshold. According to Jackendoff (1999b), the switch from a system where each sound carries meaning, to a combinatorial system where meaning is assigned to combinations of individual sounds that are meaningless in themselves, represents a major cognitive step. Nevertheless, this stringing together of sound units is observed in various kinds of animal communication as well, notably the songs of birds and whales, and there are hints of compositeness in some ape vocalizations as well, which may give a hint as to what proto-speech might sound like (Ujhelyi, 1996). The existence of composite vocalizations in three distantly related animal groups implies multiple independent evolutionary origins, from which follows that this stringing together of sound units is not evolutionarily difficult to acquire, confirming that proto-speech is not a major hurdle in the evolution of language. The sequencing ability of Calvin (1993) (see section 4.1), may be a useful exaptation.

5.3.2 Proto-gestures

As in the preceding section, only the mechanics of sign production and perception will be covered here, not its semantic and syntactic contents. This results in a very short section here, since the issue is almost trivial — it is beyond reasonable doubt that our common ancestors with the other apes, or even monkeys, had all the dexterity needed for sign language production, as well as the visual processing capacity needed to perceive signs.

Chimpanzees have been reported to use gestures for communication (Leavens et al, 1996; Leavens & Hopkins, 1998; Savage-Rumbaugh & Lewin, 1994), also in the wild (Vea & Sabater-Pi, 1998; Jucquois, 1991). The gestures are largely iconic, unlike modern spoken language, but this is not unreasonable for a proto-sign language, as iconic features are present also in some modern sign-language signs (Deacon, 1997). The evolution of sign language from the gestures of apes appears for several reasons much more plausible than the evolution of speech from animal vocalizations that Darwin referred to in the quote in section 5.1.4. The transition from iconic non-language gestures to a sign *language* has been observed in the spontaneous creation of sign creoles in deaf children without contact with sign-language speakers (Goldin-Meadow & Mylander, 1998; Saffran et al, 2001), an ontogenetic process that may have a phylogenetic predecessor (Wilkins & Wakefield, 1995). Of course, there is the important difference that the children already possessed whatever innate language abilities that humans are equipped with — nevertheless, the parallel is interesting, and as far as I know no similar development of spoken creole from iconic sounds has been observed.

5.3.3 Proto-semantics

Semantics, relating linguistic expressions with meaning, is inextricably intertwined with the ability to use symbols and symbolic thinking and communication. The 'symbol' concept is central here, but is not entirely trivial to define and operationalize, and the different definitions that can be found in the literature are not quite equivalent. Peirce (1931 35, cited by Deacon (1997), Zlatev (2001a), and many others) introduced an influential three-part division of signs:

- *Indexical:* having direct contiguity with their referent, e.g. pointing gestures.
- *Iconic:* having a non-arbitrary relationship between sign and referent, e.g. mimetic gestures.
- *Symbolic:* having the following features:
    - Conventionalized.
    - Arbitrary relationship between sign and referent.
    - Connected with other symbols in a network of *internal* relations, not through relations between their respective referents.

(adapted from Zlatev (2001a, p 182-183))

Another feature distinguishing symbols, according to Deacon (1997), is the ability of a symbol-user to disconnect the symbol from the presence of its referent. Jackendoff (1999b) emphasizes also the non-situation-specificity of human symbols.

Implicit in the ‘Conventionalized’ feature is the fundamentally *social* nature of symbols — symbols are used in communication to establish a field of shared attention, by virtue of the joint reference of sender and receiver. But a system characterized only by joint reference is regarded by Sinha (2001) as merely proto-symbolic, and ‘Conventionalized’ goes beyond joint reference in that it entails not only that both sender and receiver attend to the same referent, but also that they both know that they both know, and both know that the other knows that they know (third-level intentionality *sensu* Grice (1957)), that a certain symbol means their joint referent. The emergence of shared meaning is thus a thoroughly social process, requiring that what is shared between speakers is not just that both use the same symbol for the same referent, but that they actually share the same *instance* of meaning (Itkonen, 1983, cited in Zlatev (2001a)) — in Popperian terms (Popper, 1979, discussed in section 2.4.1), I would interpret this as both speakers having in their heads world-2 instantiations of the *same* world-3 object, or in memetic terms (section 2.4.2) them sharing the same meme, not just identical but unrelated memes. In complex cases, this may require even higher levels of intentionality (Itkonen, 1997, cited in Zlatev (2001a)).

The emergence of full symbolization *sensu* Sinha (2001) requires also *construal*, entailing the elaboration and conceptualization of the joint references of proto-symbolic systems. Construal, as I interpret it, is closely related to the network of internal relations referred to above. This relational feature is sometimes interpreted as implying that symbolicity requires syntax, that true symbols can only be used in a grammatical context — but, as Jackendoff (1999b) argues, children at the one-word stage use symbols by any reasonable definition, and adult speech also contains a number of symbols, such as expletives, that are normally used singly, not in any grammatical context.

“Meaning”, the other main component of semantics, is also a non-trivial concept to define. Zlatev (2001b) proposes a hierarchy of meaning systems, with four levels:

1. *Cue-based:* Meaning is innately assigned to predetermined cues. No learning or flexibility is involved.

2. *Association-based:* Meaning is assigned to signals through associative learning of relations between environment and action.

3. *Icon-based:* Meaning is assigned to iconic signals, through social and imitative learning.

4. *Symbol-based:* The full human system of meaning and value, with social and cultural learning. Signals are no longer iconic, but can be arbitrary symbols. Higher-order value systems, largely disconnected from the innate value systems of the lower levels, play a prominent role in the emergence of symbol-based meaning.

