Chapter 2
Stages in the Evolution of Modern Humans

From Placental Mammals and Primates to the First Humans

A convenient place to begin a brief history of the human lineage is with the placental mammals—hairy, sweaty, toothed, lidded, flap-eared four-limbed animals with lungs, four-chambered hearts and developed brains. They maintain a high constant body temperature. Their young are produced from embryos attached to the placental organ in the uterus and, after birth, are nourished by milk from mammary glands. The oldest fossil of a placental mammal, dated to c.125 Mya (million years ago), is a 'dormouse-like creature' 10 cm long.

Towards the end of the Cretaceous period (70–65 Mya), atmospheric changes, including cooling and reduced sunlight, caused, perhaps, by dust from a super volcano or by an Everest-sized asteroid led to the extinction of dinosaurs, plesiosaurs, ichthyosaurs, pterosaurs and much else. In fact no animal species weighing more than 10 kg survived this shock. Since this event, mammals and flowering plants have been the dominant groups of organisms.

Primates, distinguished by their good eyes and flexible hands and feet, are a taxonomic division (an *order*) of the placental mammals that includes the prosimians (primitive monkeys such as lemurs), apes, monkeys and humans. The earliest primates appear in the fossil record at the end of the Cretaceous (65 Mya) and become abundant during the Paleocene (65–55 Mya). They were small-clawed shrew-like quadrupeds living on the ground and in the security of trees. In the Eocene (55–38 Mya), primates finally took wholly to trees and developed many novel methods of coping with that environment. Through natural selection various innovations in body structure and function suited to an arboreal environment appeared.

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These adaptations[1] included manipulative grasping hands (with opposable thumb and forefinger) and feet for leaping from limb to limb and stereoscopic vision for depth perception (enhanced by a rotation of the eyes to the front of the skull and a reduced snout). Parallel development of the cerebral cortex (cortex is Latin for bark) led to ever-better coordination of hand and eye (important for picking fruit rapidly). Sight and touch began transcending smell and hearing as the important senses. Primates began living in social groups in more-or-less 'fixed' territories and relying increasingly on socially learned rather than instinctive behaviour. Being territorial included a willingness to expel trespassers, particularly of their own species. These adaptations can be plausibly traced to the tree-dwellers' diet of fruits from widely scattered trees. Large territories of scattered 'randomly flowering' trees can be better defended and better exploited by groups of primates with good colour vision for finding fruiting trees and fingers suited to picking the crop. The use of group 'scouts' is an effective way of amplifying the individual's senses.

Large litters are a disadvantage for mobile animals in an arboreal environment and primate reproductive strategy evolved towards more intensively caring for but one or two offspring. Also, being in a relatively tropical environment there was little need to limit sexual receptivity to certain periods of the year. Being able to mate throughout the year encourages pair-bonding and is helpful for increasing numbers in a species with a low birth rate. Having young with an extended dependency period and having a habit of living in groups for assistance, protection and food-finding were two developments promoting band cohesion and forms of social organisation that eventually led to human culture.

Throughout the Oligocene epoch (38–25 Mya), monkeys and apes, the 'higher' primates, flourished. By 25 Mya the short-tailed dryopithecine apes regarded as ancestors of humans and other extant apes were well established. Their evolutionary success was enhanced by a coevolution between the seed-distributing primates themselves and seed-producing trees, a symbiosis which led to seeds of high food value and an omnivore diet of seeds, insects and small reptiles.

During the Miocene epoch (25–5 Mya) the great ape family, the Hominidae, split into the ancestors of orangutans, gorillas, chimpanzees and humans. Some 17 Mya orangutan ancestors were the first group to diverge, with the gorilla-chimpanzee-human divergence coming towards the end of the epoch. Sarich and Wilson, drawing on molecular dating of DNA, suggested that gorillas, chimps and humans could have had a common ancestor as recently as 5 Mya.[2] Other more mainstream estimates have the gorilla splitting off some 8 Mya and put the chimpanzee-human split at 6–7 Mya.

[1] In biology, adaptation is a word used to describe both a process and its product. Adaptation is a process of natural selection (differential reproductive success of genotypes in a population) which produces adaptations. An adaptation is an unprecedented anatomical structure, physiological process or behavioural trait in a population of organisms which, at least in the short term, increases that population's capacity to survive and reproduce.

[2] Sarich, V.M., Wilson, A.C., 1967, Immunological Time Scale for Hominid Evolution. *Science,* 158, pp. 1200–1203.

The species *Ardipithecus ramidus* has a strong claim to being the earliest forerunner of modern humans to be identified. In 2001, a specimen found in Ethiopia was carbon-dated at around 5.2 Mya. Other specimens confirm that early hominines (human ancestors), including *Australopithecus afarensis*, walked upright on two feet 4.3–4.5 Mya.

Down on the Ground

Australopithecines and Their Brains

So, starting in east Africa some 5 Mya, around the beginning of the Pliocene epoch (5–1.8 Mya), the human lineage evolved from being well-adapted tree-dwellers to being ground-dwellers. It is believed that, as ecosystems changed in response to a drying, cooling climate, proto-humans, australopithecines (meaning 'southern apes'), moved from a gallery-forest habitat to a more open savanna habitat.[3] And, as they moved out onto the grasslands, they stood up. This was a key innovation which, amongst other consequences, reduced heat loads, made it easier to look over the grass for predators, to use tools and weapons, to bring food to a home base and to carry helpless infants. Thus, it was an adaptation contributing something to meeting each of the three big challenges facing all animals—food, safety and reproduction.

In time, because it allows a steady sustained gait, bipedalism (plus a unique capacity to lose heat by sweating) would allow humans to kill much faster animals, by chasing them to exhaustion. Note though that bipedalism does have an important limitation; it requires the development of a weight-bearing pelvis, one in which the birth canal cannot be too wide, which, in turn, bounds the size of the neonatal skull.

These proto-humans were small agile creatures about 1–1.3 m high, living on nuts, fruits and berries. They were a heterogeneous group, some with large teeth and huge jaws, some less robust. Over time, jaw and snout became less prominent as hands came to be used to break up food and convey it to the mouth.

Although australopithecines of 4 Mya walked like humans, they had chimpanzee-sized brains (which still made their brains somewhat larger relative to body size than chimpanzee brains). While some may have been able to use tools, australopithecines showed little sign of any cognitive (thinking power) evolution.

[3] The cause of this climate change is contentious. Starting with the northward movement of the Australian tectonic plate, there may have been a northerly movement of the connecting seaway between the Indian and Pacific oceans which then led to a flow of cold north Pacific water through to the Indian Ocean in place of warmer South Pacific water. A colder Indian ocean meant less evaporation and less rainfall over Africa. An alternative, perhaps complementary, explanation for the drying of east Africa at this time attributes it to the delayed buildup of northern hemisphere ice sheets following the closure of the Panama seaway and the loss of warm currents in the north Atlantic about 4 Mya.

Still, as the functions of fore and hind limbs differentiated, there came a parallel selection pressure for increased (frontal) cortical representation of the specialising body parts.[4] For example, a much-expanded representation in the brain of hand activity led to improved manipulative skills and, more generally, a richer neural interplay between brain and body. Neurally, these extra tasks were at first accommodated not so much by brain growth as by a rudimentary redundancy-exploiting division of labour between the brain's left and right halves: the earlier bilaterally symmetric brain was redundant in that either half could manage all motor (muscle moving) activities. With a set of new tasks being managed from the left brain, there also came a consequential need for improved channels of communication (more nerve fibres) between left and right cortical areas.

What was being initiated here was a period of hand-brain co-evolution. Once hands had evolved enough to make tools, it became advantageous for the brain to evolve in ways which facilitated the making of better tools. The important underlying principle here is that learning has evolutionary consequences. The skills an animal acquires in its life cannot be incorporated into its genome and transmitted genetically to the next generation. It does not follow, though, that such changes in individual phenotypes are of no evolutionary consequence for these changes *alter the selective forces acting on that animal*, and hence make a difference to the generation-by-generation action of selection on a lineage. For example, an animal with newly learned skills might modify its environment in a new way (use more or different resources, say) or move into a somewhat different environment.

In a savanna habitat, rich in large carnivores, the 'somewhat undersized hominids must have found themselves outclassed, outfought and outrun'[5] These circumstances led them to form cooperative teams or packs whose effectiveness for protection and food acquisition relied on coordinated action.[6] However (and for Zoltan Torey[7] this is the crucial point) since the neuro-somatic (brain-body) equipment for supporting such cooperation was not already inbuilt as instincts, the required skills (e.g. food sharing) had to be acquired and perpetuated through imitation (mimesis) and through learning.

Both of these techniques, mimesis and trial-and-error learning, are highly brain-dependent, the consequences being further selection for cortical skills and further reliance on *brain-managed behaviour*. Mimetic skill is the ability to represent knowledge (e.g. how to make a stone tool?) through voluntary motor acts. Beyond being immediately useful, the evolution of mimetic skills and their associated neural structures became the platform from which language skills would eventually evolve.

[4] Torey. Z., 1999, ibid. p. 34.

[5] Torey, Z., 1999, ibid., p. 32.

[6] In many circumstances cooperation can be thought of as a 'technology' for synergistically amplifying the capacities (sensory, physical and mental) of individuals.

[7] Torey, Z., 1999, ibid., pp. 1–38.

Habilines and Erectines

Australopithecines survived in the African landscape till about a million years ago. Along the way, perhaps 3 Mya, the first member of the genus *Homo*, namely, *Homo habilis* ('handy man') split from the australopithecine lineage. *Homo habilis* is perhaps best described as a confusing collection of transitional forms (habilines) between australopithecines and *Homo erectus*, the first large brained hominid to appear in the fossil record, about 2 Mya in both Africa and East Asia. In fact, the stone tool record suggests that erectines (*Homo erectus* and variants) could have emerged 2.5 Mya. It seems that between 2.5 and 2 Mya the forests and savannas of east Africa could have been home to a mixture of australopithecines, habilines and erectines.[8]

Australopithecines had a 450 cc brain, habilines a 450–600 cc brain and erectines a 900 cc brain. This increase in brain size over several million years was largely in regions controlling, respectively, the hand, proto-speech (of some sort) and hindsight-foresight, i.e. some appreciation of cause and effect. How and why did this transition occur? It may well have been in response to various lifestyle changes including a switch in diet from, first, leaves to fruit, nuts and roots and then to an omnivore diet containing quantities of meat. Food-acquisition techniques concurrently expanded from gathering plant parts to scavenging carcases to group-hunting of large game.[9]

Becoming meat eaters in competition with, first, scavenger carnivores like jackals and then with well-armed primary carnivores like lions required not only group cooperation but the development of tools such as stone hammers for breaking marrow bones (of particular importance for creating a secure ecological niche), sharp stones for tearing tough hides and clubs for killing game. Evolving a brain which could support the cognitive and motor skills (e.g. stone throwing) underpinning such behaviours allowed hominids to compete with better-armed carnivores. More than this, a bigger brain was an 'open ended' adaptation with the potential to coevolve in parallel with a widening range of social, cultural and cognitive skills and, indeed, to cope with a further-changing environment. Along with changes to lifestyle, brain architecture/organisation and a slowing rate of maturation (see below) came a change in hormone balance, namely, from adrenaline dominance, the mark of fearful or prey species, to noradrenaline dominance, the mark of aggressive, predatory species. Selecting hominids for delayed development automatically selects for adults with a more juvenile and hence more 'aggressive' hormone balance, meaning one more suited to hunting than gathering.

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[8] Wills, C., 1998, *Children of Prometheus: The Accelerating Pace of Human Evolution,* Perseus, Reading, p.229; Donald, M., 1991, *Origins of the Modern Mind: Three Stages in the Evolution of Culture and Cognition,* Harvard University Press, Cambridge, MA.

[9] The 'radiator' hypothesis suggests that the dramatic increase in brain size that occurred in Homo was facilitated (not directly caused) by the evolution of a radiator network of veins which relaxed the thermal constraints on overheating that previously kept brain size in check. See Falk, D., 1990, Brain Evolution in Homo: The 'Radiator' Theory, *Behavioral and Brain Sciences*, **13**, pp.333–381.

A period of major climatic fluctuations, the precursor to the Pleistocene ice ages perhaps, began some 3.5 Mya (the first major ice build-up began about 2.5 Mya). Intelligence turned out to be an ideal general-purpose highly evolvable 'tool' for coping with the associated environmental challenges while not becoming trapped in an evolutionary dead end. Most successful but specialised genetically based adaptations to currently prevailing conditions are burdened by an inability to 'go back' when conditions change once more. This is why most species that have ever been are now extinct. As Jacob Bronowski says, the environment exacts a high price for survival of the fittest—it captures them.[10]

Judging by the dramatic continuous increase in brain size between *Australopithecus* (450 cc) and modern man (1,350 cc) it can be reasonably assumed that increasing brain size (and brain complexification), with its increasing capacity for cause-effect reasoning, remained evolutionarily advantageous under a range of markedly different environments. John Tooby and Irven De Vore suggest that it was *H. habilis* who first moved from instinctive behaviour to the 'cognitive niche' where knowledge of how things work can be used to attain goals in the face of obstacles.[11] This involves what we largely mean by intelligence, namely, the building of mental models, of cognitive schemata if you prefer.[12]

Two Million Years Ago

Some 2 Mya, perhaps earlier, as east Africa continued to dry and cool, erectines migrated outwards, reaching Europe, Java, Pakistan and south China by 1.7 Mya.[13] The pressure to keep moving on, migrating, would have been a result of any net population growth in a savanna environment able to support only 1–2 people per square mile. William McNeil makes the suggestion that this first spurt in human numbers may have been boosted by the jettisoning of various tropical parasites as humans moved into colder dryer regions.[14]

Indeed, by the time the Pleistocene epoch proper began, *H. erectus* had dispersed across the still habitable parts of Europe and the near and far East. And it was around 1.9–2 Mya that erectines began to use fire and invented cooking.[15]

[10]Bronowski, J., 1973, *The Ascent of Man*, British Broadcasting Corporation, London, p. 26.

[11]Tooby, J., and DeVore, I., 1987, The Reconstruction of Hominid Evolution through Strategic Modelling, In W.G. Kinzey (Ed.), *The Evolution of Human Behavior: Primate Models*, SUNY Press, Albany, New York.

[12]D'Andrade, R.G., 1995, *The Development of Cognitive Anthropology,* Cambridge University Press, Cambridge.

[13]Stone tools 2.5 myrs old have been found in Israel and Pakistan, suggesting to Wills (1998, ibid.), that habilines also left Africa for Asia, and perhaps Eastern Europe, at least 2.5 mya, while climates were still mild.

[14]McNeill, W.H., 1979, *Plagues and People*, Penguin, London.

[15]Wrangham, R., Jones, J. H., et al.,1999, The Raw and the Stolen: Cooking and the Ecology of Human Origins, *Current Anthropology*, **40** (5), pp. 567–594.

Cooking tubers, by making their starches digestible, allowed this increasingly common cold-climate underground food source to become a concentrated and reliable (more so than fruits) part of the human diet. Together, it was fire and cooking which allowed humans to spread into cold areas. Mastery of fire would have allowed erectines to camp and live in the presence of large predators.

Increased energy intakes at this time would have lifted constraints on increased brain size, further increased reproduction rates and increased life spans, all relative to habilines and australopithecines. In turn, grandmothers would have been useful for the hard work of finding and digging tubers, and feeding them to children. Perhaps gender roles—hunting for men and food-gathering and protecting the cooking hearth for women—arose in part because women became less efficient bipedalists as their hips widened to allow the birth of larger-brained children. This natural sharing of complementary contributions to the hunter-gatherer economy may also help explain male-female pair-bonding within larger groups and the low degree of sexual dimorphism (male-female size difference) in humans relative to other apes.[16] That is, with less competition for females there could have been less selection pressure for ever-larger males to evolve.

Portending the arrival of *Homo sapiens*, another anatomical consequence of the invention of tools and cooking was the shrinking of powerful teeth and jaws and loss of the brow ridges that anchor the jaw muscles. Because cooking increases the energy-density of food, the human gut began to shrink. Also, for reasons that are not clear unless one assumes a very early development of language (as singing perhaps?), *H. erectus* acquired a greatly extended vocal flexibility due to a rearrangement of the palate and larynx. Even if, improbably, the vocal tract in erectines had been sufficiently developed for articulated speech, as distinct from other forms of vocalisation, a brain capable of managing speech still would have been lacking.

Upgrading the Habiline-Erectine Brain

While a higher-energy diet permitted a cognitively useful but energy-guzzling erectine brain to increase sharply in size over evolutionary time (to 70% of that of a modern human), what was the actual mechanism?

In large part, it was selection for *neotenous development* or, more accurately, neotenous regression. *Neoteny* is a not-uncommon evolutionary process in which successive generations increasingly retain, through to maturity, what were baby-like features in their ancestors. In humans, this means retaining such things as looking forward when standing upright, a flat face with big eyes, playfulness and unclosed skull sutures. It may be noted that modern adult humans resemble, uncannily, the juvenile forms of the other great apes, none of which has experienced neotenous development.

[16] Based on observation of many mammalian taxa, a low degree of sexual dimorphism is an indicator of monogamous mating behaviour.

This progressive infantilisation had a range of consequences. It not only allowed babies with bigger brains to pass through the birth canal (because of their flexible skulls), it allowed brain growth to continue till reproductive maturity. And it did so continue, part of the neoteny package being a delayed activation of the regulatory genes which switch the brain from a higher growth rate characteristic of juveniles to a lower, more characteristically adult growth rate. On the other side of the ledger, postponed development has meant a loss of strength, speed and agility relative to other apes.

Neoteny, Cooperative Behaviour and Individual Autonomy

Equally importantly, this just-noted delay in brain development meant that babies were being born before various instinctual 'survival-promoting' tendencies had been 'wired-in'. One consequence of this was babies who were totally dependent on parental and group nurturing to survive.

This dependence of infants might have had, plausibly, two further evolutionary consequences. One would have been a selection pressure to further enhance the group bonding and cooperative behaviour which had been part of the lineage's evolution for 50 myrs. Part of that social evolution would have been selection for cooperative and teachable children, able to evoke the support they needed.

A second consequence of infant helplessness, the antithesis of selection for cooperation at first glance, would have been a selection for autonomy, a drive to actively learn survival skills through play and other self-initiated actions.[17]

Together, as Mary Clark puts it:

> These simultaneously increasing propensities to bond on the one hand and have autonomy on the other became part of genetically ingrained 'drives' embedded in the motivational centers of the evolving brain, as are our 'drives' for water, food, shelter, and mating. Obviously the pair of them exacerbated the opportunities for inner psychic tensions as well as social stress when bonds came into conflict with independent behaviors.[18]

In contemporary humans of course, this tension, in the form of managing both the drive to individuate and the drive or need for secure attachment, to belong within the group, has come to be seen as central to the problem of achieving mental health; within the family too, where marriage is sustained by holding in tension the twin needs for intimacy and autonomy.

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[17] Drives can be thought of as generalised instincts involving much-heightened perception and motivation. In comparison, most instincts exhibit as more specific behavioural patterns which may be elicited under certain circumstances. In the case of humans, two conditions must be fulfilled for actual acting out of instinctual behavioural patterns: relevant stimuli and the absence of other modes of regulating behaviour. Drives are extremely plastic in humans. For example, sexual and feeding drives do not tell the individual where to seek release or what to eat; specific behavioural responses to these drives are acquired through socialisation. See Berger, P., and Luckmann, T., 1966, ibid. p. 181.

[18] Clark, M.E., 2002, *In Search of Human Nature*, Routledge, London, p. 130.

Neoteny and Playfulness

It is easy to overlook the importance of hominids having been selected for a prolonged capacity for juvenile, playful, exploratory behaviour as an ancillary to being selected for neotenous development; an importance beyond facilitating the learning of extant survival skills. How is this? Because play involves trying things 'at random', it leads, on occasions, to the discovery of useful new ways of behaving. And to this extent the drive to playfulness, including mental play, is the process underlying the increasing capacity to behave in a wide variety of ways (depending on context), which, as discussed below, is at the heart of the hominid lineage's 'strategy' for achieving adaptedness.

The Pleistocene Ice Ages

Earth's most recent period of ice ages or repeated glaciations (*glacials*) began about 2.5 Mya after 250 myrs without an ice age.[19] Note that while commonly referred to as the Pleistocene ice ages (including here), the start of the geologists' Pleistocene epoch is normally set at 1.6–1.8 Mya, not at 2.5 Mya. Caused by regular variations in the Earth's orbit around the Sun, there have been some two dozen warming–cooling cycles (plus and minus 3–4°C) in that 2.5 myrs, each lasting, very approximately, 100,000 years (much less till about a million years ago). Each cycle comprises (a) a long cooling period of (say) 90 kyrs, with temperatures fluctuating but getting much colder towards the end, followed by (b) a short transition (centuries) characterised by very rapid, high-amplitude climatic oscillations which leads to (c) a 'sudden' warmer *interglacial* period of (say) 10 kyrs.

For example, in the last ice age, which started 115 kya and ended 12 kya (defined as the end of the Pleistocene), huge ice sheets advanced and retreated several times over most of Canada, northern Europe and Russia. Sea levels rose and fell by as much as 200 m in concert with this locking up and releasing of much of the world's water from glaciers. The advancing glaciers, covering up to 27% of the Earth's surface, obliterated most plant and animal life in their paths and pushed the inhabited temperate zones of the northern hemisphere south. In the southern hemisphere mountain-top glaciers grew enormously. Much of the tropics became cool deserts. More generally, cold-climate vegetation types tended to replace warm-climate types. Some 18–20 kya the Earth was as cool as it had ever been in a million years, just as, now, it is as warm.

By a million years ago *Homo erectus*, dispersed half way around the world, was the only surviving hominid. And then, some 800 kya, came what was to be the second of three waves of human emigration from Africa.[20] By 500 kya *H. erectus* began

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[19] Because 250 myrs is the time it takes the solar system to revolve around the centre of the galaxy (the 'galactic year'), we can speculate that there is a cloudy, Sun-dimming region which the solar system encounters for several million years once every revolution. If that is so, there is a possibility that the present epoch of ice ages might be the last for another 250 myrs.

[20] Templeton, A., 2002, Out of Africa, Again and Again, *Nature*, **416** (6876), pp. 45–51.

to give way to several other types of Homo. For example, by 250 kya an archaic *Homo sapiens*, with a brain as big as ours (but with behaviour that showed no sign of art or symbol use) had appeared. Neanderthal man, heavy-jawed and even bigger-brained, was certainly here 100 kya. A longer lifespan and a larger brain both facilitate the transmission of culture and both began to increase in line with the increasing importance of learned behaviour some half million years ago.

As for modern humans, the fossil evidence for an African origin is strong. It is clear that modern humans (*H. sapiens sensu stricto*) were certainly present in Africa by 130 kya, and perhaps as early as 190 kya depending on how certain fossil specimens are interpreted. Modern humans, the third wave of people to emigrate from Africa, first left c.100 kya (during the last interglacial), but rather unsuccessfully, and then left again about 80 kya. Recent evidence suggests that modern humans were present in Australia as early as 62 kya.[21] In a warmer period following the particularly cold millennium triggered by the Mt Toba eruption 71 kya (see below), humans migrated into north Asia. From there, after encountering a subsequent period of cooling and glaciation, they migrated back into Europe, first appearing there (and in central Asia) c.40 kya. And, by 25–30 kya, with the disappearance of Neanderthals from Europe, *H. sapiens* was the planet's only species of human.

