Rock Art Research **2006** - *Volume 23, Number 1, pp. 3-40. D. HODGSON and P. A. HELVENSTON*

KEYWORDS: ***Palaeoart – Deception – Brain evolution – Limbic system – Cognition***

THE EMERGENCE OF THE REPRESENTATION OF ANIMALS IN PALAEOART: **Insights from evolution and the cognitive, limbic and visual systems of the human brain**

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Abstract. The organisation and evolution of the brain is beginning to provide clues as to how, why and when certain crucial behaviours may have arisen in hominins. As palaeoart constitutes evidence of such behaviour, it can therefore be understood within the broader context of hominin evolution as part of a series of connected biopsychosocial events that eventually led to the Upper Palaeolithic representations of animals. Iconic representation is accordingly shown to be linked in complex ways to how 'representation' occurred in the evolving brain in relation to the demands and dynamics of the evolutionary niche occupied by hominins.

Introduction

Visual depictions of animals, as they flourished in the Upper Palaeolithic, are thought to be a uniquely human event and an indicator of *Homo sapiens sapiens* with a truly modern brain, although not a modern mind (Helvenston and Bahn 2004). What is largely overlooked is the time depth of the process of primate evolution involved in the expression of this achievement. A detailed analysis of this issue suggests that perhaps one strand in the evolution of the production of the earliest visual depictions arose out of a common primate adaptive heritage, involving the decoding of deception and subterfuge manifested by predators and the deciphering of such diversions when pursuing prey. This would have involved a highly developed visual system, outstanding memory storage, and primordial but impressive problem-solving cognitive capacities. This essay will explore how such duplicity in representation, as it is manifest in nature, can help illuminate one reason why naturalistic pictorial representations burgeoned during the Upper Palaeolithic. An approach from this standpoint presupposes that pictorial representation did not appear suddenly during that period, but derived from a suite of interrelated activities concerning how distant human ancestors interacted with and felt about animals. It will also be demonstrated how this interdependence gave rise to certain activities relating not only to stealth in hunting and avoidance of predators, but also to proto-human feelings of awe and a primordial sense of the supernatural indicative of Donald's mimetic cultural period (1991).

Some authorities maintain that the representational art of the Upper Palaeolithic can be sufficiently explained by the customs and rituals of shamanism (Lewis-Williams 1991). This is an old theory, originally put forward in the 1960's and rejected unambiguously by André Leroi-Gourhan (Bahn and Vertut 1997). This claim continues to be highly controversial (Bahn 2001; Francfort and Hamayon with Bahn 2001; Helvenston and Bahn 2002, 2004). And, by itself, it is neither able to explain the long-standing preoccupation with animals to the almost total exclusion of any other subject, nor the existence of certain enduring formal elements in visual depictions (Hodgson 2003a). In order to resolve this issue, it is necessary from the outset to investigate why animals were such a cause for concern for hominins[1] as well as show how the evolution of the human brain in relation to the determining environmental niche can provide clues as to the neurological and behavioural precursors that led to this capability. This will involve an understanding of ethology and the way the brain has evolved in relation to the ecological niche pertaining to humans as a species. We believe that the study of both comparative primatology and comparative primate neuroanatomy provide excellent insights into human evolution, for, as Fiedler (2003: 114–5) has emphasised, the origin of representation is to be found in ethology rather than archaeology or anthropology. We are fully aware of the awesome complexity of neuro-evolution, and thus, when

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[1] Although we are aware that there is not complete agreement as to whether there is or is not a significant difference between the *Hominidae* and the *Homininae*, it is more convenient in this paper to reserve the term *hominin* to refer to taxa on the human lineage after the separation from apes, including *Sahelanthropus tchadensis, Orrorin tugenensis, Ardipithecus, Australopithecus, Homo habilis* etc.; and the term *hominid* to refer to both the ancestors of the African great apes and humans. See Berger (2001) for a brief, yet complete summary of the new taxonomy of these family trees.

we refer to the evolution of certain specific systems or structures, it is not to imply that other cerebral areas were not also developing. Rather, it is a means of simplifying a multifaceted process in order to present our specific thesis.

