An aetiology of hominin behaviour

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ABSTRACT

A rough framework for a first attempt to formulate a preliminary aetiology of hominin behaviour is proposed, based on scientific rather than archaeological evidence and reasoning. Distinctive precursors of modernity in human behaviour were present several million years ago, and since then have become gradually more established. By the beginning of the Middle Pleistocene, modern human cognitive processes seem to have been largely established. However, full modernity of behaviour can only have occurred in recent centuries, and there remain great variations in it even among extant conspecifics. This model differs significantly from all narratives offered by mainstream archaeology, which generally place the advent of modern human behaviour 30 or 40 millennia ago. These notions and the hypotheses they are based on appear to be false, however such behaviour is defined.

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Introduction

Speculations about the behaviour of hominins, which include the genera *Homo*, *Australopithecus*, *Paranthropus* and *Ardipithecus*, are traditionally provided by archaeology and palaeoanthropology. They are generally based on observations about specimens and the perceived contexts in which these are found. Other disciplines interested in this subject tend to accept such pronouncements concerning the cognitive, intellectual and cultural status of any hominins (excluding those of the sole extant representative since the introduction of written records, which are the preserve of other social sciences). In this paper it is proposed that the epistemology inherent especially in Pleistocene archaeology renders many if not most such pronouncements unreliable. There are numerous reasons for this, apart

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from the obvious lack of internal falsifiability of most archaeological and many palaeoanthropological propositions. For instance, in perceiving cultural evolution as teleological, archaeology ignores that evolution is fundamentally dysteleological—an example of the incommensurabilities between human-istic and scientific terminologies. Since devolution cannot occur in biology, but can and does occur in culture, the respective meanings of "evolution" differ fundamentally in archaeology and biology. Qual-ities such as behaviour, cognition, intellect, intention or meaning are not recoverable by archaeology. Moreover, the imposition of modern, literate narratives on properties of incredibly remote societies needs to be questioned (Helvenston, 2013). Lithocentric Pleistocene archaeology cannot even define culture reliably, because taphonomically truncated tool traditions are inert to emic identification, nor should they be expected to differentiate cultures. Rather than characterizing cultures by cultural vari-ables, such as rock art, the discipline has invented tool types (etic constructs or "observer-relative, institutional facts"; *sensu* Searle, 1995), whose combinations are regarded as diagnostic in identifying cultures. These in turn became the basis of invented ethnic entities such as, for instance, "Mousteri-ans". Obviously the concept of such a discrete society, tribe, language group, nation or ethnicity has no sound logical basis. Of the many limitations to the credibility of the discipline, one more needs to be mentioned here: for much of the last two centuries, all of the most important discoveries in Pleistocene archaeology were presented by non-archaeologists and were without exception rejected for decades—a trend that has continued to this day.

The discipline thus presents an overall impression of what Kuhn (1962) identifies as a "pre-paradigmatic" state: completely fragmented theoretically and methodologically, lacking a universal theory, and subject to fads and sectarianism. Different schools of thought that interpret the same phenomena in radically different ways determine its course. One of the most influential origins myths is the notion that "anatomically modern humans" (bearing in mind that "we have never been modern"; Latour, 1993; cf. Tobias, 1995) arose in sub-Saharan Africa and, somehow unable to interbreed with any other humans, replaced all other humans by exterminating or out-competing them. Introduced by an academic hoax (Henke and Protsch, 1978; Protsch, 1973, 1975; Protsch and Glowatzki, 1974; Protsch and Semmel, 1978), it prompted a series of hypotheses placing the origins of these "mod-erns" in Africa (Bräuer, 1984; Cann et al., 1987; Eswaran, 2002; Pennisi, 1999; Smith et al., 2005; Stringer and Andrews, 1988; Templeton, 2002), although there is no genetic, cultural, technological or palaeoanthropological evidence for this (Barinaga, 1992; Bednarik, 1991, 1992, 1995, 2003a, 2008a; Cann, 2002; Brookfield, 1997; Garrigan et al., 2005; Gibbons, 1998, 2010; Green et al., 2006, 2010; Gutierrez et al., 2002; Hardy et al., 2005; Hartl and Clark, 1997; Hedges et al., 1992; Maddison, 1991; Maddison et al., 1992; Rodriguez-Trelles et al., 2001, 2002; Templeton, 1992, 1993, 1996, 2002, 2005; Tobias, 1995; Watson et al., 1996).

This example (many others could be given) illustrates how susceptible the hermeneutics of Pleis-tocene archaeology are to capricious but unsupported hypotheses, and how these tend to dominate the public dissemination of its topics. In this paper it is proposed that, rather than being guided by the explanations this discipline tends to offer, the initiative in considering the behaviour of early humans should be taken by the relevant biosciences. Some efforts have been made to sustainably bring the neurosciences and cognitive sciences into correlation with archaeological narratives of Pleistocene hominin behaviour, but most have been severely hampered by inadequate archaeological models such as the replacement or "African Eve" hypothesis. Rather than inventing interpretations of sup-posed archaeological observations, made on the basis usually of modern Western perspectives (which are themselves the result of modern behaviour patterns), it is proposed to apply scientific reasoning.