Cultural and Genetic Evolution in the Pleistocene

While the erectine brain continued to grow and reorganise through most of the Pleistocene, culminating in the emergence 150–200 kya of modern humans with 1,350 cc brains and a capacity for structured language, this was, in some ways, a period of very slow change, almost stagnation, in human evolution.

The single most important change over that period of more than a million years was the eventual arrival, at a young enough age, of a brain organisation and size—around 750 cc—capable of supporting rudimentary speech skills. A 1-year-old sapiens and a 6-year-old erectus both have a 750 cc brain but the erectus brain, even though meeting the capacity threshold, cannot learn language simply because it has grown too slowly. That is, the parts of the left frontal cortex which might have been appropriated for learning and using language—a sophisticated motor skill—have already been appropriated for learning and using basic motor skills more needed for immediate survival.[22] Indeed, there is evidence that even in adults the cerebral cortex is constantly readjusting and fine-tuning its assignment of processing space between tasks, reflecting the constantly changing use-patterns imposed by the environment.

[21] Thorne, A., Grün, R., et al., 1999, Australia's Oldest Human Remains: Age of the Lake Mungo 3 Skeleton, *J. Hum. Evol.*, **36**, pp. 591–612; Stringer, C., 2002, Modern Human Origins: Progress and Prospects, *Phil. Trans. R. Soc. Lond. B,* **357**, pp. 563–579.

[22] Donald, M., 1991, ibid.; Torey, Z., 1999, ibid., p. 36.

Also, as Terrence Deacon points out, an individual brain which is maturing in parallel with its increasing language skills is positioned to (indeed, must) build up those skills hierarchically (words before syntax), and hence more efficiently, than a more mature brain grappling with several hierarchical levels simultaneously.[23]

Apart from cranial changes associated with brain changes, Pleistocene evolution would have seen a continuation, but slowing, of other existing trends in outward appearance such as loss of body hair, increasing height and shrinking face, teeth, jaws, gut and rib cage. In terms of cultural evolution the general view is that things moved slowly prior to a surge in the development of tools, art, burial practices, artefacts, etc., in the late Pleistocene, say, 30–40 kya.

What is of more interest here though is contemporary speculation as to the ongoing evolution through the Pleistocene of what Clark calls the *behavioural guidance system*, and the behaviour patterns generated by that system.[24] In one or another form, most of the tools or technologies or elements of that guidance system—feelings or emotions,[25] memory, skills in learning through imitation and repeated personal experience, simple reasoning skills, non-verbal communication, cultural norms—would have been present in early *Homo erectus*.

In a general way, the evolution of the behavioural guidance system through the Pleistocene hinged on bringing more and more information of various sorts to bear on and influence individual behaviour. Relatively at least, there would have been decreasing reliance on purely genetic information (instinct) and immediate sensory information (as when responding reflexively to stimuli) and more reliance on stored (memory-based) information and internally generated (e.g. reason-based) information. And, towards the end of the Pleistocene, symbolic information, particularly in the form of spoken language, would have become increasingly available.

Continuing to generalise, can something be said about the survival value of more-informed behaviour? Perhaps having more, and more sorts of, information available may have allowed the species to occupy a wider niche (live in more environments) or live in an existing niche more securely. Or, as a variation on the latter, modify a niche to make it more secure. Or, another possibility, allow the species to more readily adapt to niche change, i.e. to a changing environment. All of these can be interpreted as variously securing improvements in the magnitude and/or reliability of the energy supplies needed for maintenance and reproduction. A simple example might be the storing of information needed to crack marrow bones open.

The survival value of improved information does however come at a price, namely, the additional food energy required to maintain an upgraded information system, a bigger and better-organised brain. That is, an improved information system has to cover its own increased energy costs before it can deliver any increased

[23] Deacon, T., 1997, The Symbolic Species: The Co-evolution of Language and the Brain, Norton, New York, p. 137.

[24] Clark, M.E., 2002, p. 160.

[25] The concept of emotions as strong feelings has weakened to the point where the two words are interchangeable. An operational distinction might be that a feeling is a private experience of an emotion, one that cannot be observed by anyone else.

survival benefits. It can be argued that throughout the Pleistocene, at least up till the late Pleistocene, the survival value of an increasingly informed behavioural guidance system self-evidently outweighed the additional costs in energy terms of improving and maintaining that system; the brain kept getting more energy-demanding. And if brain size did plateau with the emergence of modern humans, was this due to an encounter with some physical limit (e.g. the exhaustion of neoteny or the speed of intra-brain communication) or due to diminishing returns to brain size, i.e. did enabled improvements in energy supplies come into balance with increased energy demands?

Memory and Learning

Some form of memory, that is, a capacity for storing acquired information in the central nervous system from where it can be retrieved for future guidance of behaviour, would have been present in the earliest mammals. Indeed, memory may well have been the first transformative development in animal information systems after a long evolutionary period in which the senses were the predominant sources of information (with motor nerves linked directly to sensory nerves). Here, we will not discuss the cellular processes which underlie the conversion (encoding) of patterns of experience into patterns of neural processes, i.e. into learning and memory. Suffice to say that these appear to be much the same for all animals from 'snails to simians'.[26]

In hominids each hemisphere of the brain has four cortical lobes, of which three—visual, temporal and parietal—are dedicated to parallel distributed (meaning simultaneously in several places) processing and storing of sensory information, creating diffusely stored patterns of experience, i.e. memories. The fourth lobe, the frontal, especially its most forward part, the prefrontal cortex, is much less involved with such processing and storing and more involved with sampling information from the other lobes and recombining it, i.e. with thinking. It is what Luria called the *planning cortex*, as distinct from the three lobes of the *sensory cortex*.[27] To this end, the planning cortex has multiple connections with the areas of the sensory cortex that are used for storage/retrieval of long-term memories.[28] Additionally and importantly, it has a capacity for holding short-term memories (lasting up to 30 s) which can be used to guide rapid-response behaviour and which have the potential to become long-term memories.

The planning cortex is also well-connected (via 'thalamocortical pathways') to the emotional centres of the brain; primarily the thalamus and the limbic system, this latter being a group of subcortical brain structures surrounding the thalamus.

[26]Deacon, T., 1997, ibid., p. 163.

[27]Cited by Clark, M.E., 2002, ibid., p. 150.

[28]Clark, M.E. 2002, ibid., p. 150.

In the course of forming a memory, data flows from the sense organs, via the thalamus, to the frontal lobes and finally to the sensory cortex where it is stored. To embed incoming information in long-term (permanent) memory storage, i.e. to form a memory retrievable in the future, a threshold degree of attention to what is being sensed and a degree of emotional arousal are required. Failing that, repeated exposure to a pattern of experience can still embed it in permanent memory. And always, as Antonio Damasio points out,[29] feelings evoked during the passage of sensory information to the sensory cortex via the brain's emotional centres are stored along with the memory; and retrieved with it.[30]

When retrieved (to the planning cortex), a memory is experienced as a sequential sampling ('frames') from the original experience, passing from detail to detail, from perspective to perspective, much like a story or narrative. At some stage during the Pleistocene the ability to voluntarily retrieve memories emerged. This meant that the 'chain' of details being retrieved could be interrupted at any 'link' and, depending perhaps on the emotional associations of that detail, the sequence could be redirected towards other memories. Modern apes and, presumably, our pre-Pleistocene ancestors, appear to retrieve memories of episodic experiences only after stimulation from the environment. As an indication of how this learning-memory process might have been upgraded over the Pleistocene, a 9-month-old human brain is too immature to firmly register experiences, while at 17–21 months it has developed enough to record and retrieve a memory of a single distinctive experience.

Learning as a Process of Percept Formation

In one sense, any act of storing a newly encountered pattern of experience in memory is an act of learning, i.e. the stock of information available for guiding behaviour has been increased. More generally though, learning is thought of as taking place when further similar patterns of experience are encountered, and the original memory is successively refined in a process of *percept formation* analogous to the use in modern humans of *inductive reasoning* to form *concepts*.[31] We might guess that a capacity for percept formation began overtaking a capacity for remembering only specific events (episodic memory) early in the Pleistocene.

[29] Damasio, A., 1999, The Feeling of What Happens; Body and Emotion in the Making of Consciousness, Harcourt Brace & Co., New York.

[30] It needs to be stated clearly that while science has learned much about correlations between brain activity and having feelings, science cannot explain how a feeling is generated any more than it can explain how a gravitational force is generated. See Harnad, S., What is Consciousness? Letter to *New York Review of Books*, 23 June, 2005, p. 56.

[31] In logic, induction is the process of generalising over multiple examples, commonly by emphasising similarities and ignoring differences between them. A percept is anything which can be identified and, in principle, named. A schema is a 'super percept' made up of multiple percepts in a stable relationship. Percepts tend to be abstractions from direct experiences. Concepts tend to be more abstract than percepts and language-based in a way that percepts are not.

How are percepts (cognitive categories is another name) formed? No two patterns of experience will be quite the same but each recurrence of any experience which is accepted as being in the same 'family' as the original experience (how? similar enough to some prototypical example?) strengthens the likelihood of certain components within the pattern being linked and being retrieved together. Components which are commonly retrieved together (i.e. the relevant neurons tend to fire together, a tendency which increases with repetition) become pieces of the percept being built up, e.g. storing and retrieving 'long neck' and 'black feathers' together contributes to building up the percept of 'swan'. Similarly, patterns of experience accepted as being outside the 'swan' family, contribute to stabilising the percept 'not a swan'.

A percept and the degree to which various inherently variable components are recognised as integral to that percept both evolve in the light of experience. Or, putting it differently, a percept is a fuzzy composite of all patterns of prior experience currently accepted as being members of the same family of experiences. A percept's boundaries can be expected to stabilise with experience and with practical success in using it. This process of learning by inductively forming percepts is also a process of acquiring *information*, at least when the sense in which that word is taken is 'that which decreases doubt concerning *meaning*' (answers to questions). And what is meaning? It is the recognition of relationships between entities. Percepts (and concepts and schemata of relationships) are thus bearers of meaning. Learning is the memorisation and refinement of meaning.

The information that learning produces can be retrieved from memory and delivered as input to the complex process of *thinking*. Basically, it is thinking which realises the potential value of memory and learning. While thinking will be further discussed presently, we can note here that, amongst other functions, it allows alternative future behaviours to be compared, cheaply, for their survival value; increasingly so with the development of verbal language, the tagging of percepts with names. Names can be thought with more easily than percepts themselves.

We might also note, finally, that while learning has been described in terms of storing and generalising patterns of sensory stimuli, the process is not restricted to acquiring information about entities in the outside world. In later hominids at least, perceptions of associations between components of distinct existing memories also emerge; a case of learning from oneself or *generative learning*. Again, possibilities for learning from others multiplied with the advent of language.

Feelings and Emotions

Evolution of Feelings-Emotions

Before mammals, animal behaviour (observable activity) was instinctual and reflexive—stimulus in, motor response out. Reptilian motor (muscle control) centres reacted to visual, auditory, tactile, chemical, gravitational and motion-sensory cues with one of a limited number of preset body movements and programmed postures. With the arrival of night-active mammals c.180 Mya, smell replaced sight as the dominant sense, and a newer, more discriminating way of responding, one directed by emotions and emotional memory,[32] arose from the *olfactory sense*. In the Jurassic period, the mammalian brain invested heavily in *aroma circuits* designed to function at night while reptilian predators slept. These odour pathways, carrying messages of threat, food, etc., gradually became the neural blueprint for what would eventually be the limbic (early mammalian) brain. By c.150 Mya, the nerve network for emotions and moods had largely evolved from neural structures previously committed to smell.

Emotions are responses within individuals to memories, other thoughts (e.g. motor intentions) and experiential situations which raise issues of survival, directly or by implication, e.g. threats, attacks, poisonous substances or the sighting of a potential mate. What form do they take? Emotions are of a few basic types (see below) and take the form of (a) a neural impulse to act, (b) a characteristic range of internal physiological changes in the digestive tract, lungs, circulatory system, etc., and, debatably, (c) feelings, meaning perceptions fed back to the planning cortex that these in-body events are happening and that they are 'pleasant' or 'unpleasant'. I say 'debatably' because psychologists are divided on whether the term 'emotions' should include 'feelings' along with the loose collections of impulses and bodily changes comprising 'emotions' in early mammals. Perhaps it is best to think of emotions and feelings as two separate but inter-related perceptual systems, the emotional system being evolutionarily earlier (from the beginning of the Cambrian) and the feelings system being associated with the late mammalian brain. The distinction is important because it is the perception of feelings in the late mammalian brain which confers on later mammals (e.g. hominids) a capacity to inhibit an initial impulse to act and initiate a 'more appropriate' response, i.e. 'appropriate' as determined in a higher cognitive centre.[33]

Emotions are mammalian elaborations of early-vertebrate *arousal patterns*, in which neurochemicals (e.g. dopamine, noradrenaline and serotonin) step-up or step-down the brain's activity level for a period, in response to sensory stimuli. It is the associated physiological changes in blood pressure, heart rate, etc., which raise the organism's capacity to react spontaneously, immediately, energetically and persistently to the triggering situation.[34] The particular type of emotional response to the brain's perception of a situation reflects the brain's prior interpretation of that situation, that is, the meaning given to it. For example, the interpretation of a situation as threatening triggers a fear response. Because it happens automatically and very rapidly in an inaccessible part of the brain, even modern humans are, for the

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[32]Emotional memory is memory involving the implicit (probably unconscious) learning and storage of information about the emotional significance of events of particular types.

[33]http://www.scaruffi.com/nature/emotion.htm (Accessed 10 Nov 2010).

[34]The physiological component of emotion has been traditionally identified as activity in the autonomic nervous system and the visceral organs (e.g. heart and lungs) that it serves.

most part, unaware of this process of interpretation or assignation of meaning to events and situations; only the subsequent emotional state.

By contrast, *instinctive behaviour* does not need to be motivated emotionally but is strictly limited in the range of trigger situations and matched responses it can recognise. The value of the new system of *emotionally directed behaviour* was that it allowed the learning (e.g. by imitating a parental example) of a somewhat broader choice of behavioural responses to a more finely classified, a more informed, perception of the environment. For a long time, behaviour would still have been largely impulsive but nevertheless, increasingly discriminating.

Emotional states, because they are sustained chemically rather than neurologically, tend to persist and, for the time that an emotional state is persisting, the individual will continue trying behaviours as if in search of an altered situation which will be interpreted by the brain as one no longer requiring an emotional response. What evolution has produced is a *reflective mechanism* which uses emotions as internally generated signals (information) for guiding behaviour towards correcting situations which cause negative emotions (anger, fear, shame, sadness). Conversely, positive emotions (sexual arousal, parental tenderness) are adaptations which accompany and reinforce behaviours that have been genetically and experientially selected as survival-promoting, e.g. the propensities in primate social groups for both bonding and autonomous behaviours. Behaviours which are successful in neutralising or gratifying emotions rapidly become learned habitual responses in similar situations. For most of the time, humans are purposive rule-following animals, living a life which, metaphorically, is like a giant chess game.[35] Novel situations tend to produce strong emotions and hence strong ‘motivation’ to find an appropriate behavioural response. We have here a *causal loop* in which emotions guide (evoke) behaviours and evoked behaviours guide (step up, step down) emotions. More explicitly, emotion rouses the individual into activity and activity ineluctably generates a change in emotion as it changes the situation being experienced. Without emotions, the hominid brain would not be aroused to initiate anything (other than instinctive behaviour), nor have any constraints on or guidance as to what to do. That is, emotions both initiate behaviour and, to a degree, reduce uncertainty as to how to behave.

This emotion-based system for guiding behaviour is sometimes described, metaphorically, as a reward–punishment system. Starting with the idea that being in a state of emotional arousal amounts to an unwanted ‘disequilibrium’, any behaviour which moves the individual into a more restful state, one of less arousal, can be thought of as having been rewarded. Conversely, behaviour which increases emotional arousal is, by definition, being ‘punished’. By moving between seeking rewards and avoiding punishments, the individual can grope (call it negative feedback) towards an emotional equilibrium. Notwithstanding, the range of behavioural options available for reducing emotional arousal under a purely emotion-based guidance system would have been limited. This brings us to the choosing brain.

[35] Peter, R.S., 1958, The Concept of Motivation, In R.F. Holland (Ed) *Studies in Philosophical Psychology*, Routledge and Kegan Paul, London and New York.

The Choosing Brain

At some stage in its evolution, moving beyond unalloyed instinct and beyond emotionally directed behaviour, the hominid lineage began to acquire an additional capacity, namely, to identify, evaluate and choose amongst (not necessarily consciously) a wider range of possible behavioural responses to survival-relevant situations. How might we envisage this emerging capability? In situations where the associated emotional response is below some threshold level (i.e. the impulse to act is not irresistible), the thinking brain is able to override the limbic brain's emotion-based impulses. What then follows, in a process that is strongly comparable to Darwinian natural selection, is that the brain imagines the consequences of alternatives to impulsive behaviour and chooses the first imagined alternative to generate sufficiently positive feelings.[36] The implication here is that imagined behaviours generate emotional responses, and then feelings, in much the same way as 'real' behaviours. Just as the bodies of terrestrial animals evolved to internalise the watery environments of their ancestors, the choosing brain is internalising (and elaborating) the exploratory sequences of impulsive behaviours and feedbacks associated with emotionally directed behaviour.

Emotions and the Social Environment

Beyond guiding individual behaviour, feelings-emotions have a second role. They consistently produce external signals and signs observable by other members of the individual's social group.[37] These include pheromones and body changes (skin colour, posture, etc.) which, being largely involuntary, are reliable indicators of behavioural intentions or propensities. Similarly, all humans, and presumably all hominids, employ the same facial muscles when expressing a particular emotion.[38] Going back millions of years, these observable accompaniments of feelings became a form of *indicative communication* about an individual's emotional state to which hominid brains have become particularly sensitised.[39] Darwin recognised the largely biological (genetic) nature of emotional expression 130 years ago, suggesting that such expressions were derived from actions that originally served biologically adaptive functions, e.g. preparation for biting became the bared teeth of the anger expression, courting behaviour spun off signals of friendship, nurturing behaviour lies

[36] Chaisson, E., 2001, ibid., says 'selection' is a misnomer—there is no agent that 'selects'. Selection is not so much an active force or promoter of evolution as a passive pruner of the unfit. A better term might be 'non-random elimination'. The brain's strategy is to try out ideas until one is found which is 'emotionally fit'.

[37] In biology, a signal is any behaviour that conveys information from one individual to another, regardless of whether it serves other functions as well.

[38] Ekman, P., (Ed.), 1982, *Emotion in the Human Face* (2nd Ed.), Cambridge University Press, New York.

[39] Deacon, T., 1997, ibid., p. 431.

behind gestures to soothe anger, to ask for help. In his classic study of emotions,[40] he concluded that while expressive movements may no longer serve biological functions, they clearly serve critical, social and communicative functions.

The evolved function of such communication of information is to regulate the behaviour of the group. For a large part of the Pleistocene, prior certainly to the arrival of functional language, the easy transmission and spread of an emotional state amongst group members would have served as an important mechanism (along with instinctual responses and a propensity to imitate others) for co-ordinating group behaviour. Indeed, the metaphor of the group behaving as a 'super-organism' is not overblown.

Sensing an emotional response in others tends to have the same effect as being exposed oneself to the stimulus which triggered the original response. More than this, such transfers of emotions convey to inexperienced juveniles how to respond to particular environmental situations. We might also note here that while the impulse to respond to an emotion-laden situation may be biologically strong, it will be filtered in that the actual response will usually depend on how the individual has been previously socialised or conditioned.

Such *emotional learning* is in keeping with *constructivist theories of emotions*,[41] which suggest that the set of situations eliciting emotional responses is co-determined (a) genetically and (b) by the individual's experiences, most particularly their learning experiences in their social environment. For example, a behaviour which is punished by a mother displaying anger will come, in time, to elicit the same emotional response in the juvenile.

The involuntary communication of emotions by indicative signs would have been augmented at some stage during the Pleistocene by voluntary forms of indicative communication, including purposive gestures, vocalisations and the simulated expression of emotion. Speech, which can be presumed to have been added to the hominid communication repertoire at a later stage again, was a dramatically different form of communication, one based on the use of arbitrary or symbolic signs rather than indicative or natural signs. Whereas indicative signs are abstracted from, are some aspect of, the information being communicated, the signs used in *symbolic communication* have no apparent indicative content but still manage to reflect a mutual understanding amongst the communicants as to what object, idea, behaviour, etc., the symbol stands for.[42] Having said that, the boundary between indicative and symbolic signs is frequently blurry, e.g. pretending to throw versus pointing.

While the set of stimuli tending to produce a learned emotional response would have been ceaselessly changing over the long Pleistocene, there is no reason to

[40] Darwin, C., 1872, *The Expression of the Emotions in Man and Animals,* John Murray, London.

[41] Averill, J.R.,1980, A Constructivist View of Emotion. In R. Plutchik and H. Kellerman (Eds.), *Emotion: Theory, Research and Experience, Vol. 1. Theories of Emotion*, Academic Press, New York, pp. 305–339.

[42] Bates, E.L., Benigni, I., et al., 1979, *On the Evolution and Development of Symbols*, Academic Press, New York, p. 64.

believe that the range of emotions available for guiding hominid behaviour would have changed in any significant way from the ancient set (with variations) of anger, fear, shame-guilt, happiness, sadness and, debatably, sexual arousal.[43] Over the Pleistocene, an increasing proportion of all situations producing emotions would involve some form of social interaction, arising mostly during the meeting of the individual's physiological and psychological (bonding, autonomy and meaning) needs and the meeting of the group's need to maintain, transmit and, occasionally, modify its culture.

A group's culture, meaning its accumulated learned behaviour (way of life), is passed on in a variety of ways from generation to generation, slowly changing in the process. When learning to habitually behave in accordance with cultural norms, children will simultaneously be acquiring the associated reward–punishment feelings that will motivate them to continue behaving in culturally compatible ways.

It can be noted here, for later recall, that if new behaviours can be attached to particular emotions and feelings, the possibility suggesting itself is that 'human nature' is malleable, that humans can be successfully socialised in multiple ways. This is also consistent with Fromm's observation that a society's social character is 'mobile' and can be changed relatively easily.[44]

The Further Evolution of Non-verbal Communication

Gestures (e.g. pointing), postures (e.g. standing tall) and body movements (e.g. shoulder shrugging) are all ways in which information could have been communicated between group members throughout the Pleistocene. Like expressions of emotion, some of these signs would have been involuntary and, originally at least, indicative, i.e. metaphorical rather than arbitrarily symbolic. But, at some stage (perhaps half a million years ago as archaic *Homo sapiens* was speciating?), evolving in parallel with an increasing cognitive capability, such non-verbal communication (popularly known as body language) must have come under voluntary, purposive control. This switch from a reactive to a proactive (goal directed) cognitive system (see below) represented the beginnings of hominids' capacity to mentally model real-world situations and reflect on them, not necessarily consciously, in order to choose a 'best available' response, e.g. to gesture or not to gesture.