Part 1 will explore the evolution of the human brain from the ethological and ecological perspective of hominins as a preliminary to demonstrating, in Part 2, how the insights gained from this analysis have important implications for understanding the emergence of representation within the theoretical context of cognitive evolution. Part 3 will look at how the representation of animals during the Upper Palaeolithic can be interpreted in terms of the evolution of cognition and the brain.

Part 1

The ecological and ethological context of brain evolution

Deception in nature

Illusional resemblance in nature is an evolved form of visual deception and takes many forms, such as a moth that looks like bark or an insect that feigns a twig. These adaptive visual attributes function to 'deceive' predators and are the result of natural selection, an evolutionary process that does not in any way imply a 'conscious' effort on the part of prey to deceive predator or vice versa. Such 'deception' can reach sophisticated levels even in the insect world; for example, there is a moth, know as the Buff Tip (*Phalera bucephela*), where the markings on the 2D wings convincingly resemble a broken 3D twig (Cott 1940) — an example of projective perspective that facilitates survival of the organism. In most of these cases, the mimicry of one species functions to deceive the perception of another. Such cues evolved in these different scenarios as a means of encouraging the unwary into 'thinking' something is there when, in fact, it is not — so that such devices might, (a) tempt a creature to respond inappropriately to something that simulates the real thing, (b) serve to beguile a potential predator, (c) assist a predator to remain concealed. Mimicry is a form of illusion because one party has adapted such that it creates a resemblance to some relevant feature in order to 'fool' the sensory system of another into responding to that feature as if it were the real thing, when it is not.

The question arises as to how the evolution of the hominin visual system relates to these concerns. Clearly, a particularly significant cue, as it had been for their distant primate ancestors, either as a threat or as an important food source (Robinson 1963; Lee and DeVore 1968; Ardrey 1976; Gamble 1999), would have been fauna — the consumption of which has been thought to be one of the crucial factors responsible for brain expansion (Martin 1983; Aiello et al. 2001; Vasey and Walker 2001). Those individuals who were able to perceive and identify animals most effectively would have stood more chance of survival and thus passed on the benefits accruing. This would have been reinforced by an evolutionary 'arms race' between the stalking and hunting expertise of those species preying on early hominins and the expertise of the hominins in evading capture. In other words, a host of predator/prey interrelationships, of which hominins constituted one strand, would have therefore led to a range of different types of camouflage whose practical function serves to defeat highly tuned perceptual systems. Thus tigers, cheetahs, leopards, monkeys and apes, etc., were capable of remaining concealed because natural selection had enabled them to evolve protective coloration mimicking the surroundings they normally inhabited, usually by simulating the spots, dapples, and shapeless lines of shadows and patterns deriving from foliage, grass or trees.

Through the evolution of protective coloration, the animals that preyed on hominins and those on which they preyed will have been intimately involved in the battle to 'fool' the other's visual system. Thus, one would expect to see a number of special advances in the evolution of the primate visual system that is represented in primordial cortical structures such as V1 (primary visual cortex) and is very ancient. Based upon the fossil skull and cranial endocast of the Eocene early primate, *Tetonius homunculus*, and its close resemblance to that of the primitive nocturnal prosimian *Galago senegalensis* (a very ancient primate) living today, Allman concluded that as early as 55 million years (Ma) ago the precursor for area 17, (primary visual cortex) was already quite well developed (1977). Primary visual cortex is the major receptive area for inputs from the sensory receptors in the retina and is involved in basic visual processing such as the perception of size, colour, form and movement. Cartmill theorised that visual adaptations in prosimians aided a hunter lifestyle (1972). For example, the tarsier and mouse lemur (modern models of the ancient prosimian) capture insects and even small vertebrates for food. The binocular overlap and concurrent increase in motor co-ordination allowed the early primate to navigate through the swaying branches and leaves to exploit fruit and insect resources. Over the long course of primate evolution, the neural substrates of the visual system were constantly fine-tuned with the development of tri-colour vision, superior stereoscopic vision, and the enhanced detection of movement, pattern, object and form discrimination (Kass and Collins 2003). The resultant human visual system, with its major interconnections to associational areas from all sensory cortices, the limbic system and its frontal lobe connections, along with refined finger-hand motor control, is the culmination of the long evolutionary process that created a creature capable of accurately depicting, through artistic expression, the most important objects in its world.