Modernity of behaviour is not determined by modern explanations of what are purported to be archaeological traces of ancient behaviour, but by the state and operation of the neural structures that are involved in moderating behavioural patterns. Therefore this paper makes no attempt to elucidate specific instances of supposed ancient behaviour, but instead considers the generic frameworks giving rise to primate behaviour. Modern human behaviour is not only determined by the intrinsic neural structures and endocrine systems giving rise to it. These are demonstrably influenced by ontogenic experiences of the individual and their effects on these neural configurations. Cultural (i.e., learned) activity modifies both the chemistry and anatomy of the brain (Malafouris, 2008), affecting the flow of neurotransmitters and hormones and the quantity of grey matter (Draganski et al., 2004; Maguire et al., 2000). Patterns of hominin behaviour at any point in history would have been determined and

moderated by the interplay of specific behavioural imperatives: social norms and pressures, the range of behavioural options perceived to be available to the individual, given a specific set of beliefs. These beliefs would have been formed by many influences, such as society's framework and individual life experience, i.e. ontogenic factors specific to the individual. Much of modern behaviour is driven by a set of powerful imperatives, especially the desires for security, peer approval and "respect". There are the desires to be taken seriously, the desire of belonging (to a place, group, or whatever), to believe in something (which is cognitively easier than not to do so). There are also desires to be useful, for control, for love, and for more of what is desired but exceeding what is essential for survival. Defining these and other properties in neuroscientific terms is well beyond present means, and the biases likely to occur when a narrow-minded organism deigns to study itself must also be considered.

The obvious epistemological impairment is that psychology explores human behaviour by analyzing its observed extant expressions, without recourse to how or why these may have developed in the phylogenic past; it lacks a scientific context, which demands causal explanations. In this paper it is attempted to show that an aetiology of human behaviour might be achievable if the orthodox models of the gatekeepers of the human past are replaced with more realistic ones.

Late Pleistocene human phylogenesis

The controversies concerning the recent development of hominins, particularly in the form of the replacement hypothesis (complete replacement of all hominins by a new species), have significantly contributed to retarding progress in questions such as those concerning hominin behaviour, or the phylogenesis of hominins in the last part of the Pleistocene. The natural selection implicit in the replacement model cannot account for the empirical evidence, for the rapid neotenization (Bednarik, 2008a), or for the retention of numerous degenerative or unfavourable alleles (Bednarik, 2008b, 2011b,c; Bednarik and Helvenston, 2012). The replacement hypothesis also lacks any supporting evidence, be it genetic, palaeoanthropological or archaeological (Bednarik, 2008a). Introgressive hybridization (Anderson, 1949), allele drift based on generational mating site distance (Harpending et al., 1998) and genetic drift (Bednarik, 2011a) through episodic genetic isolation during climatically unfavourable events (e.g. the Campagnian Ignimbrite event, or the Heinrich Event 4; Barberi et al., 1978; Fedele and Giaccio, 2007; Fedele et al., 2002, 2003) can fully account for the mosaic of hominin forms found in the Late Pleistocene (Bednarik, 2008b, 2011b,c).

More importantly, the replacement hypothesis has misinterpreted that period's human phylogeny (Eckhardt, 2000), which is marked by a suite of disadvantageous somatic, neural and genetic changes (cf. Post, 1971). Within an instant in evolutionary time, the size of the brain decreased by about 13%, cranial and other skeletal robusticity declined markedly, as did physical strength. This was accompanied or followed by the rise of almost countless neuropathologies, including the genetic preservation of literally thousands of syndromes and disorders endemic to humans (Bednarik, 2011b; Enard et al., 2002; Marvanová et al., 2003; Olson and Varki, 2003; Rubinsztein et al., 1994; Sherwood et al., 2011; Walker and Cork, 1999). These include numerous neurodegenerative diseases as well as frontal lobe connectivity problems, demyelination, dysmyelination and thousands of Mendelian disorders. Then there is a host of further deleterious conditions: cleidocranial dysplasia, malformed clavicles and dental abnormalities (genes RUNX2 and CBRA1 refer), type 2 diabetes (gene THADA), or the microcephalin D allele, introduced approximately 37,000 years ago through a single progenitor copy (but could be as recent as 14,000 years ago, at 95% confidence interval; Evans et al., 2005). Another contributor to microcephaly, the ASPM allele, appeared around 5800 years BP (Evans et al., 2005; Mekel-Bobrov et al., 2005). A host of mental illnesses has been established in the human genome since the appearance of what is often called "anatomically modern humans", especially in recent millennia, even centuries (Bednarik and Helvenston, 2012; Helvenston and Bednarik, 2011).

Why the ascent of this gamut of deleterious conditions was not vigorously selected against by natural evolution is perfectly expressed by the classic "Keller and Miller (2006) paradox", which was resolved soon after it was stated (Bednarik, 2007, 2008a,b). In a species fully subject to the canons of natural selection such numerous disadvantageous mutations would be suppressed vigorously. The suspension of Darwinian evolution had remained completely unrecognized until recently because Pleistocene archaeology and palaeoanthropology have pursued the replacement hypothesis with such

fervour that they failed to notice that it is ultimately based on a hoax by a German archaeologist (Schulz, 2004; Terberger and Street, 2003). For several decades beginning 1973, numerous fake datings of human skeletal remains had promoted this hypothesis to the point that it dominated the discipline. The distinctive changes during the final third of the Late Pleistocene are largely the result of self-domestication caused by the determination of breeding patterns by rising cultural imperatives that have been identified (Bednarik, 2008b). Domestication promotes unfavourable alleles (e.g. Andolfatto, 2001; Horrobin, 1998, 2001; Lu et al., 2006) and it can even account for otherwise unexplained features, such as the abolition of oestrus in females. Under the auspices of this process predispositions for brain illnesses and other pathologies and the growing influence of cultural choices were protected from natural selection. They are endemic to the subspecies *Homo sapiens sapiens*, whose neuropathologies tend to affect the very same brain regions that developed most recently and are the most vulnerable (Bednarik, 2008a, 2011b; Helvenston and Bednarik, 2011). All these developments marking the emergence of "modern" humans took place exclusively in the last forty millennia, and at an accelerating rate. For instance the genes CADPS2 and AUTS2, involved in autism, appear with Graciles, and NRG3 (schizophrenia) is also absent in Robusts. Using the human haplotype map to test for selective sweeps in regions associated in genome scans with psychosis, such as 1q21, is promising (Voight et al., 2006). Such selective sweeps tend to yield relatively recent aetiologies, of less than 20,000 years. Some conditions, such as schizophrenia, have been suggested to be much more recent (Bednarik and Helvenston, 2012), and so far no known relevant susceptibility alleles have been reported from robust human remains.