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[43]There are a number of candidate lists of primary emotions (collectively grouped as 'affect') in the literature. For example, Robert Plutchik developed a theory showing eight primary human emotions; joy, acceptance, fear, submission, sadness, disgust, anger and anticipation, and argued that all human emotions can be derived from these. See Plutchik, R., 1980, *Emotion: Theory, Research, and Experience: Vol. 1. Theories of Emotion*, **1**, Academic, New York.

[44]Fromm, E. 1942, *Fear of Freedom*, Routledge & Kegan Paul, London; Berger, P., and Luckmann, T., 1966, *The Social Construction of Reality: A Treatise in the Sociology of Knowledge*, Doubleday, New York, p.165; http://en.wikipedia.org/wiki/Little_Albert_experiment (Accessed 19 Nov 2010).

The Importance of Mimesis

> Mimetic action is basically a talent for using the whole body as a communication device, for translating event-perceptions into action. Its underlying modelling principle is perceptual metaphor; thus it might also be called action-metaphor. It is the most basic human thought-skill, and remains fundamentally independent of our truly linguistic modes of representation. Mimesis is based in a memory system that can rehearse and refine movement voluntarily and systematically, guided by a perceptual model of the body in its surrounding environment, and store and retrieve the products of that rehearsal. It is based on an abstract 'model of models' that allows any voluntary action of the body to be stopped, replayed, and edited, under conscious control. This is inherently a voluntary access route to memory, since the product of the model is an implementable self-image.[45]

To be useful, the meanings of non-verbal signs have to be mutually understood across the social group and need to be transmitted from one generation to the next. In Berger and Luckmann's phrase, meanings of signs must have 'sedimented'.[46] The general capability which allows groups to develop and maintain systems of non-verbal communication, and it probably evolved well before *Australopithecus*, is *mimesis*. As discussed enthusiastically by Merlin Donald,[47] mimesis (call it motor mimesis perhaps?) is most simply thought of as a capacity for imitation and rehearsal of physical behaviour, of action sequences. It takes place in two steps. Step 1 is to remember a previously observed or personally experienced sequence of body movements. Step 2 is to reproduce, to act out and to mime the remembered sequences.

Imitating others is widespread in the animal world, even amongst 'lower' orders.[48] In many circumstances it is a quick and reliable way of learning useful behaviours. When hominids' inherent tendency to spontaneously imitate others began to give way to a capacity to voluntarily control the timing of such expression, the implied increase in cognitive development may, in parallel, have allowed the memorising and imitation of more complex behavioural sequences, e.g. making fire, making stone tools.

Furthermore, in tandem with a propensity for spontaneous exploratory behaviour, the capacity to imitate oneself, to voluntarily rehearse one's own previous behaviours, meant that behavioural sequences could be practised till perfected—something that other primates cannot do. Think of how children actively and routinely rehearse and refine all kinds of action, including facial expressions, vocalisations, climbing, balancing, building things and so on.[49] Further again, the capacity to voluntarily pause when practising a behaviour sequence suggests the beginning

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[45] Donald, M., 1993, Précis of Origins of the Modern Mind, *Behavioral and Brain Sciences,* **16** (4), pp.737–791.

[46] Berger, P., and Luckmann, T,, 1966, ibid. p. 68.

[47] Donald, M., 1993, ibid.

[48] Dugatkin, A.L., 2000, The Imitation Factor: Evolution Beyond the Gene, Free Press, New York.

[49] Donald, M., 1993, ibid.

of a capacity to adapt the sequence for successful performance under a variety of conditions.[50] For example, if a sequence such as tool making is being practised and conditions such as the lack of suitable materials do not allow its completion, a pause followed by spontaneous exploratory behaviour (trial and error, trial and success) might create a variant of the failed behaviour more suited to the immediate conditions.

It seems plausible then that mimesis, the capacity to act out observed behaviour at will, could have been the instrument which allowed even early hominids to create and maintain a simple shared semantic environment, a culture of meaningful (although non-verbal) signs and behaviours. Amongst the tasks responsive to this emerging capability would have been the voluntary expression of emotions and the transfer and slow improvement of technical skills. It also opened the way for group rituals involving a number of people acting in concert. The challenge in all this of co-ordinating brain-eye-limb activity might well have provided sufficient selection pressure for explaining the rapid increase in human brain size and complexity over much of the Pleistocene.[51]

Especially Mimetic Story-Telling

Somewhat later (c.300–400 kya?), in tandem once again with a still-expanding cognitive capability, the hominid capacity for mimetic communication may have become a sufficient basis for the evolution of a further suite of cultural innovations, of shared behaviours with shared meaning.

To quote Donald again[52]:

> The 'meaning' of mimed versions of perceptual events is transparent to anyone possessing the same event-perception capabilities as the actor; thus mimetic representations can be shared, and constitute a cognitive mechanism for creating unique communal sets of representations. The shared expressive and social ramifications of mimetic capacity thus follow with the same inevitability as improved constructive skill. As the whole body becomes a potential tool for expression, a variety of new possibilities enter the social arena: complex games, extended competition, pedagogy through directed imitation (with a concomitant differentiation of social roles), a subtler and more complex array of facial and vocal expressions, and public action-metaphor, such as intentional group displays of aggression, solidarity, joy, fear, and sorrow. These would have perhaps constituted the first social 'customs', and the basis of the first truly distinctive hominid cultures.

Something not on this list of Donald's, but of great importance, is *mimetic story-telling*, the voluntary presentation by a story teller of an extended sequence of

[50] Later we will note that a capacity to 'pause', not physically as here but while mentally modelling a behaviour sequence, is a necessary part of being able to 'solve problems'. Learning to internalise behaviours which were previously physically observable is indeed a recurring feature of hominid evolution.

[51] Dunbar, R., 1998, The Social Brain Hypothesis, *Evolutionary Anthropology,* **6** (5), pp. 178—190.

[52] Donald, M., 1993, ibid.

mimetic actions—call them *mimes*—for the purpose of triggering in members of an audience an equally extended sequence of stabilised memories, i.e. percepts.[53]

Perhaps story-telling started as play or as a bonding device or as exploratory behaviour but, in time, it must have acquired purpose, namely, the conveying of information in a meaningful way, outside the context of the 'here and now'. The meaning of a single mime is the percept it first triggers plus any flow-on sequence of related percepts. A story teller's sequence of mimes has meaning to the extent that the whole sequence of percepts which the sequence of mimes produces constitutes a readily retrievable set. That is they hang together in terms of time, space, emotional content, etc. Isn't that what is meant by a 'story'? Just as in spoken language, where sentences mean more than their individual words, a mimed story would mean more than its component mimes—the beginning perhaps of an advance from lexical (word) communication to syntactic (sentence) communication.

Note also that it is the sequence of mimes as a whole which is voluntary, not just the component mimes. And that, being voluntary, a mimed story is not produced as a response to any immediate stimulatory situation; it can be told anywhere

Looked at from a higher level, the great importance of mimetic story-telling is that a case can be made that the acquisition of this capability was a key step in the evolution of both spoken language and creative thinking.

Thinking, at its simplest, involves the assembly of a meaningful sequence of percepts/schemata. For example, mimetic story-telling involves the conversion of a remembered sequence of percepts into mimes on the part of the story-teller and the conversion of that sequence of mimes into percepts by the audience. A story-teller who voluntarily mixes mimes describing aspects of several real world events into one narrative is thinking creatively, not just chronicling. Any suggestion as to when creative thinking might have become deliberately associated with an intent to deceive or entertain or solve a problem would be highly speculative though, e.g. before or after speech?

Language is not an easy word to define. Functionally, it is a tool for voluntarily conveying meaning by the use of mutually understood signs. Each sign used evokes an associated percept and it is sequences of percepts which carry meaning. At the heart of every language then there is a set of sign-percept pairs. Each sign is code for a percept. In spoken languages, for example, the signs are arbitrary phonic symbols called words[54] and each word evokes its own particular percept in speakers of that language.

[53]Note that the word being used is 'mimes', not the better-known 'memes'. Richard Dawkins defines a meme as 'a unit of cultural transmission, or a unit of imitation.' See Dawkins, R., 1989, *The Selfish Gene*, Oxford University Press, Oxford Meme is unsuitable for use here because mimes are non-verbal whereas memes can be verbal or non-verbal. Also, the emphasis when using 'meme' is on the spread of new concepts and behaviours through a population whereas mimetic actions are about communicating using known signs in a known way.

[54]Words are themselves arbitrary combinations of the three dozen or so phonemes or units of vocalisation which humans utter.

Telling a story mimetically can be viewed as using a non-verbal language. It is an activity which can only occur successfully in a group where most members share a common repertoire or 'vocabulary' of signs called mimes and where each mime presented evokes a somewhat similar percept (stabilised memory) in most members of the audience. Mimes are code for percepts. At some stage symbolic signs for percepts, as distinct from indicative or metaphorical mimes, may have begun to enter non-verbal language, although it is even hard enough to think of examples of meaningful but truly arbitrary gestures, etc., in today's world. Most seem to be highly stylised versions of plausible mimetic antecedents, e.g. pointing at something may derive from throwing a stone at it.

To the extent that a group of hominids has a common non-verbal language, they can be said to have a shared view of the world (a 'group mind') based on categories of experience which collect many similar events or objects under one sign, e.g. waving the forearms is the abstracted sign for 'bird'.[55] What seems likely is that, as the hominid brain developed over the Pleistocene, the set of mime-percept pairs available for non-verbal communication would have similarly grown. One obvious benefit from evolving such an expanded 'vocabulary' would be an improved capacity to share and collectively exploit information, e.g. consider the value of a story about the location of a fresh carcase.

Summary of Developments in Non-verbal Communication

It is likely that hominids came into the Pleistocene already equipped with a capacity for involuntarily communicating emotional states being experienced and with spontaneous propensities for exploratory behaviour and for imitating simple gestures and postures of others. There followed, it can be suggested, a step-by-step sequence of developments in non-verbal communication and thinking skills which led towards the emergence of spoken pre- or proto-language around the time of emergence of archaic *Homo sapiens*. There is no evidence to date-stamp these developments although it can be assumed that they were somehow in step with the growth and reorganisation of the erectine brain.

1. The first of these developments, representing the beginnings of purposive body language, might have been a degree of voluntary control (if and when) over the expression of a small repertoire of emotions, gestures, etc. Such voluntary control implies some cognitive capability for modelling the consequences (with awareness perhaps but not the reflective awareness of consciousness as modern humans experience it) of expressing versus not expressing some motor behaviour.
2. The further extension of voluntary control to imitating and rehearsing various behaviours of others in the social group would have been the step which allowed

[55] Allott, R., 1989, *The Motor Theory of Language Origin*, Book Guild, Lewes.

useful learned behaviours to be transferred between people and a simple culture to be maintained, and slowly modified.

3. Once a capacity for voluntary rehearsal of a remembered sequence of one's own actions had been acquired, it opened the gate to mimetic story-telling and true non-verbal language. A necessary condition for communication by language to be possible is a group whose members share a common set of sign-percept pairs and who have voluntary control over the expression of those signs (the signs being mimes in the case of non-verbal language).
4. Once established for the recounting of actual experiences, the way would have been open to use non-verbal language for new tasks (fiction? planning projects?) and for the group's common vocabulary of mime-percept pairs to be enlarged, perhaps even to include some symbol-percept pairs. We do not know.

The Transition to Spoken Language

> Given the inherent fuzziness and ambiguity of mimetic representation, it would eventually have reached a level of complexity where a method of disambiguating intended mimetic messages would have had immediate adaptive benefits. Thus it created conditions which would have favoured a communication device of greater speed and power.[56]

Mimesis Was the Springboard

Apart from being more limited in what it can convey, a mimetic language differs most obviously from a spoken language in the type of signs it attaches to mental percepts and schemata—arbitrary vocal symbols rather than indicative motor mimes. Both types of language rely on all individuals in a group being able to imitate and remember signs made by others, to correctly attach each sign to approximately the same percept as others do and to voluntarily retrieve and use signs as required for conveying the information carried by the associated percept or sequence of percepts. The suggestion here is that the cognitive skill to form percepts would have pre-dated the capacity to invent and vocalise word-signs. Or, putting it another way, vocal and mimetic signs are cognitively equivalent.

Acquiring a Vocal Apparatus

The vocalisations of our australopithecine ancestors were probably very similar to those of apes with alarm calls, grunts and squeals punctuating non-verbal language,

[56] Donald, M., 1993, ibid.

just as gestures embellish modern vocal language. Emotional states would have been expressed vocally via signals such as cries of pain and joy, laughing, crying and whimpering in fear. But vocal communication approximating human speech would have required extensive alterations to the australopithecine vocal tract, as well as a shift from predominantly subcortical (midbrain) to cortical (forebrain) control over vocalisation. The physical and cognitive apparatus required for speech can be usefully thought of as a specialised *mimetic sub-system*, one for imitating, remembering, recalling and voluntarily reproducing, not mimes, but, the sounds of spoken words.

It is this system's ability to produce a dynamic, rapidly changing stream of diverse sounds that makes spoken language possible. Unlike an involuntary vocalisation which describes a whole event and cannot be meaningfully disaggregated, advanced speech is combinatorial; it uses a small number of basic elements—phonemes or syllables—which are combined and recombined at high speed into words and phrases.

It can be plausibly supposed that evolutionary change in the vocal tract first accelerated with habitual bipedalism.[57] Whereas quadruped locomotion puts pressure on the thorax and drives breathing in time with steps, bipedal animals (and diving mammals) must be able to inhale and exhale voluntarily. Controlled exhalation is a prerequisite for laughter, song and speech. Serendipitously, selection for anatomical changes which enhanced breath control simultaneously produced changes in the vocal tract which 'pre-adapted' it for speech production. For example, the descent of the larynx (voice box) in the throat, an adaptation allowing more air to be gulped in, also produced a larger pharyngeal cavity which would later prove useful for making a variety of vowel sounds. The same requirement for better breath control, plus dietary changes perhaps, produced the fat lips and flexible tongue which would later facilitate consonant production. What we have here is an example of *exaptation*, meaning that changes being selected primarily to promote one function (breath control) create traits which, subsequently, are used in the development of quite another function (speech).

Unlike other mammals, where the vocal tract can be considered a single tube, the human vocal tract comprises two linked tubes, the pharyngeal cavity and the oral cavity, which are divided by the body of the tongue. It is an arrangement which allows a much larger repertoire of possible sounds than a single tube. Because the human tongue is important in controlling articulation, needing to move rapidly when producing speech, it is relatively small compared to the tongues of other primates, and extremely well innervated.

Human hearing is also adapted to speech. Humans are very sensitive to sounds between 1 and 4 kHz, the range of frequencies within which the human vocal tract resonates and which characterises the sound of human speech.

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[57] Bipedalism, it might similarly be noted, had also freed the hands for miming.

Origins of Words and Sentences

These changes in the vocal tract were probably not fully complete until relatively late in hominid evolution, perhaps only with the emergence of modern humans some 150,000 years ago. Meanwhile there surely would have been intermediate steps on the way to spoken language. Early erectines may have been able to produce more sounds than australopithecines but only in slow, relatively unmodulated sequences. It was Charles Darwin, in fact, who first suggested that prosody, the ability to voluntarily control volume, pitch and tone, was the initial step towards spoken language. Donald also sees prosody as more fundamental than and prior to phonetic control.[58] Perhaps music and singing, which also rely on a capacity for prosody, are equally old? Perhaps each erectine had his or her own identifying prosodic song or call?

Julian Jaynes, in his imaginative hypothesising about the origins of spoken language (as recently as 70 kya he suggests), sees the addition of terminal modifying phonemes to voluntary prosodic calls as an important turning point, e.g. modifying the ending of a danger call to distinguish between 'near danger' and 'far danger'.[59] Detaching such *modifiers* from the rest of the call and using them in differing circumstances would have made them the first words; for example, using them as *commands* to emphasise gestures when seeking to modify the behaviour of members of a hunting group, e.g. when waving someone to go far back. *Nouns* might have been next—adding a phoneme to a modifier to indicate more precisely the entity being referred to, e.g. 'near lion' or 'far lion'. Notwithstanding, the major transition from 'one sound-one meaning' to meaningful words made up of strings of arbitrary phonemes does remain a mystery.[60]

Beginnings of Syntax

Constructions such as 'near lion' are actually simple sentences. They show the beginnings of syntax in verbal language. Syntactical language has single words for objects and actions; non-syntactical language has words only for events (made up of objects and relationships between them). Whereas a different prosodic call is required for each whole situation being described, a syntactic approach to conveying the same information implies a capacity to analyse that whole situation into parts and their relationships and to attach an established verbal sign to each part/relationship. It is easier perhaps to think of spoken-language syntax as having developed from the pre-existing syntax of mimetic story-telling. For example, in

[58] Donald, M., 1993, ibid.

[59] Jaynes, J., 1976, *The Origin of Consciousness in the Breakdown of the Bicameral Mind*, Houghton Mifflin, Boston. Ch. 6.

[60] Calvin, W.H., 1997, *How Brains Think: Evolving Intelligence, Then and Now*, Basic Books, New York, Ch. 5.

miming the story of a raptor diving on its prey, any of the mimes for raptor (noun) or diving (verb) or prey (noun) could be replaced with vocal-symbol equivalents.

Nowak et al. argue that syntactic communication could have evolved gradually as the number of needed vocal signals passed a threshold where holding them all in memory became difficult.[61] Why? The number of vocal signals required increases much more slowly than the number of events or situations that can be described if the *components* of events have their own verbal signals. For example, two ‘words’ have to be remembered to describe both ‘near lion’ and ‘far lion’ whether the approach is syntactic or not. But to convey the 12 combinations of ‘near’ and ‘far’ with any of 6 species requires 12 non-syntactic words versus 8 syntactic words, Due to the possible combinatorial interrelationships between words, the addition of even one word to a modest vocabulary will sharply increase the number of additional events which can thereafter be described.

Remember that we are talking here of syntax at its simplest, i.e. associating words for percepts which are already associated in a memory. Conventions such as word order in sentences, or what constitutes a sentence, or the distinction between reportive and expective statements (i.e. tenses) would have arisen over time as unconsciously learned rules for conveying information with fewer misunderstandings. There does not seem to be much explanatory need to postulate an innate, largely genetic syntactic capability.[62]

Where Do New Words Come From?

We might imagine that names for animal species were amongst the first nouns and that, most simply, the sound of the word for a species would be an excerpt from one of that species’ calls. And, in time, with group use, the sound used to denote the pre-existing percept of that species, just like the percept itself, would stabilise. Even today, many words have such onomatopoeic origins, e.g. the hiss in ‘snake’. Similarly, we can imagine that nouns for the emotions would emerge easily from the vocalisations long-associated with the expression of emotions; thereafter, any story could routinely include a report on the narrator’s emotional state at the time of the situation being described.

But what of objects and actions without regular sound associations? Here is a scenario. Suppose someone carrying out behaviour X accidentally makes a distinctive noise, any distinctive noise, while doing so. Suppose that someone observing and imitating behaviour X includes that distinctive noise as part of the mimesis. The particular distinctive noise might first become a habitual part of behaviour X itself and then a habitual part of the miming of behaviour X during story-telling. Finally,

[61] Nowak, M.A., Plotkin, J.B, and Jansen, V.A., 2000, The Evolution of Syntactic Communication, *Nature*, **404**, pp. 495–498.

[62] Schoenemann, P.T., 1999, Syntax as an Emergent Characteristic of the Evolution of Semantic Complexity, *Minds and Machines*, **9**(3), pp. 309–346.

the distinctive noise becomes detached from behaviour X or the miming of it. Thereafter, when the distinctive noise is made voluntarily, it evokes a memory of the behaviour itself and vice versa. It has become an arbitrary vocal symbol for that behaviour. In time, the word and its meaning (referent) will become stable components of the group's language repertoire. Notwithstanding, any new word would stand to undergo continuing slow phonemic change, making it, for example, easier to say or more distinguishable from other words.

This scenario would have words being created by accident and then persisting because they are useful. Might there have been, at some time well before modern humans, a realisation that things and actions can be given arbitrary vocal labels and that this can assist communication? Such a feat of abstraction, so early, does seem unlikely.

Metaphors

New words expand the range of events and situations that can be described verbally, but so do old words used in new ways. Once a modest vocabulary has been established, metaphor becomes an important way for language use, meaning what is describable, to grow. Metaphor is the use of existing words normally used to describe or name a first entity as a way of describing or naming some seemingly unrelated second entity. But, for a metaphor to be useful, there must indeed be some kind of similarity between the entities or (in the case of analogues) between their relations to other things.

The most useful metaphors not only bestow names on newly perceived things (and actions) of importance, they draw attention to the possibility that the second entity (called the metaphrand) may be similar to the first entity (called the metaphier) in ways not alluded to in the metaphor itself, i.e. language is an organ of perception as much as a means of communication. Jaynes gives the example of 'snow blanketing the ground' with its nuances of warmth and comfort until it is spring and time to wake up.[63] Equally, metaphors may lose their richness over time and become truly arbitrary vocal symbols. For example, 'concrete' metaphors may get hidden by phonemic drift and longer metaphorical descriptions may shrink to short labels. In principle this does not matter, but it may make metaphorical words harder to remember and increasingly misunderstood, e.g. when historians misleadingly translate and interpret terms in ancient texts.

Much more importantly, as each culture built up its own metaphoric conceptualisation of the world, its verbal language would have become increasingly incomprehensible to others. Unlike mimetic language which would have been more or less understood by strangers, most metaphoric references are not to universals but are extracted from a local context and reflect only one culture's framework of reality. It may be that the origins of 'them' and 'us' thinking go back to the emergence of verbal languages.

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[63] Jaynes, J., 1976, ibid., p. 57.

Presumably the metaphors of early verbal language would all have been concrete, likening something which could be pointed at to something else which could be pointed at. Abstract concepts which are not observable and therefore can only be described metaphorically would not have arisen till there was sufficient concrete language to support them; at the end of the Pleistocene perhaps. For example, an animistic belief system requires words for the spirits which inhabit the natural world.

Why Did Language Evolve?

All manner of reasons have been advanced as to why spoken language evolved once the required preconditions (a flexible vocal tract, breath control and a capacity for mimetic narrative) were in place, even as non-verbal communication was reaching limits to what it could do.

For example, Dunbar hypothesises that language evolved to replace one-on-one grooming which becomes unwieldy as group size increases. Grooming another's fur is common amongst primates and widely held to be important for promoting group cohesion. Increasing group size, despite its negative impact on foraging success, may have been selected for in response to inter-group competition for limited resources during glacial advances.[64] Talking to and about others might help one to identify trustworthy and helpful individuals and to predict how others will behave during collective activities. In particular, he talks about the problem of dividing potentially reliable allies from 'free-riding' individuals who habitually accept favours without reciprocating. Somewhat similarly, coming from an historical perspective, William McNeill and Ernest Gellner are two who have concluded that language is primarily an instrument for maintaining social cohesion and cooperative action.[65]

Replying to Dunbar, Donald suggests that language evolved for multiple reasons simultaneously, one of which might have been 'verbal grooming'; others that he suggests include being able to coordinate fighting and hunting, food classification, teaching skills and forming functional hierarchies.[66] We might add to this list of 'common sense' reasons that speech permits one-to-many communication at night, over long distances and where there is no line of sight. Also, you can speak when your hands are busy.

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[64] Dunbar, R., 1993, Co-evolution of Neocortex Size, Groups Size and Language in Humans, *Behavioral and Brain Sciences*, **16** (4), pp. 681–735.