Each of Zlatev's meaning-levels has a multi-component structure, with a level characterized by the type of signal, the value system and the type of learning involved, as well as perceptive and emotional components. The type of signal in the different levels is related to the Peircean signal-hierarchy, with the two top levels identical in the two systems. But the learning type and associated value system adds a new layer to Peirce.

Communication systems among non-humans that may be relevant in this context are reviewed in Johansson (2001). Notable are particularly the alarm calls of vervet monkeys (Seyfarth et al, 1980). The monkey calls appear to have a mosaic of features, and do not fit neatly into any single level of either the Peircean or the Zlatevian hierarchy. But regardless of the label we assign to it, the system of the monkeys is far removed from the huge open multi-modal symbol-based meaning system available to humans. The openness of the human system, and our ability to acquire new symbols, and particularly our ability to establish joint reference, agreeing on the mapping between symbol and referent, is unmatched among wild animals.

The vervet-monkey system is not totally innate, but it shows no signs of being open either. Zlatev (2001b) assigns the vervet monkeys to the association-based meaning level, which would appear to be a reasonable assessment, even though the social component in their learning of the system may not be negligible.

Oliphant (1999) argues that the the closed nature of animal communication systems, and the consequent difference in mapping abilities and in the abilities of juveniles to acquire the system through observational learning *"is the primary factor limiting the evolution of language ability."* (p 380). But Oliphant (1999) disregards here the learning abilities demonstrated by animals in captivity.

The two chimpanzees Sherman and Austin (Savage-Rumbaugh & Lewin, 1994; Deacon, 1997), make a much stronger case for symbolic communication in non-humans, with their clearly communicative use of a non-trivial number of arbitrary tokens. Sherman and Austin definitely achieved the joint-reference proto-symbolic level of Sinha (2001). This is shown most clearly in their ability to invest new (or previously unused) tokens with meaning, e.g. in the experiment described on p 79 in Savage-Rumbaugh & Lewin (1994), where Sherman and Austin are given a novel food item, and one of them chooses a token to use for this item. Pointing back and forth between the token (on a keyboard) and the item, they establish jointly the correspondance between referent and symbol, to all appearances making sure that they both knew that the other knew the correspondance, and from then on both of them used the agreed-upon token for this food item. It is difficult to interpret this event as anything but them assigning that token as a symbol to "mean" the new food item.

Whether construal *sensu* Sinha (2001) was also present is a matter of interpretation, both of Sinha and of the chimps. Operationalizing construal in a controlled experiment is non-trivial, and as far as I can tell none of the controlled experiments performed with Sherman and Austin gives a clear answer on this issue. In other experiments, chimps have been found to understand quite abstract relationships and concepts[104]. Examples include the concept of a relation between abstract relations, as well as functional categorization of objects that are perceptually dissimilar ("tools", "food", etc.) (Savage-Rumbaugh & Lewin, 1994). This abstract conceptualization ability would appear to be a promising exaptation for the evolution of the construal aspect of fully symbolic systems *sensu* Sinha (2001). But clear evidence of the network of internal relations between symbols required for full symbolicity is still lacking outside *Homo sapiens.*

As for the "observational learning" of the connection between (proto-)symbol and referent, large vocabularies have been acquired, at least in the late stages more through observational learning than through formal training, and are used communicatively, by various apes (Lyn & Savage-Rumbaugh, 2000). This indicates that at least some non-humans appear to have the ability to overcome what Oliphant (1999) regards as a major hurdle in language evolution.

Concerning the level of meaning displayed by these enculturated chimpanzees, Zlatev (2001b) assigns them to the icon-based level. Assigning them to lower levels is clearly untenable. It is, however, not clear whether higher levels of meaning can be excluded, or whether they even fit into a single slot in the level system. For one thing, the icon-based level is supposed to be characterized by iconic signals — but many of the chimps have successfully acquired non-iconic systems, notably both Sherman & Austin mentioned above, and Kanzi, the most successful of all non-human language users. Zlatev's claim that *"[a]pes are better at learning gestures, a simplified form of "sign language" than arbitrary symbols."* (2001b, p 4), is not supported by the actual data on language-trained apes.

If iconicity were the main distinction between level 3 and 4, a strong case could instead be made for placing the chimps on level 4, together with humans. But there is no evidence in chimps for the higher-order meaning-value systems that, according to Zlatev (2001b), characterizes symbol-based meaning systems. Concerning learning, the distinction between level 3 and 4 is between imitative and cultural learning (the learning being social in both cases), and it is not clear whether the the chimps display cultural learning. Chimps in the wild do have some signs of culture (de Waal, 1999), but human-style cultural learning, the kind leading to the cumulative growth of cultural complexity (Tomasello, 1999) appears to be lacking in the wild, and may well be absent also in enculturated chimps. The enculturated apes are left hanging partway between icon-based and symbol-based meaning, fulfilling some but not all of the criteria for level 4.

As stated by Zlatev (2001b), the Zlatevian level system is not intended to be more than a schematic classification, with no expectation that every species can be pigeonholed into a level, so having apes on level "$3\frac{1}{2}$" is not really a problem.

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[104] Dolphins have similar abilities (Mercado et al, 2000), which may relate to their similar level of success in language learning (Herman et al, 1984). There are mixed reports on the abilities of monkeys, with Thompson & Oden (2000) and Fagot et al (2001) arriving at opposite conclusions.