The most prominent effect of the unintentional human self-domestication is the marked neotenization becoming evident with the rise of Upper Palaeolithic cultural traits. Hominin neotenization, which had already had a slight effect in previous physical evolution, accelerated markedly between fifty and thirty millennia ago, to the point of prompting the notion of replacement with a new species. Neoteny (pedomorphism, foetalization or juvenilization) defines the retention into adulthood of juvenile or foetal physiology (Ashley Montagu, 1989; Gould, 1979; Thiessen, 1997). Humans resemble chimpanzees anatomically most closely in the latter's foetal stage (Ashley Montagu, 1960; De Beer, 1940; Haldane, 1932). The skull of an unborn ape is thin-walled, globular and lacks the prominent tori of the adult ape, thus resembling the cranium of a modern human. Upon birth its robust features develop rapidly. The face of the ape embryo forms an almost vertical plane, as it does in the modern human all the way through adulthood, which is not the case in mature apes. Even the brains of foetal apes and adult humans are much more similar to each other, in terms of proportion and morphology, than they are to those of adult apes. Both the foetal chimpanzee and the adult human have hair on the top of the head and on the chin, but are otherwise largely naked. All male adult apes have a penis bone, but it is categorically absent in both foetal chimpanzees and all humans. The atrophy of the penis bone in humans appears to have been compensated for by the organ's significantly increased length and thickness, relative to apes (Badcock, 1980, p. 47). Similarly, in female chimpanzees, the *labia majora* are an infantile feature; in humans they are retained for life. The hymen, too, is present only in the neonate ape, but in the absence of penetration is retained for life in human females. The organs of the lower abdomen, such as rectum, urethra and vagina, are typically aligned with the spine in most adult mammals, including apes; only in foetal apes and humans do they point forward relative to the spine. The human ovary reaches full size at the age of five, which is the age of sexual maturity of the apes (De Beer, 1940, p. 75). The legs of foetal apes are relatively short, while the arms are about as long in relation to the body as in humans. In the apes, the arms become much longer after birth. Human hands and feet resemble those of embryonic apes closely, but differ significantly from both hands and feet of mature apes. In fact the human foot, especially, retains the general structure found in unborn apes, which rather contradicts the hypothesis that it is an adaptation to upright walking. It could equally well be the case that upright locomotion is an adaptation to the neotenous foot of hominins, a possibility never considered by palaeoanthropology. Even the shape of the cartilage of the ear in humans is a neotenous feature.

Neoteny is a phylogenic development in which foetal characteristics remain into adulthood, and specific processes of anatomical maturation are retarded (De Beer, 1940). "But neoteny does not only contribute to the production of large structural change; but it is also the cause of the retention of plasticity" or "morphological evolvability" (De Beer, 1930, p. 93). Adaptively useful novelties supposedly

become available as maturation genes are freed by pedomorphosis. It is self-evident that, relative to the neonate ape, the newborn human is not remotely as far developed. In the first year after birth, the human brain more than doubles in both volume and weight. It continues to grow, approaching adult size by the age of three, but goes on expanding slightly more up to adolescence and even beyond. Rhesus monkeys and gibbons achieve 70% of adult brain size at birth, the remaining 30% in the subsequent 6 months. In the great apes, the size of the brain approaches adult size after the first year of life.

In the human genus neotenous traits include an exceedingly large brain, thinness of skull bones, flattened and broadened face, lack of tori, relatively large eyes, smallish nose, small teeth and jaws, and limbs that are proportionally short relative to the torso, especially the arms (Ashley Montagu, 1989; De Panafieu and Gries, 2007; Gould, 1977). The acquisition of some of these characteristics involved enormous evolutionary costs, and most are decidedly detrimental to a primate. As in the case of adverse changes to the neural and endocrine systems, these deleterious developments need to be explained, because many of them completely contradict the principles of evolution. In the most recent phylogeny of humans these have been suspended and replaced by the rules of domestication: systematic sexual selection in favour of specific characteristics, which were determined by cultural factors rather than those determining evolutionary fitness. In other words, in the most recent history of hominins, natural selection became increasingly moderated, and eventually almost replaced, by cultural selection (Bednarik, 2008a, 2011b).

This process can be observed in the rapid gracilization among skeletal remains, especially in the females, beginning about 40,000 years ago (Bednarik, 2008b, 2011b,c). It was the females who led the neotenization in recent humans, and neoteny, although occurring in both genders, has remained more strongly expressed in women than in men. Its typical features are smaller body size, more delicate skin and skeleton, smaller mastoid features, significantly reduced or absent tori, less hair but retention of foetal hair, higher pitch of voice, more forward tilt of head but more backward tilt of pelvis, smoother ligament attachments and narrower joints, but they also include increased longevity, lower amount of energy expended at rest, faster heartbeat and prolonged development period (Ashley Montagu, 1960). Few of these features present any appreciable evolutionary benefits, although the last mentioned certainly does.