[65] Gellner, E., 1992, *Plough, Sword and Book: The Structure of Human History*, University of Chicago Press, Chicago; McNeill, W.H., 1980, *The Human Condition: An Ecological and Historical View*, Princeton University Press, Princeton, NJ.

[66] Donald, M., 1993, ibid.

Certainly, for language development to have continued as it did, the benefits must have been very substantial, given the ever-increasing cost of an enlarging brain in terms of energy required for maintaining and growing the neocortical structures needed for managing language.

But, in the full context of human history, speech must be seen as much more than a flexible tool for transferring diverse 'here and now' information between group members more efficiently (usually) than non-verbal language. Specifically, the late Pleistocene saw an acceleration and reinforcement of three trends in hominid culture which could not have occurred without structured verbal language. The three are a trend towards advanced thinking, a trend towards the accumulation of ever-more collective knowledge and a reinforcement of tribalism as a means of social organisation.

Speech Improves Thinking

As noted above, the hominid brain, at some stage, acquired the ability to voluntarily recall memories by the overt or covert use of word-symbols as well as by mimetic imagination. By covert (inner) speech we mean that words are being articulated, but without motor (muscular) execution. Imagining past acts can similarly be thought of as mimesis without motor execution. This development of voluntary control over learned behaviours, including verbal and non-verbal language use, already implies some cognitive capability for modelling the consequences of one's actions. For example, as Bronislaw Malinowski points out, even a skill such as fire making requires a 'theory' of what will work and what will not work.[67] The suggestion being probed here is that being able to use symbolic syntactical language would have further improved such modelling capability.

Derek Bickerton, for example, suggests that having symbolic language speeds up thinking and thereby reduces the time to assemble propositions, stories, etc.[68] While thinking by assembling percepts in imagination (thinking in pictures) is possible without verbal language,[69] using word assemblies instead of image assemblies allows for more complex thoughts to be generated within the limitations of short-term memory.[70] Thus, the word 'dog' makes it easier to think about dogs in general than if we only had separate words and images for 'labrador', 'spaniel', etc. The organisation of such assemblies into syntactic structures (e.g. phrases, adjective-noun pairs) would further clarify and accelerate thinking, e.g. by reducing memory load.

[67] Malinowski, B., 1944, *A Scientific Theory of Culture and Other Essays,* University of North Carolina Press, Chapel Hill.

[68] Bickerton, D., 1996, *Language and Human Behaviour,* UCL Press, London.

[69] Lyra, P., 2005, Review of José Luis Bermúdez: *Thinking without Words, Psyche,* **11**(2), pp. 1–12.

[70] The mental operation we call 'imagination' can be seen as mimesis without motor execution of the imagined acts.

Jaynes suggests another way in which language aided thinking.[71] While more instinctive behaviours do not need priming and re-priming on their way to completion, learned behaviours do and talking to oneself overtly, covertly or in the (contentious) form of auditory hallucinations may help one to keep focussed on the activity at hand.

Having an established vocabulary, attached to stabilised percepts and extracted by experience from the environment, also stood to improve thinking by refining the thinker's perception of what was being experienced. The reference here is to the speed and precision with which incoming stimuli could be either discarded or responded to.

And as that vocabulary grew, cognition would have developed beyond basic associative and reinforcement processes in the sense of being able to tell more complex stories and more types of stories. For example, an abstract cognitive category is particularly difficult to think about without using its verbal label. As for types of stories, we might suppose that verbal story telling, whether overt or covert, would have progressively encompassed (a) simple factual 'then and there' stories linking objects and actions in time and space, (b) simple fictional 'play' stories, (c) problem-solving stories assembling a sequence of actions recalling or proposing the achievement of some desired outcome (the invention of 'time'?), and (d) explanatory or 'just so' stories embodying a cause-effect chain, teasing out, step by step, how things got to be the way they are.

Being able to tell problem-solving and explanatory stories would have brought humans to the brink of 'constructivist' (as opposed to 'observational') learning, i.e. to learning without having followed any direct examples (learning from oneself!). Henceforward, a hypothetical 'what if?' model of behaviour-plus-consequences could be constructed before carrying out some novel action. Such a model (story) would or could then be tested empirically, i.e. did it work?

Nowadays, we recognise the process of generating an explanatory hypothesis that is consistent with the known facts as *abduction*, a way of reasoning that is as legitimate as induction and deduction.[72] Or, from another angle, if *meaning* is, as suggested earlier, the recognition of relationships between entities, abduction is a tool or skill for imposing meaning on what is being thought or experienced.

Uncritical Thinking

It is important to emphasise here that there are strong practical and emotional rewards (the aaahah feeling!) from imposing meaning on mental and real-world experiences. However, one perverse consequence of early modern humans being strongly motivated to 'search for meaning' is that if there are factual gaps in one's

[71] Jaynes, J., 1976, ibid., p. 313.

[72] http://en.wikipedia.org/wiki/Abductive_reasoning (Accessed 21 Nov 2010).

story, the brain's so-called interpreter tends to fill them in with entities and relationships which are fictional or out of context, e.g. introducing 'spirits' as causal agents. As is perhaps illustrated by the rationalisations offered by people carrying out post-hypnotic suggestions, the brain seems to prefer any story to no story. More than that, the brain seems to prefer a 'good' story to a 'bad' story, i.e. it tends to choose fictions which are emotionally satisfying over fictions which rouse negative emotions. Presumably there are many situations where such flawed stories are still worthwhile in terms of memorability, usability, etc., even though they contain false or redundant elements.

Presently, we will discuss Valentin Turchin's suggestion that such 'uncritical' or 'pre-critical' thinking was the norm in the early stages of speech development[73]; and that it was not till the emergence of civilisations in Mesopotamia some 5–6 kya that humans began to develop a cognitive apparatus (a technology) for changing, once established, their *verbal* models of behaviours and causal chains.

Before any arrival of such a capacity to change linguistic models, customary behaviour based on rigid verbal models was probably pervasive in hunter-gatherer societies; only an external shock which made those rules unworkable could lead to their reworking. In that era of uncritical thinking, language would have been playing a paradoxical role. On the one hand, it would have been a very useful tool for the dissemination and accumulation (see below) of practical information. On the other hand, it carried the potential to lock a group into false views of how parts of the world worked without any prospect of these being corrected, views likely to generate maladaptive behaviour in face of a changing environment.[74] Several of these perspectives, including animism (everything is alive) and the perceived reality of names and images are discussed below.

Speech Accelerates Information Accumulation

We turn now to the second of three trends likely to have been strengthened by having spoken language available, namely, a quickening rate of expansion of the stock of useful information (knowledge) hunter-gatherer groups could access for guiding members' behaviour.

Note that the reference is to a whole group's information stock, not that of any individual. A group's collective information is 'distributed' in that some information with widely agreed meaning (e.g. vocabulary) is held in memory by most members of the group whereas other information is only held by a proportion of the group or, perhaps, by just one member, e.g. specialist information held by fire makers, tool makers and hunters.

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[73] Turchin, V., 1977, *The Phenomenon of Science*, Columbia University Press, New York, Ch. 8.

[74] Turchin, V., 1977, ibid., Ch. 8.

The starting point for suggesting that the information accumulation rate would have increased with spoken language, compared with mimetic language, is the idea that information breeds (new) information. Armed with new information, people behave differently and have new learning experiences which, if they are communicated to others, provide those others, in turn, with new information. Note that we are concentrating here on the contribution to accumulation that comes from sharing and communicating with others rather than from the accumulation of new information via better thinking (see page 99) or novel experiences.

While it may have been very slow for a very long time, there is no reason to doubt that this process of near-exponential accumulation (i.e. rate of increase in the stock is proportional to its size) was already occurring when non-verbal language was the medium of communication. However, just as a group's reserves of useful information might have begun to grow more rapidly when the sharing of information through mimesis was added to sharing through genes and instincts, so with speech.

'I killed a heffelump by myself'. With speech, not only can such an important new experience be shared using less time and energy than mimesis would require, it can also be transmitted in more detail and, most importantly, at any time.[75] As Berger and Luckman put it, language provides a means of objectifying new experiences and allowing their incorporation into the knowledge stock.[76] And, for some purposes, such as teaching manual skills, words can be added to the mimetic instructions to clarify and reinforce them.

The rate at which information is accumulated depends on the rate at which it is lost as well as the rate at which it is generated. There are two points to be made here. One is that using standard 'verbal formulae' allows more memories to be held in readily accessible form. The other, remembering the hominid propensity to imitate, is that currently inaccessible memories can be readily retrieved by hearing the right verbal formula spoken by another. And, if speech did perhaps promote the formation of larger groups, the probability of such verbal formulae being lost to the group is reduced even further. That is, information would no longer be automatically lost from the group if it were lost from the memory of one or several individuals.

Finally, we come to the possibility that speech, by speeding up communication between people, leaves them with more time, perhaps, to discover useful variants on current behaviours.

Overall, spoken language is being presented as a development which increased the rate at which learned behaviour (culture) accumulated in human groups, largely by facilitating improved cognitive skills and by improving the sharing of information. And it happened through the underpinning of multiple improvements in the generation, acquisition, storage, accessibility and communicability of useful information.

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[75] Bickerton, D., 1996, ibid., p. 172.

[76] Berger, P., and Luckmann, T., 1966, ibid., p. 68.

Speech Reinforces Tribalism

Tribalism is a social system in which people live in small, more or less independent groups called tribes. Each tribe, rarely more than 150 people, comprises a number of regularly interacting clans which may or may not be related (a clan is a group of extended families whose members believe that they have a common ancestor). It is a social system in which there is no level of authority above any tribe. Within the tribe, where there may or may not be an individual leader, collective actions are agreed by reaching a consensus or agreed by tribal elders or imposed by the leader.

While this description of tribalism draws on contemporary and recently bygone examples, it is plausible to imagine that, for much of the Pleistocene, erectines and humans, ancient and modern, lived in roughly comparable social units—perhaps more in minimally interacting clans or bands rather than tribes. The scenario being suggested here is that the advent of spoken language might have changed the tribal system in various ways.

One idea that has already been alluded to is that verbal language, by supplanting time-consuming physical grooming, did allow groups to build a capacity to cooperate while opportunistically expanding numbers to levels where the group was more likely to survive various contingencies. At some group size, even speech-based cohesion must break down but whether this level is above or below maximum numbers as set by other constraints (e.g. the logistics of hunting and gathering) can only be speculated.

Leslie White[77] argues that it was speech which allowed the development of cooperative relationships between families of a tribe. As vocabulary expanded, people outside the immediate family could be designated, for the first time, as 'cousin', 'uncle', etc. This in turn opened the possibility of inventing incest taboos, a near-universal practice which allows families to be united by 'marriage' and which, by controlling marriage, can control the size of the tribe.

For the group as a whole, language can be used to construct tribal histories, origin myths and other stories which provide all the members of the tribe with a common set of meanings, explanations and beliefs about the world. The argument from there is that it is easier to bond with, act jointly with, share food, etc., with people who have the same 'mental model' of the world as you do.

The obverse of this of course is that, much more so than in a mimetic world, a tribe's language and its products inadvertently accentuate the perceived differences between tribal members and others. Even in a homogeneous environment, different languages are likely to be built on different metaphors. This in turn increases the probability of intertribal suspicion, hostility, misunderstanding, mistrust and, most importantly, the evolution of a dual moral code. Morality is largely a willingness to take the interests of others into account when making decisions. The suggestion here is that,

[77] White, L., 1959, *The Evolution of Culture: The Development of Civilization to the Fall of Rome,* McGraw-Hill, New York, p. 80.

within the tribe, attitudes towards others were driven more by amity than enmity whereas this was reversed in dealing with strangers. What is more, such shared enmity towards others would have encouraged further bonding within the tribe.

Taken together with low population densities, territorial boundaries and physical barriers in the landscape, this primal language-driven mentality would frequently have imposed an isolation on individual tribes which was conducive to their further cultural and genetic (via inbreeding) divergence.

Selecting for Language Skills

How the Brain-Language Relationship Evolved

We have already spoken of the way in which the hominid vocal apparatus first evolved to meet a need for improved breath control that came with bipedalism and then further evolved to also meet the needs of prosodic communication and, eventually, of verbal communication. Here, we briefly consider the evolution of the hominid brain over much the same period, viewing it in particular as evolving, first, to coordinate the eye-limb interaction required for complex mimetic behaviour and, second, to both service and enable a growing capacity for facial expressions, speaking and thinking. Taken together, these selective factors probably suffice to explain the brain's rapid increase in size and complexity over the last two million years; brain and language have co-evolved and complexified in tandem. Later we will return to the additional idea that over this period hominid body size was increasing and brain size was therefore also increasing—not just proportionately but, reflecting a phenomenon known as *positive allometry*, more than proportionately.

While there remains much debate over their precise functions, two areas of the human brain are regarded as centrally important to the production and processing of language. One is Broca's area, a portion of the left hemisphere's neocortex adjacent to the mouth-tongue-larynx region of the motor cortex. The other, found adjacent to the auditory cortex, is Wernicke's area. Neither is a distinct anatomical structure although Broca's area in particular is sometimes thought of as a 'bulge'. Both these specialist areas are most simply regarded as developments of pre-existing parts of the brain which have evolved to service, from nearby, the input and output routes associated with language exchange, i.e. Broca's area to service speech production and Wernicke's area to analyse incoming sound. As Deacon points out, there is no reason to expect language processes to map directly onto the structural-functional areas of the cortex, not if it is accepted that the cerebral cortex reassigns existing processing space in accordance with tasks being undertaken.[78]

[78] Deacon, T., 1997, ibid.

The fossil record shows that Broca's area (located in a region concerned since the Miocene with reciprocal gesturing) was already developing in *Australopithecus'* 500 cc brain and Wernicke's area appears in *Homo habilis* (700 cc). It seems that Broca's area was initially a locus for the spinal pathways which permit mimesis and only later developed the cranial pathways which give the very fine motor control that speech requires.

Why a Lateralized Brain?

The hominid brain exhibits 'localisation of function', meaning that, unlike other organs, its different parts do different things; and that not all parts do the same thing. In particular, for the present discussion, left and right cerebral hemispheres perform different functions. This hemispheric specialisation, this 'sidedness', is called *lateralisation*. Thus, much of the speech making-understanding process, along with numerical and logical thought, is controlled from the left hemisphere of the brain (in right-handed people). The right hemisphere is dominant with respect to, amongst other things, perception and expression of emotion, spatial abilities, visual imagery, music and, generally, diffuse and global operations. These are generalisations of course and, in normal people, the two hemispheres do work together, sharing information through a connecting bridge of 200–250 million nerve fibres called the *corpus callosum*, a bridge that would have needed increasing capacity with increasing lateralisation.

Are there suggestions as to why the left hemisphere or, better still, one hemisphere, dominates speech operations? For instance, could the possession of language induce cerebral asymmetry rather than vice versa? Given that the production of speech requires rapid and precise motor switching, any management arrangement requiring the coordination and (relatively slow) exchange of neural information between hemispheres would appear problematic. For this reason, there may have been a selection pressure for unilateral control of the speech function. And, for the same reason, there may have been selection for the speech control area to be close, in terms of path length, to the motor cortex.

An alternative view, from Jaynes (1976), speculates that the development of the language capacities of the left hemisphere occurred very late, and that they were forced into the left hemisphere by a previous specialisation of the right hemisphere.[79] In his proposal the right hemisphere became the storage place of mnemonic and hortatory/admonitory formulae ('the voices of the gods') which served to guide complex behaviours. Others have relatedly proposed that 'automatic' or 'formulaic' speech is located in the right hemisphere while 'propositional' speech is in the left.

Lateralisation is much more pronounced in the hominid than in other vertebrate brains and a more general hypothesis as to the origins of lateralisation is that it saved on the space occupied in non-human brains by symmetrical duplication of behaviour-controlling processes. That is, for the cost of losing the 'back-up' capacity

[79] Jaynes, J., 1976, ibid., p. 106.

of duplicated control, the human brain acquired a major increase in overall cognitive capacity when it evolved towards lateralisation.

Who Gets Selected?

As language moved from non-verbal towards verbal communication, those with a lower-capacity neural bridge between hemispheres may have been able to acquire speech skills more readily, or to speak more rapidly—a 'perverse' consequence of being less able to rely on good inter-hemispheric communication. Or, putting it another way, those anatomically and hormonally predisposed to using a single hemisphere for the task, and, on the evidence, that meant men more than women, had an easier time picking up the skills of spoken language.

Sexual Selection

This leads to the further idea that there may have been some degree of *sexual selection* (also called *assortative* or *non-random mating*) for speech skills, i.e. for males with smaller corpus callosa. Sexual selection is a process in which people get picked as sexual partners on the basis of physical or other traits (e.g. social class) that are preferred within their society or group, often for reasons that have nothing to do with reproductive potential. Jared Diamond gives a salutary example for Europeans of the many ways in which New Guinean men find European women unattractive.[80] In time, no matter how small the dependence of the preferred traits on genotype, this leads to significant genotypic and phenotypic differences between peoples from different societies.

In non-human primates, Small notes a 'Coolidge effect', namely, that females show a sexual preference for males exhibiting novel and various behaviours.[81] In the present case, the hypothesis is that, around 40 kya, just as women had previously picked men as procreative partners based on their (left hemisphere) talents for mimetic song and dance, they now picked men for their skills with the new storytelling tool. Certainly modern males are more laterally committed than modern females.

Just as assortative mating has proven problematic for deer with unwieldy antlers and birds of paradise with enormous tails,[82] it has the potential in humans to select physical traits at the expense of mental and behavioural traits leading, for example, to reduced intelligence.

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[80] Diamond, J., 1977, *Guns, Germs, and Steel: The Fates of Human Societies,* W.W. Norton and Co., New York, Ch. 1.

[81] Small, M., 1993, *Female Choices: Sexual Behavior of Female Primates,* Cornell University Press, New York, p. 183.

[82] An alternative, perhaps complementary, explanation for such over-developed features is that they are allometric by-products of increasing body size (see later discussion of allometry).

Baldwinian Selection

To be clear, no suggestion will be made here that language skills acquired by an individual can be directly transferred to that individual's offspring. There may be a handful of situations where that Lamarckian process operates (e.g. acquired immune responses) but the inheritance of learned behaviours (e.g. habits) is not one. What does seem plausible though, sitting somewhere between pure cultural transmission of new speech skills and traditional Darwinian natural selection for new speech skills, is the possibility that something called, variously, *Baldwinian selection, cultural biofeedback* or *genetic assimilation* is operating.[83]

The defining characteristic of Baldwinian selection is that 'phenotype change precedes genotype change—but not immediately' rather than, as classically presented, 'genotype change precedes phenotype change'. At its simplest, Baldwinian selection occurs when a change in the environment evokes a useful morphological change in certain individuals (morphological plasticity) and, eventually, in later generations, that same change becomes genetically 'fixed' or 'assimilated' within the population, i.e. it appears in most individuals whether or not the original environmental stimulus is present. In the case of learned behaviours (as distinct from other types of phenotypic change), such as inventing novel language skills, we will have a version of Baldwinian selection if, over generations, and as a result of genetic changes to brain or vocal-auditory apparatus, language-learning becomes easier or more innate or happens more reliably under diverse conditions.

While our concern here is with brain-speech coevolution, there is no shortage of respected evolutionary biologists willing to attest to the importance of Baldwinian selection's role throughout the history of multicellular life. Ernst Mayr declared that 'there is little doubt that some of the most important events in the history of life, such as the conquest of land or of the air, were initiated by shifts in behaviour'.[84] It is a process which is likely to be especially important for organisms which, like primates, have a great degree of behavioural plasticity. Notwithstanding, the actual path of evolutionary change will necessarily continue to be constrained at each step by reigning biological limits to that plasticity.

When a new useful behaviour is invented by a few individuals, there are two consequences which, in time, stand to affect what is being inherited in the larger population. One is that the innovators are likely to be more successful reproductively and hence that their genes are likely to become more common in the population's gene pool. To the extent then that above-average learning ability has a heritable genetic basis, the population's learning ability will undoubtedly improve over time, including, amongst other things, the ability to learn the behaviour that first conferred a selective advantage.

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[83] For a useful review, see Pigliucci, M., and Murren, C.J., 2003, Genetic Evolution and a Possible Evolutionary Paradox: Can Macroevolution Sometimes be so Fast as to Pass us by? *Evolution* **57**(7), pp. 1455–1464.

[84] Quoted (p.55) in Lieberman, P., 1984, *The Biology and Evolution of Language*, Harvard University Press, Cambridge, MA.

But the Baldwinian-selection hypothesis goes further than this. It suggests the existence of a process, genetic assimilation, in which the previously learned behaviour eventually becomes genetically embedded, becomes more innate. Suppose that the behaviour learned was the ability to pronounce certain consonants more distinctly. Genetic assimilation would imply that, in time, the ability to pronounce those consonants would not have to be learned but would be present in all members of the population from the time they began speaking. How could this happen? One suggestion is that a widespread genotype which is plastic enough to allow that new behaviour will be 'only a few mutations away' from a genotype which *canalises* or prescribes that particular behaviour. Perhaps, but this is not the place to explore such contested ideas.[85]

Rather, let us turn to *niche construction*,[86] this being a second consequence of individuals learning a useful new behaviour, say, to use the same example, how to pronounce consonants more clearly. Particularly in social groups, where a large part of the total environment comprises interactions between individuals, the introduction of any successful new behaviour changes the environment, the niche, to one where there is now a pressure to select for genotypes adapted to the new environment, e.g. one where clear pronunciation is rewarded. And one adaptation which would be likely (but not certain) to succeed in the newly modified niche would be the very behaviour which redefined the niche. So, while there is no guarantee of subsequent selection for better pronunciation of consonants, to the extent that there may be a tendency for mutations which favour that particular behaviour (as in the genetic assimilation argument), that is an adaptation which will tend to occur.

The idea that learned behaviour can, by altering the selecting environment and/or by altering differential reproductive success, have evolutionary consequences is not contentious. What is contentious is the degree to which that behaviour might eventually become genetically assimilated, i.e. more like an innate 'instinct', a behaviour that does not have to be learned at all, rather than something learned by imitation. In the case of speech, there is debate over whether humans have a genetic capability (genes? hard wiring?) for 'universal grammar' or have a genetically embedded 'language acquisition device'. Majority contemporary opinion would be that both speech and syntax are largely learned skills.[87] We do not need to explore this debate, apart from noting that there are both costs and benefits in terms of survival prospects from replacing learned flexible behaviours with genetic equivalents.

[85] Godfrey-Smith, P., 2003, Between Baldwin Skepticism and Baldwin Boosterism, Ch.3 in Weber, B., and Depew, D., (Eds) *Evolution and Learning: The Baldwin Effect Reconsidered*, MIT Press, Mass. A species' capacity for phenotypic plasticity under environmental change presumably reflects a past accumulation of genetic changes (mutations) which, until then, had been selectively neutral, i.e. neither adaptive nor maladaptive. Several authors have discussed whether the useful capacity to generate selectively neutral variation is itself open to selection, e.g. Conrad, M., 1983, *Adaptability*, Plenum Press, New York.

[86] Odling-Smee, F.J., Laland, K.N., and Feldman, M.W., 2003, *Niche Construction: The Neglected Process in Evolution*, Princeton University Press, Princeton, NJ.