With each level being composed of several separate requirements, that are not in all cases logically dependent on each other, intermediate stages like this must be possible. In Peircean terms, it must be possible to have e.g. a system that is conventional and arbitrary but not connected with internal relations, a system corresponding to the level Sinha (2001) calls proto-symbolic. This proto-symbolic level would appear to be a reasonable starting position for the evolution of fully symbolic communication.

It would appear, then, that the cognitive abilities necessary for proto-symbolic communication *sensu* Sinha (2001) were available in our common ancestor with the chimpanzees, as well as all the abilities required for Zlatevian level 3 and some of those required for level 4 as well. This raises the questions of why the chimps have abilities that they apparently don't use in the wild, and why chimps haven't evolved a language-like communication system, at least at the level displayed by Kanzi and other enculturated chimps (Johansson, 2001), if they already have such a central part of the abilities needed. One may wonder, as do Savage-Rumbaugh et al (1993a), whether chimp communication in the wild is richer than we have thought, possibly entailing enough aspects of symbolicity to motivate their proto-symbolic capacity? As for why they haven't evolved full (or even proto-)language, section 5.2.7 above attempted an answer in terms of different selection pressures. Another part of the answer may come from the studies of Nowak and associates (Nowak & Krakauer, 1999; Nowak et al, 2000), discussed in sections 5.3.1 and 5.3.4 respectively, who have demonstrated that the hierarchical structures of human languages are needed only when the number of concepts to be communicated exceeds certain thresholds — below those thresholds, a simple one-to-one correspondence between concepts and sounds is more economical, something which may apply to the arguably simpler world of the chimps.

Alternatively, a more likely explanation may well be that while the chimps may have all the *biological* prerequisites for proto-symbolic communication, biology is certainly not the whole story in the ontogeny of higher-level meaning systems, and the biological differences between what the chimps need for their current lifestyle and what they'd need for proto-symbolic thinking need not be large. The emergence of meaning does not take place in a vacuum, but requires both a suitable biological development program, an appropriate sociocultural environment, and the ability to have a place in and be an active agent in this environment, a set of requirements that is captured in the title of Zlatev (1997): *Situated embodiment.* The wild chimpanzees would here be caught in an apparent Catch-22 (Heller, 1961): as long as they lack the right sociocultural situatedness during ontogeny, they won't achieve symbol-based meaning — but if they don't achieve symbol-based meaning, their children won't have the right sociocultural situatedness during *their* ontogeny. Placing young chimps in a human sociocultural milieu will enable these chimps to break out of the loop, and achieve as a high a level of meaning as they have the biological equipment for, which appears to be what has happened with Kanzi and his friends.

Looking at phylogeny rather than ontogeny, our hominid ancestors did manage to bootstrap themselves out of this loop, somehow. This is likely to have been a — or even *the* — major breakthrough in the origin of human beings, signaling the takeoff of the cumulative cultural evolution so typical of humanity, and so lacking in other species, even those that do have the rudiments of culture (Tomasello, 1999; Deacon, 1997). This need not be the result of a major biological change — there may well be threshold effects involved, for example in innate value system (Zlatev, 2001b) or the fidelity of social learning (Rose, 1998; Gabora, 1997).

It has also been shown in computer simulations that, once a population has started to communicate symbolically, a system of arbitrary bidirectional signals, similar to the modern human system, will out-compete all others, assuming that accurate communication confers Darwinian fitness (Pinker, 2000).

McArthur (1987) argues for an intermediate stage in which the only words were "names": *"Dans les premiers stades du langage il y aurait peut-être eu seulement des "noms" (...): noms propres et substantifs, ..."* (p 161), but given the conceptual capabilities of chimpanzees, and the ease with which Kanzi and others have acquired symbols for actions and other non-nominal concepts (Johansson, 2001; Savage-Rumbaugh & Lewin, 1994), this stage appears rather unnecessary.

Concerning the timing of the transition to full human-level semantics, little information is available from the fossil record. Language use, of course, does not fossilize, but other forms of symbol use may, and may be used as indicators that some level of symbolic abilities has been reached. The use of ancient art as indicators that the artists were capable of symbolic thought, or even as an indicator that language had evolved (Mellars, 1998), is fairly common: *"The pieces of ochre, ... were clearly intended for decorative or ritual use. This proves that the people who made them must have been capable of subtle thought, and probably indicates that they spoke a language of syntax and tenses, Professor Henshilwood said."* (Henderson, 2002, p 1, online version). The logical connection from decorated ochre to grammatical details is, however, not overwhelmingly supported.

The argument from the appearance of art is closely related to the argument from the apparent technological revolution discussed in section 5.2.2. The supposedly sudden appearance of advanced art in the caves of Europe about 40,000 years ago is taken as evidence of a cognitive leap. However, McBrearty & Brooks (2000) documents the gradual emergence of art as well as modern tools, showing that the sudden appearance of art was also an illusion. Kuhn et al (2001) remained skeptical of the interpretation of McBrearty & Brooks (2000), but a later discovery of less ambiguous works of abstract art (Balter, 2002; Recer, 2002; Henderson, 2002; Harms & Yellen, 2002) adds further support to the long timescale of McBrearty & Brooks (2000).

Art is reasonably regarded as indicative of abstract and symbolic thought, and it is commonly argued, though not self-evident, that "*[a]bstract and symbolic behaviors imply language, ...*" (McBrearty & Brooks, 2000, p 486), but

McBrearty & Brooks (2000) certainly have a point also in the less commonly realized continuation of the sentence *"..., but it is doubtful that the point at which they first can be detected coincides with the birth of language."* (p 486). If we can observe signs of art or other symbolic behavior, we might infer, following the logic of McBrearty & Brooks (2000) and others, that the artists had language, but the converse does not apply — the absence of fossilizable art does not imply absence of language.