One of the very few significant differences between humans and other animals is that no animal, including all other primates, has any preferences in mate selection of youth, specific body ratios (e.g. hips vs waist), facial features and symmetry, skin tone or hair. In modern humans these culturally determined factors are undeniably crucial in the preference of mating partners, therefore they must have been introduced at some time in the past. Apart perhaps from facial symmetry, which may imply high immunocompetence (Grammer and Thornhill, 1994; Saxton et al., 2011; Shackelford and Larsen, 1997; but cf. Boothroyd et al., 2005, 2009), there are no biological advantages in these strongly developed "cultural" biases. Facial "attractiveness", for instance, is a cultural construct found in all extant societies (Cunningham et al., 1995), and in female humans, neotenous facial features are strongly preferred by males (Jones, 1995, 1996). These include, irrespective of cultural context, neonate large eyes, shiny hair, small noses, reduced lower facial regions, thin jaws and high foreheads (Perrett et al., 1994; Sforza et al., 2009), which are all distinctive neonate features. Obviously such pronounced preferences in female mate selection will inevitably effect significant somatic changes in populations that are totally unrelated to environmental variables. Such changes can be best observed in the hominins of central Europe, such as those from many Czech sites, of the period from about 35,000 to 25,000 years ago (Bednarik, 2008b). Darwin's laws of evolutionary theory were supplanted by Mendelian laws of inheritance (Mendel, 1866), and humans domesticated themselves, albeit unintentionally, through selective breeding that favoured specific physical characteristics (Bednarik, 2008a,b, 2011a,b,c). Neoteny was even favoured psychologically (Charlton, 2006). The neotenous psychological traits of individuals of outstanding mental faculties derive precisely from the "retention of plasticity" or "morphological evolvability" De Beer (1930) had already referred to. The baby-faced students Zebrowitz et al. (1998) refer to tend to outperform their less-neotenized peers academically today (cf. Buchen, 2011).

Domestication is the collective genetic alteration of the physiology, behaviour or life cycle of species through selective breeding. Humans are not the only initiators of domestication; many animal species, from mammals to ants, have domesticated others, for instance to modify foods indigestible by the

domesticators, or for their labour, or simply to serve as staple food source (Bednarik, 2011b). Selective breeding defies natural evolution in the sense that it can rapidly change the characteristics of a population without any natural selection in the Darwinian sense occurring. Selection for single traits inevitably results in changes in numerous others, and these changes tend to be deleterious. For instance domestication of animals typically results in decreased cranial volume relative to body size, a decrease that can be as much as 30–40%. Neotenous physical traits arising from the domestication of animals include changes in reproductive cycles (oestrus), fewer or shortened vertebra, curly tails (Trut, 1999), loss of hair, larger eyes, rounded forehead and shortened muzzle (Bertone, 2006). Several of these (and others) reflect the gracilization noted in humans, and that also applies to the changes in behaviour, towards playfulness, behavioural plasticity, exploratory pattern and pathology.

Theory of mind

Therefore the first major factor in understanding early human behaviour is that what are perceived as certain modern patterns very probably appeared together with the rapid somatic changes of the last part of the Late Pleistocene. They are then essentially attributable to human neotenization, which accelerated markedly at that time. In many ways this process resembles devolution, and it occurred almost entirely outside the canons of Darwinian evolution (biological devolution is impossible, because evolution is dysteleological). This does not, however, imply that modernity in human behaviour should be expected to have appeared as one single package during that time, which archaeologists in Eurasia call the "early Upper Palaeolithic", and which witnessed rapid gracilization of all human populations in four continents (Bednarik, 2011b). To consider the origins and aetiology of human behaviour it does not suffice to focus on these last forty or so millennia. What transpires from the above is that "it was human behaviour itself" that determined the most recent course in the development of the species, from robust *Homo sapiens* (such as *H. sapiens neanderthalensis*) to *H. sapiens sapiens*. This immediately raises the question: what were the preceding developments that set the stage for this final phase? If a viable and comprehensive aetiological history of human behaviour is to be formulated, it will be necessary to consider the possible antecedent developments that could have led to the final ascent of culturally induced neoteny.

Three factors demanding attention in any speculation about early hominin behaviour are theory of mind (ToM) and the issues of self-awareness and consciousness. ToM defines the ability of any animal to attribute mental states to oneself and others, and to understand that conspecifics have beliefs, desires and intentions; and that these may be different from one's own (Baron-Cohen, 1991; Baron-Cohen et al., 1997; Bednarik, 2011b; Frith and Happé, 1994; Happé, 1997; Happé et al., 1996; Jacques and Zelazo, 2005; Jarrold et al., 2000; Ozonoff and Miller, 1995; Premack and Woodruff, 1978). Each organism can only prove the existence of his or her own "mind" through introspection, and has no direct access to others' "minds". The presumption that other cognizing organisms have beliefs, intents, desires, pretending, knowledge, etc. is the basis of a ToM. Although present in numerous species, at greatly differing levels, it has perhaps attracted most attention in the study of two groups, children and great apes, and the level they conceive of mental activity in others, attribute intention to, and predict the behaviour of others (Call and Tomasello, 1998). It is thought to be largely the observation of behaviour that can prompt a ToM.