[87] http://en.wikipedia.org/wiki/Language_acquisition (Accessed 23 Nov 2010).

For example, a capacity for flexible behaviour will be more beneficial in a highly variable environment.

Along with the idea from developmental systems thinking that organisms inherit much more than a genome, the idea of Baldwinian selection, irrespective of how prevalent it is, reinforces the idea that the plastic phenotype, the environment, the culture and the genome co-evolve in complex ways; just as, in complex ways, genotype and environment co-determine the development path of the individual organism.[88]

Group Selection

> Now, if some one man in a tribe, more sagacious than the others, invented a new snare or weapon, or other means of attack or defence, the plainest self-interest, without the assistance of much reasoning power, would prompt the other members to imitate him; and all would thus profit. The habitual practice of each new art must likewise in some slight degree strengthen the intellect. If the new invention were an important one, the tribe would increase in number, spread, and supplant other tribes. In a tribe thus rendered more numerous there would always be a rather greater chance of the birth of other superior and inventive members. If such men left children to inherit their mental superiority, the chance of the birth of still more ingenious members would be somewhat better, and in a very small tribe decidedly better (Charles Darwin, 1871).[89]

Between writing *The Origin of Species* in 1859 and *The Descent of Man* in 1871 Darwin's understanding of the process of evolution underwent a profound but unnoticed change. As the above quote reflects, he had come to see group selection, based on the relative fitness of different tribes, to be as important as selection based on the relative fitness of individuals within a breeding group such as a tribe.

Notwithstanding, there were vigorous debates amongst evolutionary biologists through much of the twentieth century as to where in the hierarchical organisation of life—macromolecules, genes, cell lineages, organisms, groups, and structured societies—natural selection had occurred or might occur. Richard Lewontin was one who first made it clear that Darwinian natural selection is a generic process that will occur in any situation where members of a population of reproducing 'development-units' vary from each other in ways which are both (a) reliably passed on to their descendants and (b) disposed to differentially affect their capacity to produce surviving offspring.[90]

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[88] Pigliucci, M., 2005, Evolution of Phenotypic Plasticity: Where are we Going Now? *Trends in Ecology and Evolution,* **20**(9), pp.481–486.

[89] Darwin, C., 1871, *The Descent of Man, and Selection in Relation to Sex* (1st Ed.), John Murray, London, Ch. 5.

[90] Lewontin, R.C., 1970, The Units of Selection, *Annual Reviews of Ecology and Systematics,* **1**, pp. 1–18.

Tested against these criteria, it is now generally accepted, under what Brandon calls *hierarchical* or *expanded evolutionary theory*, that selection occurs at multiple levels, from macromolecules to cultures, in the hierarchy of biological-social organisation.[91] The development-units at each level in the hierarchy are being selected (sorted) by their environment, an environment made up, to a greater or lesser extent, of relatively larger development-units from 'higher' levels of biological-social organisation. In the case of an individual human, think of it this way: her fitness is a function of her adaptation to her environment *and* the adaptation of her environment to its environment

Again, a 'gene-environment' interaction occurs between DNA and the local cellular machinery. Genetic variants are sorted through a process of differential birth rates and death rates which are a function of organism-environment interactions, i.e. genetic variants are selected in the context of the cellular environment. The persistence, or continued replication, of lower level development-units is crucially dependent on the maintenance of the organised unit interfacing with the habitat.

The hierarchical perspective emphasises that the results of natural selection are not 'traits' in the usual sense of static features possessed by an organism, but relational linkages between organism and environment. Moreover, these relations are specific to the situation in which they occur. For example, there is no basis for assuming, as the trait view does, that an individual who may be socially dominant in a pairwise relationship will also be socially dominant in a group of five people working on a shared problem.

As earlier noted, moving from non-verbal to spoken language probably accelerated each tribe's accumulation of pooled knowledge and the creating of a shared way of understanding the world, as well as improving individual cognitive skills.[92] It is through speech that pooled knowledge and common mental models can be reliably transmitted between generations. Meeting that condition would have set the stage for the selection process to move towards favouring fast-learning tribes as well as fast-learning individuals within tribes. Under conditions of limited resources, a tribe of intelligently cooperating individuals stood to outgrow and displace tribes less competent.

Humans of the Late Glacial to Early Post-glacial Period

After the Mt Toba Eruption

The last ice age was a close call for humanity. Greenland ice cores confirm that 71 kya Mt Toba in Sumatra erupted with more force than almost any previous volcano, producing enough sulphurous gas and ash to darken the sky for 6 years. Temperatures plummeted by as much as 21° at higher latitudes around the planet

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[91] Brandon, R., 1990, *Adaptation and Environment,* Princeton University Press, Princeton.

[92] Berger, P., and Luckmann, T., 1966, ibid*.,* p. 68.

and, in the northern hemisphere, up to three quarters of all plants may have died. The following millennium was the coldest of the last ice age.

A number of scientists believe that this volcanic winter could have reduced the world's population of modern humans, those who had been spreading from Africa for some 30,000 years, to less than 10,000 adults.[93] It follows that all of today's humans would be descendants of those few, specifically, according to one hypothesis, those of the few who survived in (north east?) Africa. If all modern humans come from such a small and recent founder-group, it would explain why everyone today has very similar DNA despite humanity's two million year evolutionary history, i.e. there has not been time for mutations, etc., to accumulate differentially.

This is not the place to review competing models of the origins of modern human beings, but an interesting alternative hypothesis is that a handful of small isolated groups across Eurasia and Africa survived Toba and while all of these started out genetically similar, they were isolated from each other and their genomes diverged rapidly enough to produce the superficial differences in appearance of today's major population groupings, e.g. Mongoloid, Negroid and Caucasoid.[94]

Notwithstanding, within perhaps 20,000 years of Toba, humans, spreading at a rate of just a few kilometres a year, had reached and settled in Australia. This epic movement, if indeed it was out of Africa and not from further west, could have followed the Indian coastline and thence to Timor. The presumption here is that hunter-gatherer tribes kept splitting and moving on as they grew too numerous to be sustained locally. The Aborigines' final hop to Australia was helped by a period of rapid glaciation which briefly dropped sea levels by 80 m and reduced the sea gap between Timor and Australia from 480 km to a more navigable 160 km.

It is not widely appreciated just how variable climatic regimes were in the late Pleistocene. While always an ice age, conditions could warm dramatically within as little as a decade and then cool equally quickly.[95] These changes appear to have been linked to the incursion and retreat of warm currents in the North Atlantic in response to the release of fresh water lakes from behind slipping glacial barriers. As noted, glaciation reached its peak (called 'the last glacial maximum') about 18 kya and was largely over by 15 kya, although climates continued to fluctuate markedly till about 10 kya. Modern humans reached the Americas about 15 kya and New Zealand about 800 years ago. It was another drop in sea level, one associated with this final glaciation, which made the Americas accessible from Eurasia, via a dried-out Bering Strait.[96]

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[93] Ambrose, S.H., 1998, Late Pleistocene Human Population Bottlenecks, Volcanic Winter, and Differentiation of Modern Humans, *Journal of Human Evolution,* **34** (6), pp.623–651.

[94] Ambrose, S.H., 1998, ibid. This is what sometimes happens with invading species that spread rapidly across a new environment. They differentiate into observably dissimilar ecotypes. The arrival of sparrows in North America provides an example.

[95] Burroughs, W.J., 2001, *Climate Change*, Cambridge University Press, Cambridge.

[96] A contrary view, backed by some evidence, is that the Americas could have been settled by seafarers much earlier. See Burroughs, W.J., 2001, ibid., pp.207–217.

For post-Toba humans who remained in tropical Africa, the ecological niche they could exploit in a very tight web of life was small; energy was hard to capture, and sharp increases in numbers were not possible. However, as people began spreading into colder dryer regions, supported by the twin technologies of fire and (probably) clothing, they left their tropical parasites behind and found new energy sources in unexploited populations of large game animals. Together, these factors (plus better tools?) led to a population release (a boom) such that there were perhaps four million people worldwide by 15 kya.[97]

Over this period, the cultural norms (how to behave) required for successful living were transmitted between generations by imitation and word of mouth. While there would have been a degree of selection and novelty in what was passed on, most would have been handed down unchanged. Neither agriculture nor the herding of domestic animals was yet practised. Social organisation within tribes was minimal, i.e. there were few status differences and everyone did much the same work. In terms of material technology, the major advance between 70 and 40 kya was a series of improvements in stone tools, particularly flaking techniques. For example, the length of cutting edge obtainable from a source rock improved perhaps 10–12 fold over this period. At one stage, the most advanced techniques were to be found in Australia and New Guinea.

New Behaviours

From the archaeological record, it seems that a cultural shift, one significant enough to be designated the Upper Palaeolithic revolution, began about 40 kya.[98] That is, it began in step with the beginning of an intensely cold glacial period that would last till 15 kya and end the Pleistocene. This was the time when artefacts such as cave paintings and carved figurines first appeared, particularly in a European core area, and in a variety of forms which can be clearly differentiated as to time periods, regions and groups (including contributions from our soon-to-disappear Neanderthal cousins).[99]

Material Technologies

Technological changes during this tail end of the Pleistocene include the disappearance of heavy tools such as hand axes and choppers (in favour of longer, narrower 'blade' tools) and the introduction of a much wider range of special purpose tools

[97] McNeill, W.H.,1979, *Plagues and People*, Penguin, London.

[98] The Upper Palaeolithic, meaning the last part of the 'old' is best regarded as a time period, one lasting from c.40 kya till c.12 kya.

[99] Childe, G., 1936/1981, *Man Makes Himself*, Moonraker Press, Bradford-on-Avon, England, p. 51.

(e.g. harpoons, darts, needles), including, for the first time, many made from antler, bone and ivory. The new tools and fabrication technologies suggest a major change in patterns of human energy expenditure, with tools being prepared in advance and retained, rather than made and discarded expediently. Simple mechanical devices such as the spear thrower and the bow appeared and allowed muscular energy to be concentrated when despatching projectiles. Composite tools appeared, e.g. spears with stone points. More energy was also going into the construction of semi-permanent structures such as hearths, pavements and shelters (some partly underground) built of skins on a frame of bone or wood; evidence perhaps of a more settled lifestyle.

Survival continued to depend on hunting and gathering although the role of plant foods is difficult to determine. Despite the intense cold, Europe was a food-rich environment for well-equipped groups of cooperating hunters. Vast migrating herds of reindeer, bison, mammoth and wild horse grazed the plains of Russia and central Europe.

There is also evidence for the increasing use of other foods, such as rabbit, fish and shellfish. In comparison with large animals, these produced smaller amounts of food, but they were an important addition because of their greater reliability. What appear to be hunting nets have been documented in central Europe. In fact, there is conclusive evidence that products based on plant fibre—cordage, basketry, netting and perhaps textiles—were being produced in central Europe more than 25 kya and, soon after, elsewhere in Europe, the Near East, and the Far East. While tool remains are more durable, fibre technologies may have been just as important for survival. In terms of an implicit energy strategy, effort invested in making fibre products reduced subsequent energy expenditures or allowed human energy to achieve results (e.g. catching fish) which would not otherwise have been possible.

Symbolism and Representation

Representational art in the form of painting, sculpture and engraving has been widely documented at Upper Palaeolithic sites in Africa and Australia as well as Europe. Animals and humans are common subjects as well as abstract lines, dots, chevrons, etc. Around the world, people used similar natural materials such as red and yellow ochre, manganese and charcoal to create cave art. The earliest known musical instruments also come from the Upper Palaeolithic. Flutes made from long bones and whistles made from deer feet have been found at a number of sites. Deliberate and careful human burial becomes more common, often with graves containing tools and personal ornaments such as bracelets, beads, pendants made of animal teeth, ivory, shells, etc.

Trade and Migration

Through much of the Upper Palaeolithic, waves of modern humans were comprehensively colonising Eurasia and Australia, gradually replacing, one assumes, any residual populations of non-modern peoples. The details are being increasingly revealed by analyses of DNA similarities and differences amongst contemporary human populations.

Evidence of similarities in artistic styles over extended distances (e.g. podgy 'Venus' figurines) suggests that extensive social networks operated throughout Upper Palaeolithic Europe. Some materials, such as flint, semi-precious stones and shells were moved over hundreds of kilometres. Whether such movements can be interpreted as trade over trade routes is another question (a motive of 'gain from trade' seems unlikely). And to what extent did these interactions facilitate people exchanges and interbreeding between tribes, exchange of information about frontier environments and new technologies, collaborative hunting and ceremonial gatherings?

Aggression Between Groups

Conversely, did interactions between tribal groups become more violent and aggressive during the Upper Palaeolithic, particularly as glaciers advanced and reduced the land's carrying capacity (numbers of people who could be fed) during the last glacial maximum (20–15 kya)? Despite a lack of evidence, there is indeed a popular school of thought (in the writings of Robert Ardrey and Desmond Morris for example) that tribal groups of the Upper Palaeolithic and well before, had a predisposition to attack, for little or no reason, any other groups they encountered.[100] Indeed, it is often part of this perspective to suggest that, for a large part of the Pleistocene, groups were being selected for intelligence on the primary grounds that this enhanced their ability to kill other humans. Steven LeBlanc argues that lethal inter-group violence and dispossession was a commonplace response to overpopulation and hunger caused by runs of poor seasons.[101]

Such thinking has complex sources, one being the idea that things *ought* to be like that on a simple interpretation of Darwin's thinking. But there are many forms of competition besides killing. What about selection for intelligence on the primary grounds that it improves intra-group cooperation and synergy? Another source idea for the 'killer ape' hypothesis is that there are species of primates alive today which are highly aggressive (e.g. savanna baboons) and, since humans are primates, they must be intrinsically aggressive. The problem with that argument is that there are other primate groups (e.g. Bonobo chimpanzees) which exhibit little externally directed aggression. Analogical arguments across primate groups are generally unconvincing.

Perhaps a better argument is that, as noted above, early savanna-dwelling hominids began acquiring the hormone balance of a predator species as distinct from a prey species. Of course, aggression towards prey species does not auto-

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[100] Ardrey, R., 1966, *The Territorial Imperative: A Personal Inquiry into the Animal Origins of Property and Nations*, Atheneum, New York; Morris, D., 1967, *The Naked Ape: A Zoologist's Study of the Human Animal*, Cape, London; Burnet, M., 1970, *Dominant Mammal: The Biology of Human Destiny*, Heinemann, Melbourne, p. 72.

[101] Le Blanc, S., with Register, K. 2003, *Constant Battles: The Myth of the Peaceful, Noble Savage*, St Martin's Press. London.

matically translate into aggression within and between conspecific (same species) groups. And it has been further suggested, under the name of *shift theory*, that in selecting males for language skills, they were also being selected for higher testosterone (the 'male' hormone) levels and hence, eventually, for levels of male aggressiveness more compatible with a patriarchal than a matriarchal style of social organisation.[102]

Even though inconclusive, and especially if free of ideological prejudices (e.g. social Darwinism), such speculations remain important, given our need to understand the prevalence of violent conflict in today's world. To anticipate later discussion, a reasonable working hypothesis is that human groups, then and now, have/had inherent tendencies towards both amity (within the group) and enmity (between groups) and that the expression of these tendencies depends in complex ways on how the young are socialised and how stressful and difficult it is proving for a group of interest to obtain the resources it needs.[103] We need to keep remembering that behaviour is a function of nature, nurture and environment.

Social Organisation and Regulation

It has already been suggested, based largely on relative (male versus female) body size, that dominance hierarchies within groups were minimal in earlier *Homo sapiens* and there is no reason to suggest otherwise for the Upper Palaeolithic. Nor is there any hard evidence from this period that tribes were moving from a clan or collective mode of decision-making to a hierarchical or chief/leader mode of decision-making. Nonetheless, this is what happened.

Karl Polanyi, in his revelatory book, *The Great Transformation*, argues convincingly that late Pleistocene economies were based on *reciprocity* and *sharing* and that this mode of economic organisation came to influence (coevolved with?) many other aspects of social organisation, including the shared ideas which reinforced that system.[104] Thus, the suggestion is that Upper Palaeolithic humans never hunted or gathered food for just themselves or their immediate family but rather for sharing with the whole clan or tribe. This is not a new idea, or a new behaviour, it should be pointed out. Palaeontologists, including Isaac Glynn, have traced food-sharing behaviour back to the beginning of the Pleistocene.[105]

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[102] Lehmann, A., 2001, Exploring Patterns in Neuropsychology for Support for an Alternative Theory of Evolution, *Glozel Newsletter 6.5*, pp. 1–90

[103] Le Blanc, S., with Register, K., 2003, ibid.

[104] Polanyi, K., 1944/2001, The Great Transformation: The Political and Economic Origins of our Time, Beacon Press, Boston.

[105] Glynn, I., 1978, The Food-sharing Behavior of Protohuman Hominids. *Scientific American*, **238**, pp. 90–108.

Continuing the important example of food, *reciprocation* implies that when one tribal member gave food to another, they would expect something of equal worth in return, either from the recipient or someone else. So, if I give you food, you will give me equivalent food or will help with some task, etc. I might not get something back immediately, but the recipient has to reciprocate within a certain time or lose standing. An ongoing failure to reciprocate could lead to exclusion or expulsion. As an aside, a broader concept of reciprocation, one between humans and the forces of Nature, may lie behind the practice of sacrifice at a later stage in human history.

The ongoing success of such a system relies in the first instance on each individual being willing to contribute to the 'economy' according to their capabilities and trusting others to do likewise. This in turn requires that the young be so socialised. And, to reinforce such learned behaviours, there would be a place for sanctions (exclusion, shaming) against 'free riders' and cheats, and, perhaps, a place for external (cf. internal) rewards for above-average contributions. On the latter, for example, successful hunters might be preferred mates. Perhaps also, as Polanyi suggests, rituals and ceremonies evolved, partly at least, to ensure that reciprocation went smoothly.

The economic cum social system being described here is remarkably complex, involving as it does behaviours such as trust, sexual selection, socialisation, delayed reciprocity, sanctions, rewards, etc. But are such enough? Could such a system function without well-developed language? Mention has already been made of the hypothesis that language evolved to replace grooming as a bonding device in larger groups; and as a tool for 'social bookkeeping'. Paul Mellars is an archaeologist who, judging from technology shifts and the appearance of imagery as well as beads and pendants, suggests that fully modern language and symbolic expressions emerged at or slightly prior to the Upper Palaeolithic.[106] The way to view the role of language in the Upper Palaeolithic revolution might be as one of allowing, even accelerating, useful complexifications within a pre-existing but simpler economic system. That is, language improves decision-making today at the price of complicating decision-making tomorrow.

From Tribes to Chiefdoms

Except in extreme circumstances where only a few can survive, a tribal system based on self-organised reciprocity and sharing within the tribe would seem to be a sound strategy for smoothing out unpredictable food supplies and maximising group survival prospects. The process may well have been further routinised by following ritualistic procedures. And yet it is widely accepted that, by the end of the ice age, hierarchical governance systems centred on a tribal chief or leader with some degree of coercive power had been invented and become commonplace.

[106] Mellars, P., 1996, Symbolism, Language, and the Neanderthal Mind, In Mellars P., and Gibson, K., (Eds.), *Modelling the Early Human Mind.*, McDonald Inst. Archaeol. Res., Cambridge, UK, pp. 15–32.

Was this just a natural development of an established primate instinct to accept dominance-submission relationships? How else might this change in decision-making processes have occurred? As an example, think of deciding when and where to hunt. In long-established bands and small tribes, custom and tradition might simply dictate the answer. Everyone would just know what the group was going to do. Under unseasonable or other unusual conditions, and with the help of verbal language, the question might be discussed till consensus emerged. Given a strong similarity in the vocabulary, concepts and inbuilt behaviour rules understood by each individual, the perceived options might be few and consensus readily achievable. However, there could perhaps be a place for a 'chairperson' to articulate, nothing more, that consensus had been reached. And, in particularly unusual circumstances, the long memories of tribal elders might contain candidate options not familiar to younger people.

Under even more difficult and pressing conditions, during, say, emigration into new territory, the 'chairperson' might have to choose, hastily, amongst whatever options are being perceived and, in doing so, become a *leader* for a time. Or, different leaders might emerge in different situations. Still, we can only speculate about governance processes in the Upper Palaeolithic, and be informed but not blinkered by observations on contemporary hunter-gatherer societies.

So, speculating further, another area of tribal life where, on occasions, it could be useful to have non-consensus but rapid decision-making is daily food distribution. A need for some degree of task specialisation (division of labour) is beginning to appear in the Upper Palaeolithic, along with activities such as art and music and the use of new food sources. Reciprocation is quite transparent when all contributions are of the same type; symmetrical exchanges within small groups of families might suffice. But, on the (major) assumption that exchanges have to be seen as 'fair', how do you equate contributions which demand the same effort but yield different results? There is no right answer, but, so the hypothesis goes, people might accept the judgements of a leader who is trusted and recognised as trying to be fair. This in turn might lead to acceptance of pooling and redistribution of all the day's acquisitions. If the leader's redistributions came to be seen as unfair or self-serving, he or she would be simply replaced.

This idyllic system was not to last. Some time before recorded history began, leaders were becoming, to use William McNeill's word, macroparasites; tribes were becoming chiefdoms. Relying, perhaps, on religious authority, or enforcers, 'permanent' chiefs, often hereditary, were learning to make decisions reflecting a degree of self-interest as well as keeping their increasingly complex societies functioning. This was the solution which evolved from an increasingly unworkable system based on reciprocation, sharing and trust. Perhaps the value of an aggressive chief able to lead the defence of a home territory against refugee groups or covetous neighbours outweighed any loss of trust and fairness. Having a social technology for selecting a leader would certainly have been conducive to social stability at times of leadership transition. More generally, possibilities for innovative behaviour may have been greater without the inertia of group thinking; the individual mind is a better problem-solving tool than the group mind. And, once chiefdoms were established, perhaps people did not have the cognitive skills to be able to question this new system of governance.

New Minds

The Upper Palaeolithic revolution probably saw the transformation of human minds as well as human behaviours. Indeed it is that revolution's marked changes in economic and social behaviour and in material and social technologies which first suggest the arrival of new ways of thinking and new things to think about. For example, a cultural artefact such as a necklace suggests a capacity to think symbolically. Perhaps it is better to think of the Upper Palaeolithic revolution as a time of change in humanity's underlying capacity to form and use culture rather than simply as a time of rapid cultural change.

Turning from the material record to speculation, what might have initiated the Upper Palaeolithic revolution and what can be inferred about the developing mentality of Upper Palaeolithic people? Assuming that language was already reasonably well-developed (and some would disagree), the simplest suggestion here is that as the scope, vocabulary and fluency of language increased, as described earlier, there was an even faster expansion (positive feedback) in each tribe's pool of technological knowledge and their common set of meanings, explanations and beliefs about the world.

Perhaps there were genetic and neuroanatomical changes as well as language-driven cultural changes, for example a mutation which markedly increased language capabilities. Or mutations which allowed information from different parts of the brain to be coordinated rather than processed in relative isolation. There may well have been such changes but, if they occurred, it was likely to have been much earlier, perhaps 150 kya when modern humans are thought to have evolved from archaic humans.[107] It is commonly believed that there has been little change in brain anatomy since then. What cannot be revealed by the fossils on which such thinking is based are changes in organisation (pathways, etc.) within the brain.