This inference from art to language, or at least from art to symbolic capacities adequate for language, is interesting in view of the additional evidence that has been uncovered recently that appears to show that simple art actually predated the appearance of anatomically modern *Homo sapiens* (Keys, 2000), in the context of *Homo heidelbergensis*. Objects that can reasonably be interpreted as art have been found associated also with Neanderthals (Appenzeller, 1998), which would push back the origin of the biological capacities needed for art at least to the common ancestor of Neanderthals and us, some 500,000 years ago. And given that the symbolic capacities needed for art are also needed for language, and are interpreted by some as indicative of the presence of language, this adds support to the possibility of an early appearance of language, in agreement with the limits inferred from anatomy in section 5.1.4 above. As for art itself, as a cultural phenomenon, either independent invention in both lineages, or horizontal transfer between us and neanderthals, are conceivable, but a common origin of art may still be the simpler hypothesis. So far, we have insufficient data for any firm conclusions on that point.

One serious problem with the inference from art to human language, is that traces of both proto-symbolic thought and artistic acitivites have been observed in apes. Both chimpanzees and gorillas happily produce paintings when supplied with canvas, brushes, and paint. And language-trained apes have even been reported to describe what their works of art represents (Patterson & Linden, 1981), which would seem to indicate that the apes themselves regard their art as representational. One might, somewhat optimistically, argue that chimps have both art and language, saving the inference, but making it useless for elucidating the history of *human* language.

A related argument is that of Barnes (1997), who postulates language as a requirement for religion, for much the same reasons as for art — religion requires the ability to reason symbolically about abstract categories. Archeological data on the origins of religion are unfortunately sparse and controversial — much Paleolithic art, from statuets to cave paintings, has been interpreted in religious terms, but other interpretations cannot be excluded. The same is true for prehistoric ceremonial burials (Gargett, 1999). This uncertainty means that the religious argument adds no constraints to the possible origins of language.

In conclusion, the change from a chimpanzee-level proto-symbolic system to human-level semantics does not appear to entail any insurmountable difficulties, as the chimps already have the ability to fulfil, at least with training, many of the requirements of a symbolic system. The remaining requirements, notably construal and higher-order value systems, need not be impossible hurdles. The "cognitive bootstrapping" setting off the explosion of cultural and cognitive growth in human beings (Tomasello, 1999) may even generate them as a byproduct — but a byproduct that then becomes a central part of the process of cultural growth.

5.3.4 Proto-syntax

Communication is certainly possible without syntax, as shown both by agrammatics and by children at the one-word stage of language acquisition. But there are narrow limits on the complexity of the messages that can be transmitted without syntax. Nowak et al (2000) have calculated the limits of non-syntactic communication, finding that there is a critical mass of words beyond which syntactic communication becomes highly advantageous. Similarly, there is a maximum lexicon size imposed by the requirement that each new generation be able to acquire their parents' lexicon, which again limits the number of possible messages in a syntaxless system (Komarova & Nowak, 2001; Nowak, 2000a). The maximum size of the lexicon depends on acquisition efficacy, which may have provided strong selection pressure towards improved lexicon acquisition, a conjecture supported by the remarkable rate at which human beings acquire new words, one word every several hours, around the clock, sustained for years and sometimes decades[105]. This point is related to those raised by Oliphant (1999), discussed in section 5.3.3, and by Wray (1998), discussed in footnote 69.

Useful exaptations or precursors for syntax are difficult to find, though the cognitive capacity needed to handle relational concepts would appear necessary, as argued by Savage-Rumbaugh et al: *"Clearly, prior to the emergence of syntax must be the emergence of the concept that one can request that A act on B, where the speaker is neither A nor B."* (1986, p 223-224). Aiello (1998) argues for "social scripts", structured generalized patterns of social behavior, as syntax precursors, something which ties in nicely with the socio-political hypothesis of language origin (section 5.2.5), and it can certainly be argued that the concept in the quote from Savage-Rumbaugh et al (1986) above is a social script. The structure of the postulated social scripts is discussed in some detail by Worden (1996).

Ontogeny may give useful hints about a possible phylogeny of syntax. The one-word holophrastic stage can, at least in its early phases, reasonably be regarded as non-syntactical, with every utterance an unanalyzed whole (Elliot, 1981). But it still usable for communication, albeit imperfect — every parent is aware of its strengths and weaknesses, from attempts to understand the will of their one-year-old child — and can thus be taken as a reasonable point of departure for the evolution of syntax (Jackendoff, 1999b). The two-word stage is more

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[105] I am less than 400,000 hours old, and have a (passive) vocabulary well in excess of 100,000 words, summed over languages. This gives an average learning rate of better than one word every four hours.

interesting as a candidate for proto-syntax. There have been some attempts to argue, within a Chomskian innateness paradigm, that the two-word (and even one-word!) utterances of children "really" have full-blown adult-grammar deep structure, but with all but two words dropped in the surface structure (Wanner & Gleitman, 1982). But these theories impute a complexity to the children's utterances that goes far beyond that motivated by the available data (Elliot, 1981), and may be directly contradicted by more recent data, as reviewed by Tomasello (2000a) — but see also Pinker (1995) and Santelmann (1995). More plausible models of the two-word stage focus either on very simple grammars (like "pivot grammar"), or on child utterances as fragments of adult sentences, or on semantic relationships. Jackendoff (1999b) regards the two-word stage as simple concatenation of symbols, with meaning determined by semantic and pragmatic considerations, rather than by anything resembling a grammar. This is may be reasonable position for child language, and is certainly a plausible next step in syntax evolution, after the initial one-word stage.