The discovery of mirror neurons in macaques in the 1990s (Di Pellegrino et al., 1992; Rizzolatti et al., 1996) has provided much impetus in the exploration of how a ToM is formed (Gallese and Goldman, 1998; Iacoboni et al., 2005). Mirror neurons are activated both when specific actions are executed and when identical actions are observed, providing a neural mechanism for the common coding between perception and action (but see Hickok, 2009). One of the competing models to explain ToM, simulation theory (Gordon, 1986, 1996; Preston and de Waal, 2002), is said to derive much support from the mirror neurons, although it predates their discovery by a decade. These neurons are seen as the mechanism by which individuals simulate others in order to better understand them. However, mirror neurons have so far not been shown to produce actual behaviour (Provine, 2009). Motor command neurons in the prefrontal complex send out signals that orchestrate body movements, but some of them, the mirror neurons, also fire when merely watching another individual—not necessarily a conspecific—perform a similar act. It appears that the visual input prompts a "virtual reality" simulation of the other

individual's actions. However, ToM and "simulation", though related, may have different phylogenic histories (Keysers and Gazzola, 2007; Sommerville and Decety, 2006), and the roles of mirror neurons may be much more complex than anticipated; they may be involved in the formulation of constructs of reality (Bednarik, 2011b). Ramachandran (2009a) has speculated about the roles of mirror neurons in cognitive evolution (Oberman and Ramachandran, 2009), in empathy, imitation (cf. Ferrari et al., 2009) and language acquisition (cf. Rizzolatti and Arbib, 1998). His examples of germane evidence include anosognosia in a small cohort of right hemisphere stroke patients, which prompts denial of paralysis in other patients; and the suppression of the MU brain wave in humans when their hand is moved.

Neurological conditions have shown that the self is not the monolithic entity it believes itself to be. These conditions include out-of-body-experiences, apotemnophilia (alienation of a body part, especially a limb, which derives from congenital defect in the right parietal), transsexuality, Cotard's syndrome (patient is convinced to be dead), the Capgras delusion (because visual and emotional brain areas are disconnected, patient experiences familiar entities as substitutes or imposters), or akinetic mutism (patient is completely unresponsive, unable to talk or walk, despite being fully awake; caused by damage to the anterior cingulate) (Ramachandran, 2009b). Susceptibility to proprioceptive drift, demonstrated by the rubber hand illusion (Peled et al., 2003), probably accounts for out-of-body-experiences (Thakkar et al., 2011). This is one of the examples Ramachandran cites, and this susceptibility varies considerably among individuals. It is probably connected with low levels of "body ownership" and schizotypy, and such conditions can induce the belief that the patient is outside of his/her body, e.g. floating above it and actually seeing the body. Other conditions confirm that the brain's right parietal lobe contains in the superior parietal lobule an internal image of the body. Pathology affecting this body image has psychologically demonstrable, dramatic effects. For instance it is thought to be the underlying cause of anorexia nervosa and somatoparaphrenia (or apotemnophilia; cf. anosognosia). The latter syndrome, found in about 5% of right hemisphere stroke patients, leads these to deny their own paralysis. Some of these patients even deny the similar paralysis in fellow patients, which is probably attributable to the function of the mirror neurons. Ramachandran (2009a) suggests that, to make a judgment about somebody else's movements, one has to run a virtual reality simulation of the corresponding movements in one's own brain. Other phenomena probably involving mirror neurons are contagious acts such as yawning and laughing, or the odd fact that one cannot tickle oneself (Provine, 2009). There is, however, nothing trivial about the gravity of these various insights, an importance that cannot possibly be overstated. They seem to bring into focus the most profound question an intelligent organism appears to be able to contemplate: how does the brain form a construct of external reality? They raise the possibility that Plotkin's (2002) concept of an imagined world made real was closer to factuality than even he anticipated. Ultimately it must be recognized that, so far, there has not been a viable universal theory of how the neuronal mechanisms and systems of the brain create reality from the sensory input of the phenomenal world, which after all underlies all science. These above considerations suggest that, put simply, the parietal lobe might be creating a virtual-reality-like model of the external world, much in the same way as it forms a mental image of the body.

It must also be mentioned that there is evidence against attributing ToM to mirror neurons. Brain regions implicated in it are the anterior paracingulate cortex, the superior temporal sulci and the temporal poles bilaterally (Gallagher and Frith, 2003), among others. But the mirror neurons are located in the inferior frontal cortex and superior parietal lobe. Also, macaques lack a developed ToM despite having mirror neurons. Both ontogenically and phylogenically, a ToM is acquired gradually, and precursory behaviours to a ToM are recognized. Understanding attention (Baron-Cohen, 1991), understanding of others' intentions (Dennett, 1987), and imitative experience with conspecifics (Horowitz, 2003) are hallmarks of a ToM. The "false-belief task" (Wimmer and Perner, 1983), which establishes the ability of an individual to attribute false beliefs to a conspecific, is seen as a key indicator of the level of development of ToM. In humans it occurs normally around the age of four, but while it is found in children with Down syndrome, it is absent in most of those with autistic spectrum disorder (Baron-Cohen et al., 1985; Leslie, 1991), and a link with mirror neurons is suggested (Oberman and Ramachandran, 2007; Oberman et al., 2005; Williams et al., 2001). Another such test (Gopnik, 1988; Gopnik and Astington, 1988) can be passed by most 5-year-olds (see also Leslie and Thaiss, 1992; Sabbagh and Moses, 2006;