Primitive Thinking

We can only infer the characteristics of primitive minds from ethnographic studies of contemporary hunter-gatherers, from studying the developing minds of children and from some limited archaeological evidence. Even then, questions abound. Would a person from the late ice age, say 20 kya, be able to understand and answer a question as to whether they had a spiritual sense of feeling at home in their environment? Or who they were? Or which tribe they belonged to? Or why they had behaved so in some what-to-do situation? By 'what-to-do' situations I mean situations of hesitancy or doubt or stress where none of habit, tradition, custom, instinct, emotion, etc., dictates automatically how to behave; in general, problems that have not as yet been routinised. Indeed, did anyone ask any questions then? Were they

[107] Mayr, E., 2001, *What Evolution Is,* Basic Books, New York, p. 252.

conscious in the same way as readers of this book are conscious? The answer to the last is almost certainly No, but we will come to that.

Still, despite the ignorance and uncertainty, there is a measure of agreement amongst paleo-anthropologists as to what post-speech minds may have been like prior to, and, probably, for a while after, the Neolithic Revolution (see page 149). We will discuss this mainstream view under the headings of (a) animism and magic and (b) cognitive and representational skills.

Animism and Magic

It was suggested earlier that, under a broad rendering of their motivations, humans and their ancestors have drives (generalised instincts) for autonomy (self-assertion), for bonding with others and for meaning, the last being an urge to explain things. *Animism* is the belief system widely held to have been at the heart of the primitive or pre-critical mode of thinking and imposing meaning on the world which emerged in parallel with the emergence of spoken language. In animism, the behaviour of natural phenomena, both living and non-living, is explained by assigning (all) objects (including places) and processes a human-like agency, a *spirit*, with a capacity to act intentionally. To take an important example, this means that dead people are still alive in some sense. That might further mean, for instance, that one leaves food out for corpses or that the dead can still speak.

Furthermore, in many of the world's contemporary hunter-gatherer populations, and perhaps in the most recent ice age, a common extension of animistic thinking is the idea that the world is further populated with invisible spirits, 'ancestors' perhaps, which are not attached to particular real objects and processes. Other elaborations of animistic thinking include 'essences' such as souls and 'real' objects which are only visible to certain people.

It is challenging to even speculate as to the origins of animism but one suggestion is that it is an unsurprising product (as indeed is the drive for bonding with other humans) of the sort of *symbiotic consciousness* (to use Arthur Koestler's term) or *participatory consciousness* (to use Jay Earley's term) which early Upper Palaeolithic humans enjoyed.[108] It is hypothesised that this form of consciousness involved people having feelings of being connected to and belonging, metaphorically, to the world around them. More prosaically, it can be suggested that people had not yet learned to distinguish between external objects and events and the mental images representing them. Given that these people would hardly have been able to express (inadequate vocabulary) or see introspectively that they were having such feelings (if they were!), consciousness seems too grand a term here, except

[108] Earley, J., 1997, Transforming Human Culture: Social Evolution and the Planetary Crisis, SUNY Press, Albany; Koestler, A., 1970, *The Ghost in the Machine,* Pan Books, London, p. 277.

perhaps that it flags a contrast with the sort of reflective self-aware consciousness that emerged after the advent of civilisation. While we cannot step outside our own consciousness and imagine symbiotic 'consciousness', perhaps it was like being in a vivid dream where things just happen (no sense of causal process) and one responds reflexively.

Magic goes hand in hand with animism and is the idea that the behaviour of the 'spirit people' in things and processes can be influenced advantageously by appropriate human activity; for example, that the weather can be influenced through symbolic activities and rituals such as rain dances. A *shaman* is someone with developed magical skills.

Early anthropologists, such as James Frazer of 'Golden Bough' fame, described magical thinking in terms of two 'associative laws', contagion and similarity.[109] The *law of contagion* is summed up by the idea that when objects come into contact, there is a permanent exchange of properties between them and they remain causally connected thereafter. For example, contact with an object considered to be impure will transmit the impurity to the handler, who cannot be rid of it without recourse to purification rituals. The *law of similarity* is based on the notion that 'image equals object' or, more generally, that similar things are causally connected. Operations on one are automatically (magically) carried out on the other. For example, when a 20,000-year-old Cro-Magnon cave painting shows a spear in a bison, some real bison was being supposed to have a similar experience in store. Rituals are behaviours which imitate some aspect of the desired result, e.g. sprinkling water on the ground during a rain dance.

Words are treated in the same way as images and rituals. Once the percept has been formed, every time a swan (say) appears, the word 'swan' also reliably appears. It is a small step from there to believing that the name of an object is part of the object, a belief behind many magic rituals, taboos, etc.

Before smiling, take note of the survival of these two principles of magical thinking into modern times, for example when demonstrators hang or burn public figures in effigy. Also, to the extent that it is introducing an associative sense of cause and effect, magical thinking is the precursor of scientific thinking. And painted images may have been precursors to writing. Here is Ashley Montagu's sympathetic perspective on magical thinking:

> The trouble with the non-literate is not that he isn't logical, but that he applies logic too often, many times on the basis of insufficient premises. He generally assumes that events which are associated together are causally connected. But this is a fallacy which the majority of civilized people commit most of the time, and it has been known to happen among trained scientists! Non-literates tend to adhere too rigidly to the rule of association as causation, but most of the time it works, and by the pragmatic rule what works is taken to be true.[110]

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[109] Frazer, J.G., 1922, *The Golden Bough*, Abridged Edition, Macmillan, New York.

[110] Montagu, A., 1957, *Man: His First Million Years*, World Publishing Company, New York.

Cognitive and Representational Abilities

First, it bears repeating that hypotheses about the minds of Upper Palaeolithic people rely heavily on backcasting from ethnographic studies of remnant hunter-gatherer populations. Having said that, let us speculate boldly.

What is most surprising to present-day people about the minds of early hunter-gatherers, as hypothesised, is not their animistic-magical models of reality but the extreme resistance and insensitivity of these 'pre-critical' minds to the data of experience. To moderns, pre-critical thinking is inconceivably conservative and closed. Not only is there no capacity to question beliefs, rules, customs, etc., there may not even have been a capacity to formulate any questions, given that asking a question implies the possibility of alternative answers. Obvious facts which, in our opinion, would, ineluctably force someone to reconsider certain convictions do not, for some reason, have any effect on them at all.

While it is not an explanation, it helps to recognise that the pre-critical mind made no distinction between belief and knowledge. Or perhaps not helpful: Bertrand Russell in *Analysis of the Mind*[111] says that, at first sight, knowledge might be defined as belief which is in agreement with the facts. And then says, 'The trouble is that no one knows what a belief is, no one knows what a fact is, and no one knows what sort of agreement between them would make a belief true'.[112] Notwithstanding, for pre-critical minds, animism and magic constituted a knowledge system, not a belief system.

Valentin Turchin provides a further insight into pre-critical thinking by contrasting it with *critical thinking*, a capacity which he sees as only beginning to emerge in the irrigation civilisations of the Middle East some 6,000 years ago.[113] Critical thinking allows alternative verbal models of problem-solving behaviour or explanations of reality to be compared and for just one of these to be adopted as a working model. In logic, this selecting of the particular explanation which is better than its rivals is called the *law of sufficient grounds*. The law of sufficient grounds is absolutely foreign to pre-critical thinking. It is here that the 'metasystem transition' which separates modern thinking from primitive thinking is seen most clearly. Turchin locates this transition from the uncritical brain to the *choosing brain* in the emergence of linguistic activity directed to linguistic activity, i.e. in thinking about thinking. Thus, it is not enough to think about something: one must also ask why one thinks that way, whether there is an alternative line of thought, and what would be the consequences of these particular thoughts. If a chosen action does not work, one asks why not.

Because pre-critical thinking cannot reject a belief once formed and stands to generate multiple animistic explanations for any situation and, also, because it

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[111] Russell, B., 1921, *Analysis of the Mind*, Allen & Unwin, London.

[112] Russell then relents enough to say that, speaking broadly, it is our 'verbal habits' which crystallise our beliefs, and afford the most convenient way of making them explicit.

[113] Turchin, V., 1977, *Phenomenon of Science,* Columbia University Press, New York, Ch. 8.

cannot organise or integrate these multifarious beliefs, pre-critical thinking is riddled with contradictions and misperceptions. Not to put too fine a point on it, pre-critical thinking would appear to be next to useless for yielding rational (i.e. likely to succeed and likely to improve things) responses to novel what-to-do situations. Despite their cultural developments and their practical achievements, Upper Palaeolithic people would still have been reliant on instinctual responses and random exploratory behaviour in what-to-do emergencies not envisaged by custom and tradition. Thinking was not a tool for solving problems at this time.

Representational Abilities

> I remain, therefore, entirely unconvinced that there is any such phenomenon as thinking which consists neither of images nor of words, or that 'ideas' have to be added to sensations and images as part of the material out of which mental phenomena are built (Bertrand Russell, *The Analysis of Mind*, Ch 11).

We can suppose that over the long Pleistocene humans developed an increasing capacity to mentally reproduce (imagine) visual and auditory perceptions that had been stored in memory. Without (imagined) images, there can be no awareness of past or future, only a fleeting present filled by impressions, emotions and bodily impulses (e.g. defecation). There can be no differentiation of inside and outside; no awareness of a boundary between self and other; and no different categories for internal experience versus perceptions of external objects and events. A sense of time is not possible if past perceptions cannot be retained in the mind and then invoked.

We can also suppose that this process of forming stable cognitive categories would have been much enhanced with the emergence of language, both non-verbal and verbal. This is because the scope (what is to be included) of a percept associated with a 'fixed' linguistic symbol could be cumulatively refined over time. The 'symbiotic' external world would increasingly have been categorised into discrete parts by cerebration, by a process of 'carving nature at the joints' in search of practical distinctions.

Notwithstanding, people's repertoires of verbal representations (likenesses) of persons, relationships, social systems, mortality, the self and many other less-concrete concepts familiar to contemporary humans would have been small. Another way of saying this is that those ancestors did not yet have a vocabulary which would allow them to think about these things; a characterisation that depends on the idea that a large part of what we call *thinking* is talking to oneself (perhaps out loud in those days?). Sometimes the conversation is one-sided, sometimes not. *Thoughts* are the separate sentences in that conversation.

The more general suggestion to be made here is that cognitive and representational achievements would have advanced arm in arm through the Upper Palaeolithic. You can't think about thinking if there are no words for thoughts, memories, questions, etc. A tribe's vocabulary and shared verbal habits was its collective model of reality, changing but slowly over many generations, e.g. words changing meaning, beliefs falling into disuse (as distinct from being rejected).

Consider, for example, how the very useful concept of *oneself* might have evolved. Once language had developed to the point where individuals were given names, the stage would have been set for people to be able to learn to represent themselves mentally and verbally, to develop an inner working model of oneself, a self-sense. Drawing on Thomas Jordan's speculations,[114] something of what this might possibly have meant initially can be suggested, namely, an ability to describe one's own behaviour in the third person, although largely in bodily rather than mental terms. The capacity to recognise that one is having thoughts and that these are an important part of oneself (and ditto for other people) would come much later. This elaboration of the sense of self is called *individuation*, the term being the same whether it is taking place over an individual life or over hundreds of generations.[115]

We will return to the evolution of critical and conceptual thinking when we come, presently, to the next great revolution after the Upper Palaeolithic, namely, the post-glacial Neolithic Revolution.

Dependence of the Individual on the Group

Notwithstanding the emergence of language and, later, of chiefdoms as means of social coordination in hunter-gatherer societies, it seems likely that Upper Palaeolithic tribes functioned like super-organisms, made up of people with a very weak sense of self; not as collections of individuals well aware of their bodily and mental differences from others. In *The Gutenberg Galaxy*, Marshall McLuhan suggests that tribal people learn to regard themselves as rather insignificant parts of a much larger group and not as independent, self-reliant entities.[116] Personal ambition and initiative are permitted little outlet and a meaningful integration of experience along personal individualistic lines is never achieved. Indeed, the very possibility of 'thinking for oneself' is scarcely even acknowledged; and, if it does occur, it is shunned, not only by others but by the thinker himself or herself. In contrast to this intellectual constriction, tribal society allows the individual considerable temperamental freedom—to be extroverted and express one's feelings freely.

As noted above, people then would have had little capacity to model consequences and choose, neither consciously nor unconsciously, between alternative behavioural options in what-to-do situations. But would that evaluative skill have been needed anyway? In a reasonably stable environment, habit, custom and tradition based on past learning would have adequately guided behaviour much of the time. And in a few recurring classes of emergency situations, instinctual and spontaneous group responses, guided by rapid communication of emotional states

[114] Turchin, V., 1977, ibid.

[115] Fromm, E., 1942, *Fear of Freedom,* Routledge and Kegan Paul, London, pp. 23–25.

[116] McLuhan, M., 1962, *The Gutenberg Galaxy: The Making of Typographic Man,* University of Toronto Press, Toronto, p. 18.

(anxiety, fear) would have been triggered. Imitating the behaviour of a recognised chief, and obeying his or her verbal commands, would have further served to synchronise and co-ordinate individual behaviours. Because role differentiation was minimal (male hunters, female gatherers, the old and the young), there would have been little need for unique individual responses.

In fact, it goes further than that. In the harsh conditions at the end of the ice age, many tribes would frequently have been on the brink of extinction. Under those circumstances, any innovative deviation from inculcated 'proven' behaviours would have carried high risks. Perhaps, until conditions improved as the ice age ended, there could even have been selection against cognitive skills!

Implications of a Weak Sense of Self

Tribal people would have had physical and stage-of-life differences from each other of course, but mentally, it is being suggested, they would have had few differences and little awareness of how they differed from others—what has been called the membership mind.[117] They probably had short time-horizons, a poorly developed sense of past and future which, if so, would have made it difficult for an individual to undertake sustained tasks (e.g. travelling to a distant hunting ground) for which the rewards were not immediate; they would have been unable to envisage an extended sequence of activities and consequences leading to a goal. Here, perhaps, lies the origin of group rituals which use rhythmic, coordinated, invariant, mimetic movements which reinforce the emotional appeal to the individual of the task or wish being pursued, e.g. singing and chanting. Indeed, ritual, and imitative behaviour in general has to be recognised as a social coordination mechanism, along with drives-instincts, shared emotion, tradition, custom and verbal commands.

We might also note that having short time horizons and a weak self-sense would make it difficult for individuals to play and sustain specific roles within the tribe. Even chiefs might have needed group support on occasions.

Another implication of weak self-sense is that impulsive, emotional behaviour stands to swamp the individual's fragile, tentative attempts to act intentionally to satisfy his or her vague wishes. To control antisocial behaviour, the tribe would have had to rely on individuals conforming to custom and obeying taboos (avoiding forbidden behaviours).

Conscience (internalised social rules) and guilt about breaking rules would not have, as yet, appeared.[118] Morality would have consisted in 'not getting caught'. Conversely, active deceit of others would have been minimal prior to people having an awareness of how their own minds functioned. Without such awareness a deceiver would have no basis for modelling and then exploiting another's behaviour. What is

[117] Wilber, K., 1996, *Up From Eden: A Transpersonal View of Human Evolution,* The Theosophical Publishing House, Wheaton, p. 270.

[118] Berger, P., and Luckmann, T., 1966, ibid.

that person thinking about me? Once established though, a capacity to deceive would have been much facilitated by language. Especially amongst people who had little capacity to critically evaluate linguistic statements, lies about others would be readily believed.

Reflections on Hominid Evolution

This chapter is yet another version of the story of how the human lineage and human social groups might have evolved. And, like all stories, it has a provenance, foci, in-built constraints and a purpose. The very word 'lineage' signals that this is a story which assumes that humans and prehumans and their social groups have been changing in significant ways even as they have been surviving for millions of years.

Thus the chapter takes up the story of hominid evolution with the evolution of placental mammals (125 Mya) into primates (65 Mya) who took to the trees to live during the Eocene (55–38 Mya). There, in east Africa, they stayed until the branch[119] of the great ape family from which humans evolved moved from their declining gallery-forest habitat to an open forest (savanna) habitat (5 Mya). Perhaps 3 Mya the first 'species' of the *Homo* genus (*Homo habilis*) became identifiable; and, by 2 Mya, as the Pleistocene epoch and its ice ages approached, *Homo erectus* had not only evolved from *H. habilis*, but was on the brink of migrating out of Africa into distant parts of Eurasia. It was from the erectines who remained in Africa that archaic forms of *H. sapiens* evolved circa 200,000 years ago. And it was perhaps a 100,000 years ago that groups of modern *H. sapiens* began moving out of Africa *en route* to settling the whole world, displacing any remnant erectine populations in the process. The chapter takes the story to the end of the last ice age (15 kya) and into the period just before the Neolithic Revolution (12 kya) when some humans stopped being full-time hunter-gatherers and began growing crops and domesticating herd animals.

It has been necessary, for space reasons, to keep the chapter as short as possible consistent with telling a story which does not leave too many gaps and which is substantive enough to yield—if they are there—some principles and facts applicable to better managing social change today. Despite the considerable competent effort that scholars have put into reconstructing the human story, hard evidence is limited, particularly when trying to understand such important intangibles as the emergence of language, beliefs and cognitive skills. Often the difficulty is more one of knowing when some change occurred rather than what occurred. For example, estimated dates for the emergence of developed language vary by more than a 100,000 years. Unequipped as I am to explore every alternative hypothesis, I have used a 'satisficing'

[119] I am reminded of the joke about the aristocrat who claimed that his ancestors' family tree went back to the time when they lived in it.

approach of looking through the literature for answers to my what-when questions up to the point where something 'plausible enough' turns up.[120]

How then can we most simply understand, give meaning to, this fragile story of hominid evolution? A good starting point, so obvious that it might be overlooked, is that the hominid lineage was there at the start of the Pleistocene and there at the end. Unlike most biological lineages that have ever existed, it survived. Tautologically, just as survival of the fitter means no more than survival of those that survive, extinction is the fate of species that fail to reproduce themselves!

When Is a Species Vulnerable to Extinction?

More usefully, we might ask what makes a lineage more or less vulnerable to extinction, to becoming the end of the line. But still there are no operational answers. Any lineage and the environmental niche (adaptation zone) in which it is located are undergoing continuous change, sometimes faster, sometimes slower. Considered together, a lineage and its niche constitute a *developmental system*, importing and exporting energy and materials like other dissipative systems.[121] What is transferred between generations is not traits, or blueprints or symbolic representations of traits, but developmental means, call them resources or interactants. While some resources persist independently over generations (e.g. sunlight), others are transmitted from parent to daughter generation (e.g. genes). Once brought together, the resources in a developmental system spontaneously interact (self-organise) to produce a new generation of organisms.

There is, in principle, a joint set of niche specifications and of lineage specifications within which the lineage can survive (its 'survival space') and vice versa; the developmental system can be thought of as ineluctably moving through 'survival space'. So, it can be suggested that when the specifications of the niche-lineage system are approaching the boundary of the system's 'survival space', the lineage is vulnerable to extinction. Unfortunately, those boundaries are only knowable in a very general way.

Adaptation

One well-recognised process which tends to make a species less vulnerable to extinction is *adaptation*. Somewhat confusingly, this word is also the name given to

[120] *Satisficing* is Herbert Simon's (1956) word for adopting a strategy which is 'good enough' when decision-making resources are limited, as they usually are, i.e. any strategy which yields adequate, albeit not optimal, results is acceptable. See Simon, H.A., 1956, Rational Choice and the Structure of the Environment, *Psychological Review*, **63** (2), pp. 129–138.

[121] Griffiths, P.E., and Gray, R. D., 1994, Developmental Systems Theory and Evolutionary Explanation, *Journal of Philosophy*, **91**, pp.277–304; Walker, B.H., 2008, *Building Resilience: Embracing an Uncertain Future*, The Alfred Deakin Lectures, Deakin University, Vic.

the products of the adaptation process—these products being themselves processes. Adaptation is a process of natural selection[122] which produces adaptations. An adaptation is an unprecedented capability or process (including physiological-biochemical processes, behavioural traits, building anatomical structures), which, once spread through a population of related organisms, increases that population's capacity to survive and reproduce, at least in the short term. In general, adaptations work by amplifying/reshaping some of a species' behavioural or reproductive possibilities, e.g. natural selection for incrementally longer necks made it possible, eventually, for the giraffe to browse on tall trees. In energy terms, successful adaptations allow a species to maintain or increase energy throughput.

But the consequences of adaptation do not end there. When a species' behaviour changes, the environmental niche it is occupying will necessarily be changed also, in as much as the species will be taking in and exporting energy and materials in a somewhat different way. The effect may be large or small but, either way, there will be a tendency for natural selection to then produce further adaptations in the species. This in turn will further change the niche; what is being initiated here is a process of circular causation in which the lineage and the niche will continue to co-construct each other.[123] For example, the giraffes' browse trees get eaten out (local extinction) or the trees themselves co-adapt, generation on generation, by growing still taller. In the latter case there will be a tendency for giraffes with even longer necks to be selected.

The giraffe example illustrates the point that some traits in some interbreeding populations continue to evolve, over very long periods of time, through a cumulative or 'directional' sequence of adaptive changes, implying that each successive change does something to increase the population's capacity to survive and reproduce—not necessarily in absolute terms but relative to reproductive capacity in the absence of such adaptation.[124] A trait will stop evolving when its further change is no longer genetically possible or reproductively useful, whichever comes first. Here it can be noted that, like all animals, hominids have been somewhat restricted in their genetic plasticity, their intrinsic possibilities for directed evolution, simply because, unlike plants and single-celled protista, they have a fixed body plan under which, for their effective functioning, limbs and organs depend on each other in complex ways. That makes it difficult to change one character without disrupting other characters, a limitation called *channelling* or *canalisation*.[125]

In a classic paper on adaptation, Richard Lewontin points out that adaptive evolution requires 'quasi-independence'.[126] By quasi-independence he means that selection

[122] Formally, *natural selection* is the process of differential reproductive success of heritable variants of developmental systems due to relative improvements in their functioning.

[123] The rich idea that the niche and the organism co-evolve is explored under the rubric of *constructivism* in the literature. See Odling-Smee, F.J., et al. 2003, ibid.

[124] Thomas Huxley called this a process of 'progressive adaptation' but 'progress' is a problematic word, to be avoided when possible.

[125] Conrad, M., 1983, *Adaptability*, Plenum Press, New York, p. 260.

[126] Lewontin, R.C., 1978, Adaptation, *Sci. Am.* **239**, pp. 156–169.

must be able to act on a trait without causing deleterious changes in other aspects of the organism. If all the features of an organism were so closely developmentally integrated that quasi-independent variation did not exist, then 'organisms as we know them could not exist because adaptive evolution would have been impossible'. In terms of defining an organism's further evolutionary possibilities, the related idea of *modularity* is the suggestion that most changes in a body process only have to be compatible with processes in the same regulatory module, not other modules.

A niche's characteristics are changing continuously, not only being modified in response to its lineage's adaptive disturbances, but also in response to ongoing noise, fluctuations, shocks and trends in the material-energy flows through the larger systems which enfold every niche-plus-lineage developmental system. For example, there will be changes in energy flows through the food web of the lineage's enfolding ecosystem, e.g. changes in populations of parasites, predators or food species. In turn, these changes might be reflections of flow-rate changes in climate, landscape, soils, waterbodies or other aspects of the Earth's larger, slower material-energy cycles. As a consequence of niche changes, formerly adaptive traits can become maladaptive (hinder survival and reproduction) and disappear from the gene pool while other pre-adaptive as-yet-uncommon traits[127] might acquire an enhanced survival value and become increasingly common.