Furthermore, there is a fair degree of continuity in the ontogeny of language, with no clear gaps or sudden jumps separating the different stages: *"...we recognize in these simple processes forms of language not separated by a break from our more complicated ones. We see that we can build up the more complicated forms from the primitive ones by gradually adding new forms."* (Wittgenstein, 1969, p 17, quoted in Zlatev (2001a)). This continuity in ontogeny argues for at least the logical possiblity of continuity also in phylogeny, with the gradual evolution of "more complicated forms from the primitive ones".

Armstrong et al (1995, cited in Carstairs-McCarthy (1996) and King (1996)), who support a sign-language origin of language, invoke the temporal structure of signs as the roots of syntax. They raise an intriguing point, since an iconic sign sequence describing an action indeed naturally possesses a rudimentary structure that might be a reasonable syntax precursor. If nothing else, iconic sign sequences certainly facilitate the understanding of relationships among concepts (King, 1996), which, as noted above, is one step that must be taken on the road towards syntax. Unfortunately, Armstrong et al (1995) take their thesis too far, when they argue not only for signs as proto-syntax, which makes some sense, but also attempt to derive the specifics of human syntax, notably the ubiquity of SVO word order among the languages of the world, which is an unnecessary and poorly supported extension that distracts from their main point (Carstairs-McCarthy, 1996).

Possibilities for the very earliest stages of proto-syntax have been discussed above. What happens if we look at the other end, at modern human grammar, and contemplate which components might be removable?

As noted earlier, it is sometimes argued that modern human grammar is a monolithic system that cannot be built piece by piece. But I will argue that this stepwise construction (or deconstruction, from the perspective of modern syntax) is perfectly possible if the structure of grammar is looked at from an appropriate perspective, and the pieces are added in the right order — not all aspects of grammar are totally interdependent. Certainly, if any component of modern human language is removed, what is left is not equal to modern human language — but it may still be a functional language, if not as rich and expressive as what we're using today. A language with proto-syntax, missing one or two principles of modern grammar, may not be adequate to write this text — but may nevertheless be adequate for the daily life of proto-humans.

A definitive analysis of the removability of different components or principles of grammar requires that we know what these principles are. However, even though the Chomskian paradigm dominates the scene, there are several competing theories of grammar that remain viable (Dooley Collberg, 1991), e.g. Gazdar et al (1985) or Bresnan (1982). And Chomsky himself comes up with a new version of grammar about once every decade (Chomsky, 1957; Chomsky, 1965; Chomsky, 1982; Chomsky, 1995), and I see no reason to take for granted that the current incarnation, however elegant, is the ultimate one. Instead, I'll adopt a slightly different perspective, and look at a few features that modern human languages incontrovertibly possess, regardless of the details of grammatical theory, and see which of those features may be removable, and in which order.

Human languages are universally:

- *Structured* in the sense that a sentence is not just a random juxtaposition of words, but a sequence ordered according to certain rules (whatever these rules may be).
- *Hierarchical* in the sense that there are several levels of structures within structures.
- *Recursive* in the sense that the same rules and structures may recur at different levels in the hierarchy, so that a structure may contain a substructure that is another incarnation of the same structure, in theory repeated *ad infinitum.*
- *Flexible* in the transformational sense that there are many different ways to express the "same" meaning by moving around words and restructuring sentences according to certain rules.

The list of features above is structured, in the sense of the first list item, in that the features are listed in a non-random order. The *Structured* feature is fundamental — it makes little sense to talk about syntax at all for a non-structured language, and all the other features presuppose *Structured.* But it is perfectly possible to imagine a language that is *Structured* without possessing any of the other features — the two-word stage of child language may be an example, if it has any syntax at all. Some pidgin languages may be clearer examples. This means that *Structured* must be the first syntax feature to evolve.

A *Hierarchical* language must be *Structured*, but need not be either *Recursive* or *Flexible.* The main breakthrough in achieving *Hierarchical* may be the grouping of words into headed units, and the application of structural rules to headed units as a whole, rather than to individual words (Jackendoff, 1999b). It is possible to have a hierarchy of structures, without the same structure being allowed to recur in infinite recursive chains. I know of no examples of natural human languages like this, but some computer languages (e.g. FORTRAN) do not have full recursivity. Having years of experience of FORTRAN programming, I can testify that this is inconvenient but not fatal — there are always ways to get around the lack of recursivity.

In fact, nothing else in language, as far as I can tell, requires the *Recursive* feature (whereas *Recursive* certainly requires *Hierarchical*). As argued above, it is quite possible to have a language with only partial recursivity, or even none at all, something further supported by the existence of children with SLI (see p 71) whose language apparently lacks recursivity (Bloom, 1999). Therefore, *Recursive* is a prime candidate for being a late evolutionary addition to human grammar.

Flexible, like *Recursive*, appears to be an optional feature that can be removed without fatal effects. *Flexible* definitely requires *Structured* to be meaningful, and may require *Hierarchical*, but none of the other features require *Flexible*. Depending on the exact grammatical theory, there may be a lot of obligatory moving around of constituents in a sentence — but in modern human grammar there are also lots of optional movement possibilities, constituents that can be moved or not at the discretion of the speaker. Language would be perfectly functional, if less rich and nuanced, without these discretionary movements. Therefore, *Flexible* is also a candidate for being a late evolutionary addition to human grammar.