Zaitchik, 1990). These abilities would seem to mark the threshold of human ToM, but since precursory behaviours indicative of ToM are found widely among non-human species, such behaviour would be expected in primate phylogeny well before the australopithecines. Similarly, in a credible model well-developed stages of ToM would realistically need to be attributed to such species as *Homo habilis* or *Homo erectus*. The ontogenic parallels are relatively well understood. Intentional behaviour can be detected by infants 5–9 months old (Woodward, 1999), while at 15 months infants can classify actions according to their goals (Csibra et al., 2003). The same abilities are available to chimpanzees and orangutans (Call and Tomasello, 1998), but apparently not to monkeys (Jellema et al., 2000). Between 18 and 24 months, the child establishes joint attention (Franco and Butterworth, 1996), as well as engages in pretend-play, and it develops an ability to understand desires (Rapacholi and Gopnik, 1997; Wellman and Wooley, 1990; Wellman and Liu, 2004). Again, apes use gaze monitoring to detect joint attention (Hare et al., 2000), but monkeys apparently do not. But it is with the appearance of "metarepresentation", the ability to explicitly represent representations as representations (Baron-Cohen, 1995; Leslie, 1994; Perner and Garnham, 2001), and with recursion that human ToM emerges, as these are lacking in the great apes (Call and Tomasello, 1999; Suddendorf, 1999). Similarly, the apes have so far provided no evidence of episodic memory or future planning (Suddendorf and Busby, 2003). Episodic memory, which is identified with autonoetic consciousness, can be impaired in humans, e.g., in amnesia, Asperger's syndrome, or in older adults (Gardiner, 2001). It can be attributed to differential activity in the medial prefrontal and medial parietal cortices, imaging studies of episodic retrieval have shown (Lou et al., 2004).

Homology would then suggest that precursory ToM behaviour such as the detection of intention, goals and joint attention would have appeared in human ancestors during the Miocene, while metarepresentation and recursion are likely to have emerged in the Pliocene. Planning of future action, self-representation, complex syntax and creative thought are rendered possible by these, as well as metamemory and counterfactual reasoning (Samson et al., 2004; Saxe and Kanwisher, 2003; Shimamura, 2000; Shimamura et al., 1990; Suddendorf, 1999; De Villiers, 2000). It is roughly at the age of 40 months that the child surpasses the ToM level of the great apes. Thus the executive control over cognition unique to humans, together with metarepresentation and recursion, must have developed in the last 5 or 6 million years. Although the brain areas accounting for the latter two faculties remain unidentified, executive control resides in the frontal lobes. Since the frontal and temporal areas have experienced the greatest degree of enlargement in humans (Bednarik and Helvenston, 2012; Semendeferi et al., 2001), uniquely human abilities would be expected to be most likely found there, although inter-connectivity rather than discrete loci may be the main driving force of cognitive evolution. But it is precisely the expansion of association cortices that has made the human brain disproportionately large (Preuss, 2000).

Self-awareness and consciousness

Turning to self-awareness, the sentience of one's own knowledge, attitudes, opinions and existence, it is again obvious that various levels apply to different species. Some of the great apes, the elephants and bottlenose dolphins are among the species that have passed the mirror test (De Veer and Van Den Bos, 1999; Gallup, 1970; Gallup et al., 2002; Heyes, 1998; Keenan et al., 2003; Mitchell, 1993, 1997, 2002; but see Swartz, 1997; Morin, 2003 for critical reviews), and interestingly they are much the same species shown to possess von Economo neurons (Seeley et al., 2006; Butti et al., 2009; Hakeem et al., 2009). This is perhaps not so much a relationship of direct supervenience; the connection may be via social complexity. Von Economo neurons seem to occur in relatively large species with large brains and extensive social networks (Bednarik, 2011b), and it may be that constructs of individuality evolved in tandem with these networks. Indeed, it is difficult to see how social complexity could have developed beyond that of ants, bees or termites without some level of self-awareness, just as the advent of self-awareness is hard to account for.

Self-awareness is seen as a superior, more developed form of consciousness. The hallmark of consciousness may be a transparent representation of the world from a privileged egocentric perspective (Trehub, 2009) but this does not reveal how it could have come about. Consciousness focuses attention on the organism's environment, merely processing incoming external stimuli (Dennett, 1991; Farthing,

1992), whereas self-awareness focuses on the self, processing both private and "public" information about selfhood. The capacity of being the object of one's own attention defines self-awareness, in which the individual is a reflective observer of its internal milieu and experiences its own mental events (Carver, 2002; Gallup, 1998; Gallup and Platek, 2002). What is regarded as the "self" is inherently a social construct (Seyfarth and Cheney, 2000), shaped by the individual's culture and immediate conspecifics (Leary and Buttermore, 2003). But the self is not the same as consciousness (Natsoulas, 1998), as shown by the observation that many attributes seen as inherent in the self are not available to conscious scrutiny. People invent the neurological computation of the boundaries of personhood from their own behaviour and from the narratives they form, which also determine their future behaviour. Thus it needs to be established how the chain of events from sensory input is established and how behaviour is initiated, controlled and produced (Carruthers, 2002; Clowes, 2007; Koch, 2004; Nelson, 2005). It appears that subcortical white matter, brainstem and thalamus are implicated in consciousness (Fernández-Espejo et al., 2011), although it is assumed that unconsciousness mainly involves the cortical brain (Velly et al., 2007) and the thalamus is not believed to drive consciousness. Ultimately consciousness is self-referential awareness, the self's sense of its own existence, which may explain why its aetiology remains unsolved. Hofstadter (2007) likens this quest to finding a self-consistent set of axioms for deducing all of mathematics, which Kurt Gödel has shown to be impossible, due to the self-referential nature of mathematical statements.