Concomitant with advances in the visual system, central processing mechanisms also evolved such that some neural substrates became increasingly preconditioned, allowing for the rapid accommodation of significant environmental cues, which thereby minimised the need for learning associated with the most basic survival behaviours. Hominins will, therefore, have become pre-programmed to visually detect certain key cues unique to their specific evolutionary niche. This dynamic involved the capacity to rapidly perceive various categories of objects — living, inanimate, members of the same species, predator, prey, etc. Many primate species, including our closest relatives, the chimpanzees, already have a well-developed ability to sort by such visual categories (Tomasello and Call 1997; Vauclair 2002). This process is additionally premised on the assumption that the lifetime of any early individual hominin would have been too fleeting for a visual system to learn how to discriminate objects from the prodigious complexity of the ambient optical array (Cosmides and Tooby 1994).

Deception in non-human primates

From the perspective of outward physical appearance, a number of primate species have developed protective coloration. For example, the tamarins' striking coloration is a wonderful disguise in the wild, as is the camouflage of the pygmy marmoset. The dark coloration of chimpanzees and gorillas makes them difficult to perceive in the depth of the forest with its deep shaded areas. Wild chimpanzees are known to have a marked piloerector response that makes them appear much larger than they really are. Such responses have been observed in reaction to highly aggressive and excited moods, some of which occur during hunting (Goodall 1986: 122), and it is easy to see how this adaptation would be useful in fooling both predator and prey. Unlike 'lower' primates, however, hominins came to consciously devise strategies and tactics of disinformation, deception, threat and stealth beyond those produced by way of primary evolutionary processes, eventually making humans the ultimate predator (Levy 2003).

We can surmise these evolutionary developments in early hominins because chimpanzees in the wild employ deceptive techniques to fool prey during the hunt, in that they have been observed to utilise complex hunting strategies that trick monkeys into rushing toward chimps stationed in a spot to which the prey have been driven. In fact, all the elements of the behavioural repertoire constituting such deceptive practices have been observed. For example, the chimpanzee Michael was observed to mount a threat display in which he picked up two large cans, banging them together while hooting and charging swiftly down a hill. This behaviour catapulted him from one of the lowest ranking males to alpha male (Goodall 1986: 112–13). One can easily imagine such behaviour being utilised during hunting, especially since chimpanzees hunting in groups have been seen breaking trees to obtain clubs with which they threatened, chased and beat leopards (Kortland 1975; Hiraiwa-Hasegawa et al. 1986: 12).

Moreover, chimpanzees are certainly capable of deceptive social behaviour. For example, 9-year-old Figan withheld food calls to hide a bunch of bananas that he then consumed himself (Goodall 1986: 125). Most interesting, he appeared highly uncomfortable during the process of inhibiting this call response, for it is neurologically determined, has obvious adaptive advantages for the species, and is usually involuntary. Indeed, this example demonstrates that even in chimpanzees, there are some occasions on which a given individual may, although not without conflict, exercise some voluntary control over innate communicative vocalisations that appear to be accompanied by a positive emotional valence for that specific individual. As this illustration reveals, deception can clearly play a role in the natural communication of chimpanzees (de Waal 1986).

The significance of an enlarged hominin brain

The first major expansion of the hominin brain is dated to about 2.5–1.8 Ma BP (Holloway et al. 2004: 16) [2] and may be associated with a genetic mutation (c. 2.4 Ma BP) that resulted in a reduction in the size of masticatory muscles in hominins. Since the huge temporalis muscles of hominins required the saggital crest to attach and anchor them, the resulting decrease in their size eventually led to its elimination. According to the authors, the presence of the bony crest prevented the skull from expanding in hominins (Stedman et al. 2004: 373–4); so, as it was selected out, the brain, and most particularly the cerebral cortex had space in which to expand in response to already existing developmental neurogenic processes (Finlay et al. 2001), perhaps beginning with the appearance of *Homo habilis* (about 1.8 Ma BP). These, along with the reorganisation of certain critical areas of the association cortex (Holloway 1999), may have been two factors sparking the enhanced encephalisation of the brain and the evolution of flexible problem-solving capacities, as it is well known that increased encephalisation is strongly correlated with behavioural complexity (Jerison 1991).