This adds up to an allowed sequence of successive grammar elaboration, that may be a candidate evolutionary sequence:

1. One-word stage — semantics with no syntax
2. Two-word stage — *Structured*, but with none of the other features.
3. Hierarchical structure, much like a basic phrase structure grammar, but with no recursivity. This means a language without subordinate clauses and other forms of embedding.
4. Recursive syntax (alternatively, *Flexible* may be added before *Recursive*, since they are largely independent of each other).
5. Full modern human grammar.

Each step in this sequence corresponds to a functional communication system, if not as elaborate and rich as the modern human system. And none of the gaps that need to be bridged when going from one step to the next looks anything like the huge chasm commonly pictured between non-syntax and syntax.

Jackendoff (1999b) presents a similar sequence, with a similar number of syntactic steps (he has more steps in total, but many of them do not concern syntax, and are covered in section 5.3.1–5.3.3 above). The main difference appears to be that he concatenates symbols into longer strings than two words before adding *Structured*, and that he does not make a clear distinction between *Hierarchical* and *Recursive*.

The first step towards syntax, getting started on the sequence at all, might be thought the most difficult — but since we have compelling evidence that proto-syntax at stage 1 and very likely 2 is within reach of chimpanzees, that step involves nothing but activating already existing capabilities, which cannot be an insurmountable problem.

Furthermore, depending on exactly what the underlying grammar looks like, it is not inconceivable that some of these steps can be subdivided even further, with e.g. simple additive recursion evolving before central-embedding sentence-level recursion. Expressed in phrase structure rules:

$$S \rightarrow NP\,VP \tag{1}$$

$$NP \rightarrow Adj\ NP \tag{2}$$

$$NP \rightarrow NP\ Comp\ S \tag{3}$$

Rule 2, which adds very little complexity in either production or comprehension, may well be an earlier development than rule 3, which is much more difficult to handle even for adult modern humans.

The steps roughly resemble the stages of child language acquisition, where recursivity is a fairly late addition (Goldin-Meadow, 1982). Recursivity is plausible as a late addition in phylogeny as well as ontogeny, also because adults have trouble with it — comprehension is poor on sentences with multi-level recursion (Christiansen & Chater, 1999), such as the following sentence built by triple application of rule 3 above:

The rat the cat the dog the man hit chased caught squeaked (4)

In theory, such sentences are grammatical — but they are commonly judged as ungrammatical[106] (Christiansen & Chater, 1999), and are exceedingly rare in natural language. Even in simpler cases, we don't handle recursion quite as automatically as we do most other syntax — we commonly have to stop and think consciously about the parsing of a recursive sentence, at least with more than one level of recursion, which we rarely need to do in non-recursive cases. The central-embedding recursion discussed here appears to be the worst case for our language processing, and breaks down with no more than three or four nested levels, but with a sufficient number of levels of embedding I find other types of

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[106] Seidenberg & MacDonald (1999) have a point in that such discrepancies between the theoretical competence grammar, and the actual performance of people, is a problem for the Chomskian paradigm.

recursion non-trivial to parse as well, as long as the recursion amounts to more than simple concatenation.

Recursion was invoked by Chomsky (1957) as a language feature that was impossible to learn without an innate grammar (cf. footnote 93 above), which may be true for infinite recursion. However, as noted above, human language does not in practice allow recursion more than a few levels deep. And recursion to the same depth that humans can handle, has been learned by a connectionist network (Christiansen & Chater, 1999). The network "understood" sentences with the same structure as (4) at about the same level as humans do[107].

Concerning earlier levels of grammar, it is worth noting that the postulated social scripts of Worden (1996) and Aiello (1998) have the features *Structured* and *Hierarchical*, and even rudimentary recursivity. Other hypotheses of the functioning of primate social intelligence imply similar levels of structure and complexity (Worden, 1996). This is a consequence of the structure and complexity of observed behavior, making it highly plausible that apes had a structured and hierarchical conceptual system available as a language exaptation. If the cognitive machinery of the social scripts of Worden (1996) is available and can be used for language, we immediately reach stage 3 in the evolutionary sequence above. Byrne (2000) goes one step further, and postulates more general cognitive structures for dealing with structured, hierarchical problems, which would be eminently exaptable to syntax processing.

Pidgin languages, with their highly simplified grammatical structure, can also be invoked here, at the very least as examples of functional languages without all the features of full human syntax (McMahon, 1994), and possibly as a modern-day example of what an intermediate stage in the evolution of syntax might have looked like (Bickerton, 1995). Pidgins commonly lack both *Hierarchical* and *Recursive*, consisting of just a linear structure of words, illustrating level "$2\frac{1}{2}$" syntax, with the same basic complexity level as the two-word stage, but with more words and longer, more semantically complex utterances. Jackendoff (1999b) invokes "The Basic Variety" (BV), a kind of minimalistic acquisition of a foreign language up to the level where basic communication can take place but no further, as another type of "fossil proto-language". BV has no morphology and no hierarchical structure, and a very simple semantically based word order.

The selection pressures driving evolution from one stage to the next, can be related to the increasing complexity of proto-human society, along the lines of the calculations of Nowak et al (2000) which indicate that a simple one-word language is optimal in a simple world, but that structured hierarchical language

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[107] Networks of this kind have another interesting feature — the same network that's used and trained for comprehension, can also be used for production of grammatical sentences within the same grammar (Christiansen & Chater, 1999). This circumvents the argument that language evolution is unlikely since both production mechanisms and comprehension mechanisms have to evolve in tandem as argued by e.g. Vaneechoutte & Skoyles (1998). That argument is specious anyway, since coevolution of two coupled features is a common and fairly well understood phenomenon in biology, but it is nevertheless nice to have it undercut so cleanly.

becomes advantageous once a complexity threshold is passed in the contents of the communication that the language is used for. In a computer simulation, Hashimoto & Ikegami (1996) have shown that if reproductive success is based on communicative success, a successive evolution towards more and more complex grammars can result.