In a general way, any extant species has to adapt genetically at a sufficient rate relative to the rate at which it is changing its niche, or its niche is changing, or it goes extinct. Needless to say, what constitutes a sufficient rate is context-dependent. Still something, admittedly non-operational, can be said. In a rapidly changing environment a genetically diverse species, one with a heterogeneous gene pool, is more likely to survive on the grounds that it is more likely to be pre-adapted; as is one which is *adaptable*, i.e. which generates adaptations relatively rapidly.[128] Succinctly, species die out when the rate of environmental change exceeds the species' capacity to adapt.

Specialised Versus Generalised Adaptation

Before coming specifically to hominid survival, there is one more distinction to be made to fill out this much-simplified discussion of the determinants of extinction. It is, to use a modification of Edgar Dunn's terms, the distinction between *specialised*

[127] Gould, S.J., and Vrba, E.S., 1982, Exaptation—A Missing Term in the Science of Form, *Paleobiology,* **8** (1), pp.4–15. Gould and Vrba use the term *exaptation* rather than pre-adaptation on the grounds that exaptation has no teleological flavour of purpose. I prefer pre-adaptation as being more immediately understandable. There is no implication that the organism 'knew' in advance that some adaptation would acquire further utility at a later time. *Cooption* is another term for pre-adaptation.

[128] *Adaptability* is the capacity to thrive and survive when the environment changes whereas *evolvability* is proactive, i.e. the entity has capacity to try something different in the absence of environmental change.

adaptation and *generalised adaptation*.[129] The former refers to sequences of adaptations which make survival in a species' existing environmental niches more likely and the latter to adaptations which expand the environmental niche within which the lineage can survive. Commonly, but far from always, the difference between the two can be understood as the difference between being able to get the same food more efficiently versus getting access to more foods in more situations and locations.

Specialised Adaptation

The giraffe's neck is an example of specialised adaptation. Others involve such things as changes in colouration, size and shape of body parts. The process is one of fine-tuning a species to be more energy-efficient in a more or less trend-free environmental niche, e.g. the honeyeater's beak is reshaped to better extract nectar from the local flowers. Eventually, under specialised adaptation, a stage might be reached where the existing state of adaptedness[130] is simply maintained (called stabilising selection) with genetic variation across the population being progressively reduced to a stable level, i.e. with alleles of various genes being eliminated from the species' gene pool. Such a process may or may not leave the species experiencing it with some pre-adaptive traits but, either way, that species will become vulnerable to extinction, even under slow environmental change, simply because its former specialist adaptations are now increasingly maladaptive (and largely irreversible); and, also, it has little genetic variability from which adaptations appropriate to a changing niche might be generated. On the matter of genetic variability it can be noted though that to the extent that the niche is spatially or temporally heterogeneous, and to the extent that sub-populations within parts of the niche (sub-niches) can interbreed, the species will tend to remain genetically diverse and somewhat less specialised.

Specialised adaptation is also the process by which a common ancestral species evolves into two or more species (called cladogenesis). This is what happens when different sub-populations of the common ancestral species become and remain separated (no interbreeding) for long enough in differing sub-niches of the ancestral species' niche. As the separated sub-populations accumulate their own unique adaptations (called disruptive selection) they first diversify into different subspecies and then different species within the same family. While geographical separation is particularly important here, separation could be reproductive (e.g. different breeding seasons) or ecological (e.g. living in different strata within the tree canopy).

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[129] Dunn, E.S., 1971, *Economic and Social Development: A Process of Social Learning*, Johns Hopkins, Baltimore. Dunn's terms (Ch.2) are *adaptive specialisation* and *adaptive generalisation*. Other terms for the same distinction are specific versus general evolution and cladogenesis (branching evolution) versus anagenesis (upward evolution). See also Rensch, B., 1959, *Evolution above the Species Level,* Columbia University Press, New York.

[130] *Adaptedness* is an absolute measure of the capacity to survive and reproduce. Fitness is a relative (to others) measure of survival and reproductive success.

Generalised Adaptation

The clearest examples of *generalised adaptation* occur when a species comes to occupy a radically different type of niche (in contrast to specialised adaptation where a species radiates into 'sub-niches'). Thus, the development of the wing in the reptilian lineage opened up the aerial niche to the avian descendants of that lineage. The development of homeothermy (internally regulated body temperature) in birds and mammals was a generalised adaptation which vastly extended the terrestrial habitats of these groups.

When a lineage evolves in ways that allow it to occupy a new type of niche, the products of that process will normally be recognised, taxonomically, as being species in a new family (group of related species) or higher taxonomic category. In contrast, specialised adaptation by either disruptive or stabilising selection results, at most, in new species within the same family or variants of existing species.

How does generalised adaptation happen? When, with hindsight, a line of evolutionary change is recognised to have been one of the generalised adaptations, of major change in organism characters and environment, it can be seen that each adaptive step made possible further adaptations which were formerly not possible or not adaptive or even viable. It is this 'unshackling' effect which explains the paleontological fact that, when they do emerge, new families and orders emerge much more rapidly than new species emerge within families.

For example, as noted, the Cambrian 'explosion', some 540 Mya, is the well-known phenomenon during which, over 10–20 myrs, all extant animal phyla, and several others now extinct, arose abruptly in the geological record. But even though generalised adaptation produces large changes, often quite rapidly, such are still produced by a succession of genetic changes, just as happens in specialised adaptation. Theories about new orders, phyla, etc., emerging as a result of multiple small mutations occurring simultaneously (the so-called hopeful monsters) have few supporters.

What helps here is to understand that, sometimes, a single viable and 'harmonious' mutation—a sudden alteration of heritable characteristics in a gene, a chromosome, a genome, a plastid or a plasmon—can have dramatic effects on the developmental trajectory (ontogeny) of a mutating organism's offspring.[131] Thus, as discussed in Chap. 1, it has been learned in recent years that around the time of the Cambrian explosion, not only were there major environmental changes (e.g. in atmospheric oxygen, in the extent and composition of coastal waters), but a new system of genetic control, one not present in unicellular organisms, was evolving from duplicated copies of pre-existing genes. The innovation here was *homeotic or regulatory genes* which control the positioning of major structures in an animal's body plan; which can change the relative growth rates of various organs, limbs, etc., and so produce phenotypes with characters that are exaggerated or reduced relative

[131] An organism's *plasmon* is the aggregate of its cytoplasmic or extranuclear genetic material. A *plastid,* a specialised component organelle in a photosynthetic plant cell that contains pigment, ribosomes and DNA, serves specific physiological purposes such as food synthesis and storage.

to the parents; and which act as on-off switches for repressing or evoking activity in (non-regulatory) *structural genes*.[132] For example, in a mammal, a single homeotic mutation might produce an arm that is shorter, or longer, or broader. Regardless, it will probably still look and work like an arm. It is now accepted by mainstream biologists that a single homeotic mutation may have multiple effects on diverse characters, including behaviour, development pattern and morphology, without rendering the offspring non-viable, especially when those offspring are not being subjected to strong selection pressures. It seems that the Cambrian explosion could have depended in part on a flush of newly possible homeotic mutations occurring at a time of broad-scale environmental change.

Extending One's Niche

If a species is to successfully extend its niche, changing markedly in the process, there would seem to be at least three preconditions to be met. One is that the new niche needs to be geographically accessible from the old. For example, an aquatic species adapted to a deep-ocean niche could not have served as a 'phylogenetic bridge' to amphibian and terrestrial existence; it would have to be a species at home in the shallows. Second, the colonising species would need to have some minimal set of selectively neutral pre-adaptations.[133] For example, an aquatic animal species colonising the land would need to be pre-equipped with a means of locomotion there such as wriggling or walking on its fins.

A third precondition for achieving successful occupation of a new niche is what might be called *ecological access*. That is, within geographical range there must be an ecological web sufficiently developed to contain niches which the colonising species is somewhat equipped to fill but which are not already occupied by other well-adapted species. For example, at intervals during the evolution of multicellular life there have been mass extinctions of species caused by cosmic and planetary events such as large-scale volcanism or impacts by asteroids, comets, etc. While new, different ecosystems are quickly re-established after such catastrophic events, there are inevitably many empty niches for some time. Thus, on the (debateable) assumption that dinosaurs were cold-blooded and that this partly explains their demise during a long winter triggered by a comet strike some 65 Mya, a niche was created for mammals, these having some pre-adapted capacity for regulating body temperature, to emerge as the dominant form of animal life.

While not preconditions, there are several other situations that appear to be conducive to the onset of generalised adaptation. One of these, sometimes called the *law of the unspecialised*, suggests that new families and orders tend to emerge out

[132] Carroll, S.B., 2000, Endless Forms: The Evolution of Gene Regulation and Morphological Diversity, *Cell* **101**, pp. 577–580. Structural genes are genes that code for polypeptides or other structural units of a cell.

[133] 'Selectively neutral' means that organisms with these pre-adaptations were as reproductively successful as those without them.

of less specialised subgroups within a species or out of the less specialised species in a family of species. One reason for this might be that in a specialised species all its tissues have already acquired highly specific functional tasks whereas in unspecialised species there may well be tissues that have not yet been co-opted for specialised tasks and which may therefore be available for reshaping into generalised adaptations.[134] A related observation here is that generalised adaptation tends to occur in (geographical) transition zones between major ecological provinces, perhaps because the *ecotypes* (variants within a species) located there are already pre-adapted to some extent and because the environment in the transition zone, being the ‘edge’ of the niche, is more variable than in the ‘core’ part of the niche. Because they have to cope with multiple environments, species in transition zones are under less selection pressure to specialise. Indeed, such species may well get selected for phenotypic plasticity, the capacity to develop or behave differently depending on the reigning environment.

It does seem that, when conditions are right, new families and orders do enter the fossil record very quickly in terms of geological time and seldom through a succession of many small genetic changes (gradualism) within a given environment such as envisaged under specialised adaptation. This is the process that Stephen Gould and Nils Eldredge termed *punctuated equilibrium*[135]; perhaps *periodic acceleration* (in the rate of phylogenesis, meaning differentiation through evolution) would be a more informative name. What the fossil record suggests is that, following the occupation of a previously unexploited niche or a newly created niche, in a situation where selection pressures are low, it is common for the invading species to rapidly split into a diversity of ‘fit enough’ species, most of which then begin their own journeys towards specialised adaptation.

Constraints and Trajectories in Phylogenesis

To what extent are the evolutionary possibilities open to a species at any time channelled in a particular direction or moulded by internal constraints on what is physically, developmentally (e.g. bodyplan constraints) or biochemically possible or by

[134] Sometimes, because genes can have multiple effects, non-functional tissues can arise as by-products of selection for some functional character. Unspecialised tissues can be formed as allometric ‘by-products’ and then be later coopted for new functions. Specialisation removes surplus unspecialised tissues which otherwise might have been available for moulding into generalised adaptations.

[135] Gould, S.J., and Eldredge, N., 1977, Punctuated Equilibria: The Tempo and Mode of Evolution Reconsidered, *Paleobiology,* **3** (2), pp. 115–151. A common argument against gradualism is that forms with characteristics intermediate between orders or even families are essentially unknown.

external environmental parameters such as atmospheric-oxygen levels or the presence of other species? From knowing what has gone before, i.e. what past adaptations have produced, are there things that can be said about what tends to happen or about what cannot happen? As an illustration of the latter, we might note that the development of the wing deprived birds of potential hands that could be used to manipulate the environment and, in the interests of flight, limited potential size—including a brain of size sufficient for the development of intelligence.[136] As a trade-off for these 'lockouts', birds acquired high mobility and, thereby, access to new food sources.

As a sample of what tends to happen, consider one of palaeontology's basic generalisations, namely, that trends are common, i.e. morphological, etc., changes in a particular direction tend to continue once initiated, as with the giraffe's neck. A more important example, one with many flow-on effects, is the tendency of body size to increase in many lines of descent. Historically, there has been much debate as to whether such trajectories can be plausibly explained by natural selection alone or whether there is a need to postulate additional *orthogenetic mechanisms*, ones which imply goal-directed evolution. Today, most opinion would be that a sufficient explanation for most persistent trends is that internal and external constraints on what changes will be viable have left just a few feasible directions of change available for natural selection to find. To quote Gould[137]:

> …the constraints of inherited form and developmental pathways may so channel any change, even though selection induces motion down permitted paths, the channel itself represents the primary determinant of evolutionary direction.

Notwithstanding, once a favourable 'biological technology' has been 'invented' (no purposiveness intended), it might be expected to persist (with or without some trending) in the lineage for as long as no better way of carrying out that adaptation's function emerges.[138] Thus, chromosomes, structures which transmit synergistic genes in tandem, have persisted since their emergence because they help ensure that all new cells contain all genes. The cell itself is a similarly favourable and persistent 'invention'; it is a modular 'building block' which has the property of selectively limiting the influence of its chemical environment on its contents. As a third important example, the emergence of a nervous system conferred an enhanced ability to react appropriately to external stimuli, e.g. by prompting muscles to contract for fleeing when danger appears. In general, organs and organ systems such as the

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[136] Dunn, E.S., 1971, Economic and Social Development: A Process of Social Learning, Johns Hopkins, Baltimore, p. 57.

[137] Gould, S.J., 1982, Darwinism and the Expansion of Evolutionary Theory, *Science*, New Series, **216** (4544), pp. 380–387.

[138] Rensch, B., 1959, *Evolution above the Species Level*. Columbia University Press. New York, p. 71.

brain, blood vessels, nephridia (insect 'kidneys'), labyrinth (internal ear), etc., have remained largely unchanged since their beginnings.

Some Rules of Phylogenetic Development

As already noted, sequences of adaptive changes can cumulate directionally (directional selection), either in response to a changing or changed environment or via a process of coevolution between lineage and environment. In practice, knowledge of an animal's mode of life and habitat often allow a degree of prediction as to the direction of its functional-anatomical evolution. Bernhard Rensch[139] has collated some of these insights as 'rules of phylogenetic development'. For example:

Large terrestrial vertebrates must develop heavy columnar legs with disproportionately large bones because, as body size increases, body weight increases much faster than the strength of the animal's leg bones, e.g. elephants, extinct orders of large birds and giant reptiles.

Speed through air and water is increased by streamlining the body.

Sessile animals can only evolve in water, an environment where they can rely on eddying to bring them food.

There are only a limited number of models for evolving legs for jumping or for digging.

Heterotrophs (mainly animals) could not evolve before the evolution of autotrophs (mainly plants) to feed on.

Autotrophic organisms require a large surface area because their uptake of nutrients and energy is through those surfaces.

Evolution of larger bodies in multi-celled animals requires a transport system for food and oxygen (blood vessels, tracheae). Without such systems, tissues must be close enough to the sites where food and oxygen molecules enter to allow for the slow rate at which these diffuse through tissue. Flatworms, for example, have no circulatory or respiratory system but succeed because of their flat bodies and richly branched intestines.

Generalised adaptation in multi-celled animals results in major reorganisation and specialisation of internal organs and their increasingly centralised control from the brain.

Some of these rules illuminate the well-recognised phenomenon of *convergence* in which different species follow parallel evolutionary paths, i.e. the same sorts of adaptations appear quite independently in diverse species that have become adapted to a similar habitat or way of life, e.g. the similar body shapes of the North American grey wolf, a placental mammal, and the Tasmanian tiger (*Thylacine*), a marsupial mammal.

[139] Rensch, B., 1959, ibid., p. 73.

The Importance of Allometry and Heterochrony for Evolutionary Trajectories

Allometry is the term recognising that, in most animals, different body parts grow at consistently different rates as the size of that organism increases. Empirically, the results of such differential growth rates can normally be expressed as power law relationships of the form:

$$\log X = a \log Y$$

where *X* and *Y* are the sizes of any two allometrically related body parts.

While the relative growth rates of organs and parts of organs remain constant during much of an individual organism's development, there can be periods when an organ or structure grows faster than the body as a whole (positive allometry) or more slowly (negative allometry). For example, the human head exhibits positive allometry till birth and negative allometry thereafter.

Such relative growth rates and the length of time for which they operate during the organism's normal development sequence are under regulatory-gene and hormonal control and open to adaptive selection. Within limits, allometric relationships are as subject to selection as static morphology itself.[140] In principle then, in a well-adapted organism each body part grows to a size where it can meet the 'peak performance' needs of other body parts, and have its own needs met, in a balanced way, i.e. without surplus or insufficient capacity.

The reality is more complicated. The functions of regulatory genes appear to be organised hierarchically with, in many cases, a single regulatory gene controlling the development of not one but a whole group (module), or even whole groups, of allometrically linked body parts/traits. This means that one or a few mutations in a lineage's regulatory genes can dramatically change the timing and duration of developmental events during morphogenesis—a change called *heterochrony*—and hence change the allometric relations (proportions) between the body parts of the phenotype. Selection for neotenous development in early hominids, as described earlier, provides a clear example.

Selection for Increasing Body Size

In most mammalian lines of descent there have been, at times, increases in body size, e.g. giant types evolving from smaller ancestors. Why? In many environments, there are a number of advantages, up to a point, in being larger.[141] Thus the last glacial age saw an increase in types of large homeotherms such as mammoths, giant elk, red deer and giant wombats, all benefiting from needing relatively less food to maintain body temperature than their smaller ancestors.

[140] Gould, S.J., 1966, Allometry and Size in Ontogeny and Phylogeny. *Biol. Rev.,* **41**, pp. 587–640.

[141] Rensch, B., 1959, ibid., pp. 211–218;. See also Reiss, M.J., 1989, *The Allometry of Growth and Reproduction,* Cambridge University Press, Cambridge.

Because of genetically embedded allometric correlations, selection for larger body size commonly brings with it the ‘overdevelopment’ or ‘underdevelopment’ of various body parts, compared with smaller ancestors. Some of these, like proportionately stouter legs for enlarged vertebrates, are necessary in an absolute sense. Some may prove maladaptive, others adaptive. For example, positive allometric growth of the permanent teeth in many lines leads to excessively (fatally?) large canines and incisors, e.g. the sabre-toothed tiger. Conversely, under the negative allometric growth typical of the smaller organs (heart, liver, etc.), there is more space available in the body cavity of larger types for intestines and a developing foetus. While the brain is relatively smaller in large types the ‘newer’ forebrain is relatively larger, the individual neurons are absolutely larger and have more dendrites (extensions) per neuron, implying a brain with more possibilities for associating images and perceptions with each other.

It might be noted here that the allometrically guided evolution of the vertebrate brain illustrates the idea that excess ‘overdeveloped’ tissue can, in time, be employed for new functions or even to form new organs. Thus, several functions located in the midbrain shifted to the forebrain once its relative size increased by positive allometry during the amphibian-reptile stage of vertebrate evolution. That same shift may have initiated the eventual development of the cerebral cortex possessed eventually by all higher vertebrates. Thus, in hominids, as noted earlier, new cortical tissue became available for allocation to new or expanded functions such as making plans, making associations between ideas and between percepts and, eventually, managing the motor functions of speech.

Selection for increasing body size then is likely to bring, along with major changes in body proportions, both adaptive benefits and adaptive costs; size will only continue to increase for as long as the costs of the ‘allometric by-products’ of increasing size remain tolerable. Or, and this is genetically difficult, until the allometric links between favourable and unfavourable traits are broken. And, to the extent that there is already pre-adaptive variation within a population in the genetically embedded allometric and heterochronic relations governing organ development, selection for increasing body size stands to bring not one but a range of major changes in body proportions. These variations could, in turn, trigger rapid speciation, especially if the accessible and actual environment were itself spatially variable.

To round things out here, recall, from earlier discussion of Baldwinian selection, that accumulated genetic modifications which, before environmental change, were selectively neutral, and perhaps ‘invisible’, might, under environmental change, trigger a plastic response in the phenotype. That is, genetic change, phenotypic change and environmental change may all be contributing to any change in body proportions.

Notwithstanding some discussion in the literature,[142] what is not clear is the source of the genetic plasticity which allows a trait such as body size to keep increasing over, perhaps, hundreds of generations. Part of the answer might lie in selection for alleles of the regulatory gene or genes which control the timing between switching on and switching off the secretion of growth hormone. Again, the pituitary gland's capacity for secreting growth hormone may itself be allometrically dependent on the organism's past size increases.[143] Or, perhaps it is nutritional levels rather than genes that limit increases in body size—size improves nutrition, improved nutrition increases size.

The Hominid Experience

While the story will continue to be refined, or even recast, the main stages in hominid evolution—from (say) the hominid-chimpanzee divergence until modern humans precariously survived the last ice age—are clear enough. In those six million or so years, the lineage radiated into a small number of species several times (punctuated equilibrium?); just like many other vertebrate lineages. While several coexisted at times, all but one of these species has now died out. But just why the *Homo sapiens* lineage survived and others did not is a topic we have not explored.

Not only did the human lineage survive massive global-scale climatic and ecological changes during its evolution but, by the beginning of the Holocene epoch (10–11 kya), which is where this chapter ends, populations of modern humans had migrated to and were established in all lands except Antarctica and some south Pacific islands. The world's human population at that time could have been five million, all organised into hunter-gatherer bands of up to 150 people. Developmentally, morphologically and behaviourally, these people were markedly different from the ancestral great apes who first adapted to a shrinking of their tree-top habitat by obtaining an increasing part of their food on the ground and, eventually, becoming ground-dwellers.

Of three previously noted requirements for a lineage to successfully occupy a new niche, *geographical access* to savanna habitats came ineluctably as grasslands replaced drying forests in the east Africa of the late Pliocene. Understanding of how hominids had *ecological access* to an unoccupied or uncompetitively occupied niche is more speculative. Still, apparently there was room for a forager-scavenger-food-sharing species capable of coordinated group behaviour.

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[142] For example, http://www.science.siu.edu/zoology/king/metapt.htm (Accessed 3 May 2006); Heyland, A., Hodin, J., and Reitzel, A.M., 2004, Hormone Signalling in Evolution and Development: A Non-Model System Approach, *BioEssays,* **27**, pp. 64–75.

[143] Shea, B.T., 1992, Developmental Perspective on Size Change and Allometry In Evolution, *Evolutionary Anthropology,* **1**(4), pp. 125–134.

This leads to the third requirement for successful niche extension, namely, that the immigrant species be 'sufficiently' pre-adapted to the new conditions and not be too burdened with specialised adaptations carried over from their previous niche. For example, over millions of years of arboreal life, the primitive grasping hand continued to function without any specialised adaptation (such as becoming claw-like), maintaining its versatile mobility and its direct nerve-connections to the forebrain. Indeed, it is hard to think of any adaptations to tree-life which would subsequently prove patently maladaptive once the lineage moved to the ground. In this sense proto-humans were remarkably unspecialised.