Internally directed aspects of cognition, such as ToM, episodic memory, self-evaluation and self-awareness derive from the default mode network (DMN), which is considered to be a functionally homogeneous system (Sestieri et al., 2011). Relative to ToM, conscious self-awareness is even less understood and accounted for ontologically. Neuroscience and neuropsychology favour the view that it is located primarily in a neural network of the prefrontal, posterior temporal and inferior parietal of the right hemisphere (Decety and Sommerville, 2003; Gusnard, 2005; Stuss et al., 2001; but see critiques in Morin, 2002, 2004; Morin and Michaud, 2007). In humans, a diminished state of self-awareness occurs for instance in dementia, sleep or when focusing upon strong stimuli (Cavanna and Trimble, 2006). Ultimately self-awareness must be the result of interplay of many variables, starting from the input of the proprioceptors to the engagement of several brain regions. It includes the operation of distal type bimodal neurons (moderating anticipation and execution; Maravita et al., 2003). What can be said about it is that it can be safely attributed to all hominoids and hominins, and there is a reasonable expectation that it became progressively more established with time. In contrast with the dogmatic rejection of Lower Palaeolithic beads by some archaeologists, from a biological perspective it is rather surprising that such artefacts, quintessential to defining self-awareness archaeologically, appear so late on the available record (during the Middle Acheulian technological traditions; Bednarik, 2005). As in so many other issues, biological, empirical and scientific perceptions clash irreconcilably with the fictitious narratives of Pleistocene archaeology (Bednarik, 1992, *et passim*).

Towards the aetiology of behaviour

Thus the relevant scientific information would provide a rough framework for a first attempt to formulate a preliminary aetiology of hominin behaviour, in which archaeological dogma, however, has no place. Lower levels of ToM certainly have to be expected in the Miocene and Pliocene ancestors of humans (i.e. for much of the last 20 million years) and beyond, and could reasonably be presumed to have developed during these periods (Foley, 1997). The behaviour of these primates must be assumed to have been attuned to the level of ToM and self-awareness that was available to them. In view of the dysteleological nature of evolution, the archaeological, teleologically guided assumption of a development of increased complexity cannot apply to a natural system. If it did, the system would cease to be natural (governed by Darwinian evolution alone). On the other hand, *culture can develop teleologically*, via incremental improvements involving a moderating intellect of gradually increasing autonomy. Therefore hominin intellect is neither archaeologically recoverable nor can it be inferred from stone tools, which is the underlying "lithocentric" mantra of most scholars in the field. The sciences, on the other hand, are perfectly capable of providing some of the crucial goalposts, and since these account for the most dramatic aspect of hominin evolution, encephalization, they need to gain priority in explaining the human ascent, including how modern behaviour originated. Given that

natural selection can only select expressed abilities, not latent ones, the indices Pleistocene archaeology fields in its speculations about behaviour, cognition or even technology are always flawed. The absurdity of archaeology's "explosion" or "great leap" around 40,000 years ago illustrates this, when it is contrasted with the empirical observation that the human brain approached its modern size many hundreds of millennia ago. Just as language can only be selected for after it has appeared, so can larger brain size, and to suggest, as archaeology implies, that for millions of years this brain increased relentlessly without being much used, is unacceptable to the biological sciences.

According to these deliberations, distinctive precursors of modernity in human behaviour were present several million years ago, and since then have become gradually more established. At the upper end of the time scale, the rapid neotenization and incidental self-domestication of the human line over the last forty or so millennia (Bednarik, 2008a,b, 2011b) were such that they would have completed the journey to fully modern behaviour patterns (but not necessarily behaviour identical to modern). However, in the task of beginning to formulate a first outline of the aetiology of human behaviour these are merely preludial considerations. Human priorities in studying the neotenous ape define the shortcomings of such an approach, particularly when they are dominated by a Western righteousness that has yet to learn that all human groups exist, and have existed, in different constructs of reality. As Helvenston (2013) argues cogently, conflating literate minds with the oral minds that inhabited the human past, which "cognitive archaeology" does without realizing, is the result of one such epistemological impairment.

"Modern behaviour", therefore, does not refer to the behaviour of modern Westerners, or to that of any other extant human group. Instead it is defined by the state of the neural structures that are involved in moderating behavioural patterns, which ultimately are determined by inhibitory and excitatory stimuli in the brain. The behaviours mapped onto these structures are more different than the countless languages that have been mapped onto similarly inherent systems of language centres. After all, human behaviour is not only determined by the intrinsic structures giving rise to it; these are demonstrably influenced by ontogenic experiences of the individual and their effects on these neural configurations. Just as there can be no doubt about the ontogenic plasticity of behaviour, it follows that the behaviour of all individuals must be different, each reflecting individual experience—just as the precise realities in which human individuals exist must all differ from one another. As Malafouris (2008) states, "the functional structure and anatomy of the human brain is a dynamic construct remodelled in detail by behaviourally important experiences". Cultural activity modifies the chemistry and structure of the brain through affecting the flow of neurotransmitters and hormones (Smail, 2007) and the quantity of grey matter (Draganski et al., 2004; Maguire et al., 2000). For instance the general introduction of writing in recent centuries has dramatically changed the brain of adult humans: although they start out as infants with brains similar to non-literate peoples, these brains are gradually reorganized as demanded by the thinking implicit in literacy, which is totally different from the thought patterns found in oral societies (Helvenston, 2013). The same applies to the more recent introduction of computers. The use of all symbol systems (be they computer languages, conventions for diagrams, styles of painting) influences perception and thought (Goodman, 1978). Therefore the complexity of the issue cannot be overestimated, but this does not change the underlying proposition that there must have been dominant patterns of hominin behaviour at any point in history. These would have been determined by the interplay of specific behavioural imperatives: social norms and pressures, the range of behavioural options perceived to be available to the individual, given a specific set of beliefs. These beliefs would have been formed by many influences, such as society's framework and individual life experience, i.e. ontogenic factors specific to the individual.