In conclusion, the gradual evolution of modern human grammar, through several functional intermediate stages, appears perfectly possible. The exact path of evolution is speculative, due to the dearth of data on the structure of actual proto-languages, but no insurmountable obstacles are visible. Some of the required transitions can actually be observed today, either in ontogeny, or in e.g. transitions from pidgin to creole language.

5.3.5 How can all the protos be combined?

As shown in the preceding sections, there are plausible gradual paths for the evolution of all the main aspects of language. But in order for language as a whole system to evolve, the various components have to be combined. Some of them are independent, but others need to be assembled in a certain order, in order to maintain a workable and stepwise improved communication system.

Two points are immediately apparent:

- At least one modality for production and perception needs to be up and running, at least at a primitive level, right from the start, otherwise language cannot be used for communication.
- Semantics must come before syntax. Semantics without syntax is a workable communication system (Bookless & Mortley, 1996), but syntax without semantics is pointless for communication.

Given those two conditions, there is considerable freedom to choose different evolutionary paths. In table 3, I attempt to summarize the first steps. As stated earlier, the starting point for the evolution of the human language abilities is taken as the abilities of our last common ancestor with the chimpanzees, which, in the absence of parallel evolution, can be assumed similar to the abilities of modern chimpanzees.

Signing capacity is available right from the start, and primitive speech, at the level of MacNeilage & Davis (2000), is not far off, so the modalities need not concern us further here. As for semantics, the results from ape language studies, e.g. Savage-Rumbaugh & Lewin (1994) indicate that the conceptual and proto-symbolic abilities needed for language at the one-word stage, the first step in my proposed evolutionary sequence on page 121, are within the reach of chimpanzees — full symbolicity, with its emphasis on relations between symbols, would hardly appear vital at the one-word stage, where symbols are processed one at a time.

	Speech	*Gestures*	*Semantics*	*Syntax*
Linguistic status of chimpanzees	Rudimentary and poorly controlled sounds, but adequate perception	Good dexterity and perception	Can be taught many symbols, and use them for communication	Can be taught rudimentary syntax
Useful exaptations in chimpanzees		Communicative gestures	Basic symbolic, conceptual and relational capacity	Social scripts?
Possible for early hominids, without additional prerequisites	Neural control of vocalizations, e.g. MacNeilage-syllables		Spontaneous symbol acquisition, leading to one-word utterances	
Steps remaining	Full neural and sequencing control, moved larynx, improved tongue motor control	(none needed)	Hierarchical semantics, abstract multi-level classification	Structured Hierarchical Recursive Flexible

Table 3: A summary of the starting position and possible exaptations and early evolutionary steps, in the four areas of proto-language discussed in this section.

After that, a co-evolution of semantics and syntax would appear likely, with the various aspects of syntax appearing in the proposed order. The evolution of syntax would be driven by more and more complex communication demands, very likely caused by a socio-political arms race. The same communication complexity would affect also semantics in the same direction, first simply towards more and more words, but later also towards a more structured semantics, with derivations and verb frames and hierarchical structures of concepts supplying the complex expressive abilities needed. The details here are of necessity speculative.

As the number of words grew beyond all bounds, increased demands would be placed on the modality used for language, providing selection pressure towards the production of clear and unambiguous and economical distinctions between large numbers of closely spaced sounds or signs. This is precisely what the modern human vocal apparatus provides today, so its evolution very likely took place at this stage, driven by these demands for communicative clarity and precision.

6 Conclusions

Humans have evolved from ape-like ancestors who lived perhaps five million years ago or a bit more. Some details of the family tree are still obscure, but four periods are quite clear:

- *5–2 million years ago:* Our ancestors were australopithecines, bipedal creatures with ape-sized brains.
- *2–0.5 million years ago:* Our ancestors were *Homo ergaster/erectus*, people with human bodies but not quite human-sized brains.
- *0.5–0.1 million years ago:* Two types of humans with full-sized brains evolved and lived in parallel, Neanderthals in Europe and *Homo sapiens* in Africa.
- *0.1 millions years ago – today:* Modern humans, *Homo sapiens*, spread out from Africa and conquered the world. Other types of humans disappeared.

Concerning the bodily equipment needed for language, the following conclusions can be drawn:

- *Speech production:* Several changes were needed, both in the anatomy of the vocal tract, and in the neural wiring and control circuits. These changes are evolutionarily expensive, and have no apparent function other than speech, so speech must have supplied the selective pressure for their evolution. Signs of these changes can be seen in Neanderthals, which implies that speech was used by our common ancestor with the Neanderthals.
- *Speech perception:* The equipment of apes, and for that matter most mammals, is perfectly adequate.
- *Brain size:* The human brain has increased tremendously in size during evolution, at considerable cost, but the reasons for this are not well established. Social pressures driving the evolution of “Machiavellian intelligence” appears to be the most plausible hypothesis.
- *Brain modularity:* The evidence concerning the existence of dedicated modules in the brain remains inconclusive. Primary sensory data appear to be handled in dedicated vision modules and hearing modules and so on, but these are not genetically hardwired. In the case of language, there are some signs of modularity, but not anything resembling a monolithic encapsulated dedicated language module. The evidence rather points towards language being handled by several subsystems, many of which also have nonlinguistic functions.