Indeed, one can readily list a number of pre-adaptations (some predating arboreal life) which, immediately or with further selection, appear to have improved survival prospects for australopithecines in a drying, cooling world. For example:

Capacity to regulate body temperature
Group living (important for cooperative scavenging and gathering, food sharing, defence)
Forward-facing eyes for stereoscopic vision
Good hand-eye coordination
Omnivore dentition and digestive tract
Feet which would adapt easily to walking and running
Erect posture of the trunk (an essential prerequisite for erect walking)

Once on the ground, adaptation to a savanna niche could begin, starting with selection for increasingly efficient bipedal locomotion and a larger body size than would have been practical for life in the treetops. And as body size increased (a distinct advantage in that new habitat), so did brain size, the forebrain in particular. The long march from a chimpanzee-sized brain to a modern human brain had begun. Indeed, the paramount feature of hominid evolution over the last two million years has been the growth and reorganisation (e.g. lateralisation) of the brain, along with closely associated changes in morphological traits (e.g. vocal apparatus), in behavioural traits (e.g. cultural practices) and in the timing of life-cycle events (e.g. neotenous development). Over the same period a large number of proto-human traits have persisted with relatively little change.

Improving Adaptedness

The *adaptability* of an evolving lineage is its proficiency in generating, via natural selection, adaptations that, within its niche, improve *adaptedness* (fitness, reliability), i.e. improve survival and reproduction prospects. Like other higher animals (less so for plants and simple animals), the hominid lineage has relied on ongoing evolution within a particular family of adaptations, namely, *phenotypic plasticity*, to maintain and improve adaptedness in what has proved to be a variable environment. Recall that an individual organism's phenotypic plasticity is its capacity to continue surviving and developing in a changing environment, by changing physiologically, morphologically and behaviourally. Anurag Agrawal, discussing the 'adaptive plasticity hypothesis' says that 'the modern view of plasticity can be generalised to the statement that phenotypic plasticity evolves to maximise fitness in variable environments'.[144]

Focusing here on behavioural plasticity, the basic requirement for achieving flexible behaviour—meaning context-sensitive observable activity, particularly in terms of mobility and discrimination—is a developed centralised nervous system linked, on the one hand, to organs for perceiving the environment and, on the other, to a skeleton and muscles capable of versatile movement. But, to move beyond the reflexive and instinctual, achieving flexibility in observable activity eventually requires a brain that is also capable of learning and memorising. A lineage with limited behavioural plasticity will necessarily be more reliant on physiological and morphological responses to achieve adaptedness. For example, prokaryotes synthesise their own metabolites to a degree multi-celled animals cannot match; plants have a putative 'strategy' of acquiring resources by extending into the environment.

As noted severally above, a variety of processes have been implicated in explaining the growth and reorganisation of the hominid brain over the Pleistocene epoch: the allometric relationship between brain (parts) and body size; selection for neotenous development; selection for tighter neural control of the hand following the transition to bipedalism; the management of mimesis and, eventually, prosody and speech; the impact of shifting between niches; and variability/change in both the abiotic and biotic (including socio-cultural) selecting environments.

How have these processes expanded phenotypic plasticity, the individual's ability to respond appropriately to changing circumstances? In particular, how has an increasing emphasis on *brain-managed behaviour* led to increasingly plastic behaviour? At one level, increasingly plastic behaviour is nothing more than a many-to-many elaboration of the one-to-one stimulus-response mechanism recognised in the simplest plants and animals (e.g. the oyster that closes when touched). In brief, the plastic organism, compared with the implastic organism, differentiates incoming stimuli more finely, has more motor options available and uses a more elaborate comparative procedure to select a motor response to a received stimulus.

So, behavioural plasticity increased over the Pleistocene as:

Streams of sensory inputs from the external and internal environments were being represented in a centralised brain in ever more categorical detail and being coordinated more closely.

The range of motor actions (behavioural outputs) available to the organism increased as the brain acquired finer control over evolving sets of muscles and their movements.

The brain acquired an increased capacity for memorising experiences and associating them (equals learning); and using these capacities for generating and modelling the consequences of alternative motor actions in response to current

[144] Agrawal, A., 2001, Phenotypic Plasticity in the Interactions and Evolution of Species, *Science*, **294**, pp. 321–326.

sensory inputs. In novel situations the brain's capacity for generating images of alternative motor actions depends on its capacity for exploratory *mental* behaviour which in turn is linked to earlier selection for delayed development and, with it, extended childhood.

The brain acquired a (preconscious) decision-making or choice-making capacity for searching candidate motor responses until it identified, and then implemented, one with consequences which were 'good enough' in terms of the emotional associations attached to those consequences.

The range of traditional and routine behaviours available to the individual accumulated reliably from generation to generation.

Evolutionary Ecology of Hunter-Gatherers

For most of the Pleistocene, hominids were hunter-gatherers organised into nomadic bands that roved between relatively more productive (in food terms) patches distributed across a loosely defined territory. Their basic means of acquiring food (there being no imports or exports) was to harvest available plant and animal biomass, while paying a degree of attention to securing the ongoing reproduction of that biomass, e.g. taboos on certain food sources at times.

In good times (plentiful food) band numbers may have grown and, in bad times (high population relative to the territory's immediate carrying capacity), contracted as a result of increased mortality and emigration by some of the band (called fission) into new territory. On coarser spatial and temporal scales, a further factor driving hominid spread during the Pleistocene was 'biome shift', this being the ways in which various biomes (forests, deserts, coasts, etc.) shifted backwards and forwards across Eurasia as glaciers and sea levels responded to warming and cooling periods within and between the epoch's several dozen ice ages. Like other animal groups, hominids would have moved with or tracked the expansions and contractions of biomes to which they were adapted. In some situations biomes may have contracted rather than shifted, forcing groups into competition for declining resources and, perhaps, for we do not know, into violent conflict.

In these ways, we can imagine erectines and, possibly, australopithecines, colonising much of Eurasia by a process of slow frontier expansion. That is, while the global hominid population probably zig-zagged slowly upwards, through glacial and interglacial periods, for much of the Pleistocene (until the post-Toba crash), the process was more one of growth by extensification (more occupied hectares), not intensification (more people per occupied hectare).

Depending on the type of biome being exploited, omnivorous hominids would have been in competition with carnivores for herbivore prey and with herbivores for plant foods; and would be prey themselves sometimes. But, having control over no energy sources beyond their own somatic energy (at least till fire was mastered), and despite a growing phenotypic plasticity, hominids are unlikely to have extinguished other species, except very locally perhaps. There may even have been a degree of coevolution with prey species and with other predator species (leading in places to hominids focusing on some subset of the available prey species).[145]

What seems likely is that in most seasons, in most biomes, the hunter-gatherer population would have harvested only a small proportion of the available biomass (much less than 1%) and, even in harsh seasons, it is unlikely that resources would have been depleted to the point of being thereafter unusable.[146] The persistence (many would call it sustainability) through geologic time of the hunter-gatherer mode of livelihood (or, in economic language, system of production) and its extension into the most demanding of terrestrial habitats are indications of the success, under a diversity of changing and changed conditions, of the core hominid evolutionary trajectory, namely, the cumulative amplification of the lineage's brain-based behavioural plasticity.

Without hindsight, that conclusion would not be obvious. Maintaining and, over evolutionary time, growing a centralised, albeit functionally differentiated, nervous system requires the unceasing delivery of large quantities of metabolic energy. Even allowing for the decreasing specific metabolic rate which accompanies increasing body size, this is a strategy premised on being able to capture large quantities of energy and using much of that yield to maintain the very organ which allows larger quantities of energy to be captured in the first place. Expressed in that way, the 'big brain strategy' is a continuation of the homeotherm strategy; compared with cold-blooded animals, warm-blooded animals need to capture large quantities of energy to maintain their capacity to be more independent of external temperatures.

Considering the lineage as a whole, as a metaphorical 'super-organism' perhaps, hominids were processing and extracting more and more energy from their environment as the Pleistocene progressed (the 'super-organism' was growing). More correctly, this is a general trend which has to be seen against a background of major shifts in the type and level of productivity of the larger environment.

Within this trend, two component trends can be distinguished; one in the extensification of energy extraction and one in the *intensification* of energy extraction. The process of population growth by extensive spread was equally a process by which the hominid lineage, as a whole, was extracting more energy from the environment—not by capturing more joules per ha, but by capturing much the same joules per ha from many more hectares.

As regards the intensification trend, what is being suggested is that hunter-gatherer societies were also *netting* increasing amounts of energy per ha (per unit body-weight?) from their territories as the Pleistocene progressed. That is, the difference between energy captured and energy expended to capture it was increasing. To the extent that energy captured per unit of energy expended was also increasing, hunter-gatherers were also capturing energy more efficiently. And, perhaps, also more

[145] Brantingham, P.J., 1998, Hominid–Carnivore Coevolution and Invasion of the Predatory Guild, *J. Anthropological Archaeology*, **17**, pp. 327–353.

[146] Haberl, H., 2002, The Energetic Metabolism of Societies Part II: Empirical Examples, *Research And Analysis*, Massachusetts Institute of Technology and Yale University.

reliably, meaning less variability over time in the net amount of energy captured—a most important determinant of group survival, sometimes interpreted, misleadingly, as greater independence from the environment.

Lumping these variations on the intensification theme together, what might have made such intensification possible? An answer has already been suggested, namely, the cumulative amplification and application of the lineage's brain-based behavioural plasticity, in combination with the advent of a number of physical and developmental adaptations. Apart from changes in the brain itself, these latter include adaptations in body size, in vocal apparatus, in the hands, in the pelvis and, of course, in the timing of maturation.

Cultural Liftoff

One way of thinking generically about the contributions to hominid adaptedness of the increasingly plastic brain is to see it as having generated a succession of *technologies* or *behavioural recipes*—stepwise procedures for completing tasks, for realising imagined goal states. And, to the extent that they persist, that they survive in the selecting environment, all such technologies, indirectly but ultimately, raise, at least in relative terms, the (net) mean quantity of energy captured by the group and/or reduce variability in the (net) quantity of energy captured over time. The Darwinian assumption being made here about the selecting environment is that newly generated technologies or new variants of existing technologies will not be adopted and persist unless they 'save' or 'earn' more disposable energy than existing technologies. The ability to acquire disposable energy is central to adaptedness. Nonetheless, the forces of habit and tradition or side effects on the availability of non-energy resources or high transition costs (the effort required to switch from an old to a new technology), could all militate against the adoption of a new technology on the basis of its energy gains alone.

But what were these technologies? While it could be seen as stretching the concept of technologies too far, it can be suggested that technologies group readily into:

Material technologies involve making things from source materials, including prostheses such as tools and weapons, cooked food, clothes and shelters.

Social technologies which involve habitual, cooperative, coordinated action between people, e.g. food sharing, hunting and gathering in groups, defending the group, attacking other groups, rituals, taboos, division of labour and the invention of leadership.

Communicative technologies involve the transfer of information and knowledge between people using, for example, mimesis, demonstration, stories, displaying emotions and spoken language.

Cognitive technologies which use the resources of sensory inputs (both internal and external), memories and learned relationships to model, in words and images, the consequences of alternative behaviours and events. Applications include making decisions, classifying entities and solving what-to-do problems.

A group's *culture* is largely defined by the extent to which the habitual application of particular technologies within these categories is common to, or, at least, understood by the group's members. And, in this sense, Pleistocene cultures evolved as these various shared behaviours became better adapted to existing circumstances or became modified to suit changing circumstances. Most of these evolving technologies can be seen to have had roots in pre-Pleistocene minds and social relationships (the first hominids were already social animals with sizeable brains) and appear to have changed only slowly thereafter and in readily understandable ways, e.g. achieving more cutting edge per stone core.

Then, some 40 kya, came the Upper Palaeolithic revolution in which developments in material, social, communicative and cognitive technologies, both singly and in concert, began accelerating the rate of cultural change; and, overall, a group's capacity to reliably capture energy from its territory. The oldest known flute and the oldest known ground stone axe both date from 35 kya. Was this largely a matter of separate technologies having accumulated to a point, a critical mass, where synergistic possibilities between them began to appear? Were pre-existing simpler technologies now being brought together to create, incrementally, more complex new technologies, e.g. combining sharper flakes and straighter shafts to produce a new generation of spears? Perhaps, but it seems more likely that the development of extended spoken language, the master technology, massively augmented the lineage's capacity to create, transfer, bequeath, accumulate and integrate the sweep of material, social, communicative and cognitive technologies.

And, we might note, assuming that fire had been mastered well before the Upper Palaeolithic revolution, this cultural transformation was achieved without a bonanza of technologies for accessing radically new energy sources (e.g. wind) or for accessing prior energy sources (e.g. photosynthates) in fundamentally different ways.

The essence of the scenario being presented here is that during the Pleistocene, particularly towards the end, the human lineage was unconsciously building up its repertoires of two sorts of *intellectual capital*. One was working knowledge of material, social, communicative and cognitive technologies which, directly or indirectly, gave groups an enhanced capacity to reliably capture biomass energy from an area. The other was knowledge (information, understanding, a model, etc.) of how the world works, meaning its constituent cause-effect relationships, both hypothetical and observed. It is not too bold to suggest that without verbal language there would have been little accumulation of intellectual capital; just as there was little opportunity for mobile nomads to accumulate material capital beyond portable possessions.

Cultural Evolution and Population Trends

As noted above, group sizes would probably have expanded in good times and contracted in harsh times. Increasing levels of technological competence (adaptedness) might have slowed any fall in group numbers in harsh times and, in better times, at least till numbers grew to match the territory's rising carrying capacity, the dividend from better technologies might have been more ‘leisure’ or ‘play’ time for practising and further improving all types of technologies. And there could have been more time for devising behaviours for dealing with emerging what-to-do situations; and more time for transmitting traditional behaviours through rituals, mimesis, etc.

But when it comes to judging the significance of cultural evolution in raising average population density and lowering its variability there are too many factors involved to allow generalisations. For example, how often did improved technologies lead to over-harvesting? How draining was the overhead cost in energy terms of maintaining an ever-larger suite of material, social, communicative and cognitive technologies? How often did entrenched technologies become maladaptive under changing conditions?

A reasonable guess for the Upper Palaeolithic, and it is nothing more, is that advancing technologies tended to facilitate small increases in average population density, moderate reductions in population variability and somewhat larger improvements in groups’ capacities to survive major changes in environmental conditions, the sudden bitterness of the last glacial maximum for example. It would not be until the invention of fundamentally different energy-acquisition technologies (farming and herding), well after the end of the last ice age, that population densities would rise markedly.

Is This Story Remarkable?

We have now traversed the prehistory of the hominid lineage from well before the Pleistocene epoch to its end. Our lineage entered the Pleistocene as primates and mammals and left the same way. Indeed we are still mammals and primates and will, almost certainly, long remain so (widespread species undergo little evolutionary change[147]). We might ask then, is the human story remarkable?

An entity (or a process) is remarkable to the extent that it is observably different from other entities in the same *family*, the word ‘family’ here meaning a set of entities which have some defining characteristics in common, e.g. primates have good eyes and flexible hands and feet.[148] Humans have all the characteristics of mammals but they are remarkable mammals in terms of their easy bipedalism, their slow maturation and the large highly organised brains which make their material, social, communicative and cognitive technologies possible. Reflecting their own adaptive paths, other mammals are remarkable too of course; for strength, speed, sensory acuity, etc.

We might also ask whether the hominid lineage has been remarkably lucky, because it probably has! ‘Lucky’ here means lucky to have survived; and not too

[147] Mayr, E., 2001. *What Evolution Is,* Basic Books, New York, p. 254.

[148] Lakoff, G., and Johnson, M., 1980, *Metaphors We Live By*, University of Chicago Press, Chicago, p. 117.

cruelly. Most obviously, if the Toba eruption, 71 kya, had been a little bigger, or had lasted a little longer or had been followed up with some more large eruptions—and any of these scenarios would have been unsurprising—the lineage may well have not survived.

In terms of the large dissipative systems within which the hominid lineage (itself a dissipative system, albeit dispersed in space and time) is embedded, the Pleistocene was, luckily, more or less stable. The Earth suffered no impacts from large meteors/comets and no extended bursts of high-energy radiation. Insolation levels, the composition of the atmosphere and the positions and tectonics of the continents were all effectively stable, i.e. were changing slowly, in human terms. After all, the Pleistocene is a very short period relative to the lifetimes of these large systems. It was mainly shifts in climate, over decades and centuries, and associated changes in shorelines, ice cover and biomes that provided the challenges to which the hominid lineage had to adapt or die out. Behaviours (technologies) which acquire food successfully in one environment need not necessarily be successful in others.

Metaphorically, phylogenesis via natural selection is a short-sighted process which, almost always, takes species down adaptive paths that turn out to be dead ends, i.e. most species that ever were are now extinct. The hominid lineage however experienced a sequence of adaptations which, despite being routinely short-sighted, did not become maladaptations when the selecting environment changed and indeed turned out to be useful pre-adaptations for new environments. A good example is the adaptations to arboreal life which turned out to be useful pre-adaptations for life on the savannas. That's luck.

Can this line of argument be taken further? Did hominids who were evolving on the cooling, drying savannas of the early Pleistocene acquire adaptations which pre-adapted them and did not maladapt them for the ice ages to come? One positive example is that the mobility acquired on the savannas allowed later Eurasians to survive the harshest of glacial times by intercepting and butchering animals from migrating herds during the short spring-summer and cold-storing them for the following winter.

And next, as modern humans came through the last glacial maximum, did they turn out to be pre-adapted, not maladapted, to the warmer, less variable conditions of the Holocene epoch? A partial answer here is that Pleistocene hominids were never selected to any extent for physiological and morphological characters which might plausibly be viewed as specialised adaptations to ice age conditions, e.g. hairiness. In this sense they were again lucky because these are the sorts of adaptations which, when conditions change, tend to become maladaptations. Rather, hominids were largely being (naturally) selected for brains that showed an appetency and an increasing capacity, in terms of size and organisation, to create material, social, communicative and cognitive technologies. And, as these technologies were evolving and co-evolving, hominid culture was selectively accumulating, from generation to generation, a *capital stock* of shared ideas, percepts, potential behaviours, experiences, etc. A pool of acquired behaviours could accumulate despite the deaths of those acquiring them.

This remarkable process, this *cultural evolution*, was and is strongly analogous to natural (biological) selection and that includes being shaped by analogues of the necessary and sufficient conditions under which natural selection occurs, namely, phenotypic variations which (a) are directly related to variations in reproductive success and which (b) are more or less heritable.

Corresponding to the triplet of phenotype-genotype variation, fitness differences and parent-offspring transmission under natural selection, the necessary and sufficient conditions supporting cultural evolution in hunter-gatherer times were:

Generation of variation—spontaneous exploratory behaviour in what-to-do situations and in atypical situations where existing technology recipes require some adjustment/modification before they can be successfully applied.

Selection for fitness—a tendency for such technological innovations to be selected to replace or be added to previous technologies in situations where trials confirm they improve the group's ability to capture energy, either directly or (like food-sharing) quite indirectly. We might note though that for existing technologies to be replaced, the gains would need to outweigh the 'transition costs' of overturning existing traditions and habits in societies which experience would have taught to be highly conservative.

Perpetuation through 'inheritance'—reliable transmission between individuals and retention within the group memory (social learning) of recipes for successful technological innovations. Initially, transmission was through non-verbal mimesis but, late in the Pleistocene, through verbal instructions on how to implement technology recipes.

Technologies are like genes in several ways. Indeed, they are prime examples of the 'imitable behaviours' which Richard Dawkins' called 'memes' and Edward Wilson called 'cultural genes' or 'culturgens'.[149] They can appear spontaneously like mutations, they are available for use as needed and they can be recombined to create new capabilities.

While the rate of biological evolution slowed after the human brain reached its present size, the rate of cultural evolution, and hence of technology accumulation or *cultural-capital accumulation*, began to speed up at that time and has continued to speed up until the present day. This 'swamping' of biological change by cultural change in human populations is (like biogenesis, sex, multicellularity, sociality, etc.) one of the truly remarkable emergent developments in the evolution of life on Earth. And, at least till the Neolithic Revolution (10 kya), when new energy-capturing technologies emerged, it was developments in one technology, namely, language, particularly vocabulary size, which uniquely allowed, no, hastened, the ongoing upgrading of cultural evolution's processes for generating, selecting and retaining new technologies.

[149] Dawkins, R., 1989, *The Selfish Gene*, Oxford University Press, Oxford; http://en.wikipedia.org/wiki/Culturgen (Accessed 17 Dec 2010).

Bye-Bye Pleistocene, Hullo Holocene

So, there we have it. About 15 kya the end of the ice age was signalled by rising temperatures, rising seas, melting glaciers, declining populations of large food animals and spreading forests (in Europe) and deserts (in north America). The species of present interest, *Homo sapiens*, was to be found over most of Eurasia and Australia and poised to spread through the Americas and the Pacific. Humans would appear to have been remarkably well placed to meet the challenges and opportunities posed by niche loss and niche gain at this time. They had adapted to but escaped capture by low-temperature environments. Their implicit (probably non-conscious) strategy for achieving this had been to develop an 'extended phenotype', a variety of 'prosthetic' technologies—material, social, communicative and cognitive—for amplifying individual and group capabilities in diverse ways. Paramountly, these were not genetically fixed like instincts but available for use as situations demanded, e.g. shedding clothes in warm weather.

For human populations everywhere, this was the strategy they would take forward into the Holocene epoch, accumulating further technologies suited to and possible within the particular biomes they occupied; creating a hunting culture rather than a fishing culture for example. Trade and other contacts (e.g. ceremonial) between groups would continue to ensure a degree of technology transfer between populations and sufficient genetic mixing to preclude further speciation.

With hindsight, many of the technologies coming out of the Pleistocene were precursors to and components of more developed Holocene technologies. For example, fire management comes, and has to come, before metal smelting; the social technology of chiefdoms is the first step towards the role specialisation and stratified societies of the Mesopotamian civilisations; in cognitive technology, magical thinking sets the stage for scientific thinking; and in communicative technology, pictorial images lead to writing.

And, at some stage, as the range of extant technologies increased, 'compound' technologies involving the combining of existing technologies began to be invented with increasing frequency. Why? Because the (theoretical) possibilities for new compound technologies increase in proportion to the square of the number of existing technologies. For several reasons however, the process of technology invention did not thereby 'explode'. One is that most combinations of existing technologies are either infeasible or not useful. Another is that in hunter-gatherer and early Holocene village societies there may not have been enough discretionary time or enough surplus food energy to support the exploratory behaviour that can generate new combinatorial technologies.

Nevertheless, a process of fitful compound growth in the available suite of technologies was now under way and has continued till the present day. Remembering our broad conceptualisation of *technology*, cultural evolution can be usefully viewed as a process of inventing and applying new technologies. Cultural evolution was and is a response which human societies make to changed conditions, to changes in their environment. But it is not a necessary or universal response—'do nothing' is also a possible response.

Nor is there any guarantee that the invention and application of new technologies will improve the species' adaptedness. Certainly it is a strategy which created a new mode of production, a new social and economic system under the enormous shift from Pleistocene to Holocene conditions. And, as measured by the subsequent increase in human population numbers, cultural evolution did not fail this test. Perhaps cultural evolution is a strategy which would have failed under other environmental lurches but that is unknowable.

Whether or not cultural evolution improved quality of life for most people in a Holocene environment is, as we shall see, more debateable. But the even more important question which has now been opened up is whether adaptation by cultural evolution is a dead-end strategy which, if continued, will lead to the extinction of the species, for example, by generating overwhelming rates of cultural and environmental change. At this stage we might just note, with the benefit of hindsight, that by the beginning of the Holocene, cultural evolution had produced a variety of technologies with the potential to become maladaptive in the longer term, e.g. anthropomorphic models of the natural world, a dual morality (amity and enmity) and tradition.

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