Behaviour is the outcome of neuronal activity and its interplay with the endocrine system (hypothalamus, pituitary gland, and pineal gland). Specific neurons can have considerable influence on behaviour, for instance the von Economo neurons have already been mentioned. The tonically active neurons, functioning as a gating mechanism between the matrisome and the striosome regions, modulate the orbital frontal cortex and anterior cingulate by adjusting the degree to which the thalamus drives both areas (Bednarik, 2011b, p. 177). The protein tau, a component of intracellular neurofibrillary tangles, has profound effects as neurons and synapses die and axons degenerate in Parkinson's disease. The current Human Microbiome Jumpstart Reference Strains Consortium (2010) has even offered the suggestion that gut microbiota may be involved in neural development and function, e.g.

in mood disorders (Forsythe et al., 2010). Similarly, *Helicobacter pylori* (a bacterium implicated in ulcers and stomach cancer) may help trigger Parkinson's disease. In short, human behaviour is the result of an exceedingly complex aetiology that currently defies comprehensive explanation.

Nevertheless, this paper has attempted a scientific definition of the broad parameters of the likely behaviour of hominins to probe the origins of modern behaviour. It has done this not by offering speculative musings about specific behaviour patterns, but by introducing relevant issues from the biosciences, thus facilitating the formulation of propositions that are testable within these. Archaeological appeal to plausibility has been explicitly excluded as being merely a stratagem to preserve a false dogma. That dogma demands that modern behaviour appeared with the purported speciation to recent Graciles, which is expressed in the Final Pleistocene cave art of south-western Europe (from 40,000 years BP onwards), therefore any preceding evidence of human modernity must be either false, incorrectly dated or its presenters must be mistaken. All of the assumptions underpinning this notion are false: the first Upper Palaeolithic cave art is not the work of Graciles (Bednarik, 2007); the amount of Middle Palaeolithic rock art surviving today is probably much greater than that of Upper Palaeolithic rock art (Bednarik, 2010); and empirical evidence of "behavioural modernity" precedes the Graciles by hundreds of millennia (Bednarik, 2011c). Attempts to sustainably bring the neurosciences and cognitive sciences into correlation with archaeological narratives of Pleistocene human behaviour have been made, but have been severely hampered by false archaeological models, especially the replacement hypothesis. Human modernity, be it somatically, culturally or behaviourally, did not appear as a single package at a particular time, but emerged as a series of progressive developments culminating in the recent neotenization episode in the last part of the Late Pleistocene. Human behaviour 30,000 years ago would have certainly differed dramatically from today's patterns, and yet it was fully modern in the sense that the biological structures producing patterns of behaviour were largely similar to today's. However, these similarities had been developing for eons prior to the emergence of that crown of evolution, *Homo sapiens sapiens* (Bednarik, 2011b).

The core trait under selection in the evolution of cognition is not tool use, or even ToM; it is high order control capacity (Christensen, in press). ToM, self-awareness, consciousness, technology and culture were all available to non-human species, but were not developed to an integrated system of a self-reflective brain that observes itself and then makes conscious decisions based on excitatory/inhibitory neural functions. For instance, the sleeping nests or tools of the great apes were not improved upon; there was no volition to do so. The same applies to the early stone tools of hominins up to mid-Early Pleistocene times. Therefore volition becomes the prompter, and it needs to be explained how its ability to derive abstract goals from the prefrontal cortex arose (R. Dielenberg, pers. comm.). The answer, it is proposed here, lies in the rise of cultural behaviour and its growing conscious comprehension of cause and effect. This development apparently took place at some stage in the Early Pleistocene. By the beginning of the Middle Pleistocene, 780,000 years ago, modern human behaviour as a neurological and endocrine process was well established, in the sense that the structures involved in moderating behavioural patterns were substantially in place. For instance the earliest evidence of maritime colonization, from that time (Bednarik, 1999, 2003b), demands that *Homo erectus* then possessed relatively complex communication, presumably in the form of speech. This clashes severely with the model expounded by Donald (1993, 2001) and its three-stage explanation. It also differs dramatically from all narratives offered by mainstream archaeology. The neural structures underwriting human behaviour at that time should be visualized as being not significantly different from those of present humans of, say, 8–12 years of age that have not been modified by written communication, or other forms of exograms (extra-cortical memory records of ideas; symbols). Thus consistent and skilled making and use of exograms is perhaps the most realistic indicator of essentially modern behaviour. It is evidenced in several forms during the Middle Pleistocene (Bednarik, 1993, 1995, 1997, 2005), which mainstream archaeology has yet to discover.

It also follows from the above considerations that "fully modern" human behaviour did not appear until recent centuries. The archaeological claims placing its advent 30 or 40 millennia ago are therefore false, however such behaviour is defined. For the rest of the Pleistocene and for most of the Holocene, human behaviour was modern in the sense that it used much the same structures as today, but it was certainly not modern in its expressions. Indeed, even among contemporary conspecifics, it can differ widely, for instance according to degree of literacy and sophistication of cause and effect

reasoning. Both these factors still vary greatly today: the behaviour of most present-day humans remains moderated by magical thinking-type mental processes (lack of integration between left pre-frontal cortical areas and memory), underwritten by sub-optimal cause and effect perception. In short, most of the rationalizing about past human behaviours has been conducted in unrealistic frameworks, and modernity of behaviour needs to be carefully defined.

Acknowledgments

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