			Adaptation		Spandrel	
			Early	Late	Early	Late
Gradual	Speech	Innate	Possible	**No**	No	**No**
		Learned	Possible	No	Unlikely	No
	Gesture	Innate	Possible	**No**	No	**No**
		Learned	Possible	No	Conceivable	**No**
Sudden	Speech	Innate	**No**	**No**	**No**	**No**
		Learned	No	**No**	No	**No**
	Gesture	Innate	No	**No**	**No**	**No**
		Learned	Unlikely	**No**	No	**No**

Table 4: Evaluation of the viability of different combinations of locations along the five dimensions of language evolution hypotheses discussed in section 5.1. The salience of the text indicates the confidence level of the assessment. The evidence and arguments that the table is based on are spread out throughout section 5.

There are many conceivable paths of language evolution. But some hypothetical paths are more plausible than others, and some hypotheses are wholly untenable. Returning to the five dimensions of language evolution hypotheses discussed in section 5.1, table 4 summarizes the viability of their 32 possible combinations.

As can be seen in the table, the preponderance of the evidence favors language being an early gradual adaptation. All other possibilities are either totally untenable or highly unlikely, with the possible exception of early non-innate sign language emerging as a spandrel based on available exaptations.

Late language is excluded mainly because there is evidence of speech adaptations earlier in the fossil record than the proposed timeframe for late language. Sudden emergence of language is largely excluded as well, and totally excluded if grammar is innate, because complex genetically specified systems, such as our speech adaptations, and particularly an innate universal grammar, take time to evolve (Worden, 1995), which implies gradual emergence.

Given an early gradual adaptive emergence of language, either innate or learned language are defensible hypotheses, as are either speech or sign language as the primary modality. The innateness debate will not be resolved here, but a few more things can be added concerning modality. Gestures first has the clear advantage that the production capacity was already available, but since speech is the dominant modality today, Occam would favour speech as dominant from the start. A hybrid solution is an attractive possibility, with the earliest stages of language mainly signed, but with the signs supplemented by the simple sounds that these early speakers could produce, a scenario much like the fictional one depicted by Auel (1980), though much earlier in history. Within such a hybrid system, selective pressure towards improved communicative clarity would drive the evolution of the modality which had room for improvement — speech, but not really sign, as the dexterity used for signing was already highly optimized. Our vocal apparatus would then be optimized for speech, the results of which we see today.

Fossil evidence indicates that this speech optimization got started well before the emergence of *Homo sapiens*, almost certainly more than half a million years ago, and possibly more than a million, probably in *Homo erectus*[108]. As the speech optimization, with its accompanying costs, would not occur without strong selective pressure from heavy demands for complex verbal communication, this implies that *Homo erectus* already possessed non-trivial language abilities.

There is no evidence indicating just how complex syntax *erectus* had. They may have been at the two-word stage, or they may have had effectively full human language — it is difficult to imagine any way to tell. On one hand, *erectus* is the first hominid with a brain size approaching the modern human range — there are modern humans with *erectus*-sized brains and excellent language skills — and they were also the first to spread out to many different habitats on different continents, but on the other hand their comparatively simple, static culture argues against modern human cognitive skills.

Both modern humans and Neanderthals are descendants of *erectus* (with possibly one or two intervening chronospecies), which implies that both inherited the language abilities of *erectus*. We know the language skills of modern humans — but this common inheritance implies that Neanderthals also had language, at the very least at the *erectus* level.

Modern humans, after parting company with the Neanderthals perhaps half a million years ago, acquired the remaining features of modern language in parallel with acquiring modern human anatomy. Both aspects were finished before modern humans started spreading over the world, more than 60,000 years ago. The last common ancestor of all humans today, probably living in Africa shortly before this exodus, is the likely speaker of Proto-World, the common ancestor of all the modern language families, and the earliest language which we may have any remote hope of reconstructing (Ruhlen, 1994). But there is no reason to believe that this Proto-World was the *first* language spoken — as discussed above, our ancestors may have had language for a million years already. The details of those earlier proto-languages are likely to remain opaque for the foreseeable future.

Concerning the causative side of the issue, the question of what drove the evolution of language, the socio-political hypothesis appears the most plausible, though it is unlikely that any single factor dominates in the evolution of such a versatile tool as language — social, political, teaching, sexual, economical, and technological factors may all have contributed to greater or lesser extent to the

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[108] In the unlikely case that Bermudez de Castro et al (1997) are correct in their assessment, *Homo antecessor* would also be a candidate first speaker.

evolution of language. I have listed them in probable order of importance, though this is rather speculative.

There is much we still do not know about the origin of language, and much that we may never know. It is an issue of enormous complexity. But the field is not totally devoid of relevant data, and it is not open to unbridled speculation once all pertinent data are taken into account — the dictum of the Linguistic Society of Paris from 1866 is no longer motivated. Unfortunately, all the knowledge that bears upon the issue of language origins is spread over many different disciplines, and workers within a single discipline rarely capture the full story. I have made an attempt here to integrate as much as possible across disciplines, and tried to determine which hypotheses of language evolution remain consistent with all available data, and which can be excluded as untenable or unlikely.

The result is that I can conclude with some confidence that the evolution of language is possible, in a process in which both biological and cultural-memetic evolution play prominent roles. There is no single uniquely determined history of language origins, but major avenues of speculation have been closed off, and the possibilities have been narrowed down considerably. We have an ancient history as speaking and probably signing apes, our language gradually evolving memetically over many hundreds of millennia towards improved communication and learnability, and us evolving biologically even more gradually towards improved speakers and learners of language.

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