In fact, many analytic capacities were probably latent in the brain of the common chimp/human ancestor. This is suggested by the fact that bonobos, who when raised in an artificial culture especially designed to facilitate the production, modification and purposeful use of tools, the understanding of sentences of naturally-spoken English and the acquisition of a large lexicon of visual symbols (Savage-Rumbaugh et al. 1993) 'do not act, think or communicate like the same species' (Donald 1998), thus revealing latent cognitive potential that is not apparent when observing them in their natural surroundings. Furthermore, chimpanzees evince a pattern of associational cortex pointing toward the hominin line with more greatly increased associational visual cortex in some individuals than others (Holloway et al. 2003). This is in marked contrast to the brain organisation of pongids, where primary visual cortex (area 17 in humans) is much larger than in humans, because of the development of a large associational visual cortex (area 18) in the latter. [3] Overall, the visual associa-

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[2] We follow Holloway et al. in summarising general increases in hominin brain size as follows: there was a major increase 2.5–1.8 Ma BP from *A. africanus* to *Homo habilis*. There was a small increase in brain size 1.8–0.5 Ma BP from *Homo habilis to Homo erectus*. There was a modest size increase from 0.5 to 0.10 Ma ago from *Homo erectus* to *Homo sapiens*

[3] Areas 18 and 19 are associational visual cortices and are involved in perceptual processes, including translation and interpretation of visual impressions projected from area 17. Both regions receive bilateral visual information, whereas area 17 receives mostly monocular inputs. Area 19, especially, also receives multimodal inputs from the parietal and temporal lobes and performs numerous integrative tasks.

tion areas appear to be involved in the initial analysis of form, pattern, distance and depth perception, as well as in integrating visual inputs with inputs from other sensory cortical areas (Joseph 1996: 476–7). The major reduction of striate cortex (area l7) probably occurred in the australopithecines (Holloway et al. 2001), or at the latest in *Homo habilis* (Falk 1985; Tobias 1988). The enlargement of visual associational cortex, with its improved capacity to interface with enhanced neural mechanisms of memory, learning, problem solving, and motoric expression, points the way toward the relative behavioural flexibility thought to be characteristic of early hominins.

Thus, instead of relying upon evolutionarily-cued forms of deception as in 'lower primates', the hominin's enlarged brain enabled better co-ordination of information to defeat ambiguous signals. One outcome of increased encephalisation was the fact that eventually the human brain became specifically adapted to cope with visual information through a massive process of multiple cross-referencing. Byrne and Corp (2004; see also Jones 2005) have shown that that the size of the cortex, the outer layer of the brain responsible for advanced cognitive functions, is a good predictor of the degree of deception to be found in primates. This suggests that deception may have been an important driving force in cognitive evolution. In this respect, the learning involved in the acquisition of the skills of stalking and hunting will have provided some of the impetus for the development of abstract thinking in which previously learned information could be used to solve new problems. The greatest development of such innovative practices is found in humans, although we know that chimpanzees in the wild practice fairly sophisticated techniques of hunting (Goodall 1963, 1968) in which they prey upon birds (eggs and nestlings primarily), the occasional human infant, and several species of primates (mostly monkeys or chimp infants; Goodall 1986: 269). Thus, it seems most likely that the common primate ancestor of both chimps and humans was already a skilled hunter.

The hominin exploitation of mimicry and the emotional brain

As the expansion and reorganisation of cortical areas accelerated from about 1.8–0.5 Ma BP, it is likely that hominins were capable of interpreting any given situation in multifarious ways that may have led to the capacity to consciously imitate the mimicry they were able to observe in the natural world in ways unavailable to our common hominid ancestors. For example, chimpanzees search for prey based upon visual, vocal or olfactory spoor (McGrew 1992: 218), and no doubt so did early hominins. It would have been a short step to enhance the look of animal skins so that they appeared more like hunted animals, thus leading to the procurement of greater amounts of protein-rich meat, with all the advantages arising therefrom.

Some of the earliest disguises utilised probably included mimicking animal vocal calls, or olfactory cues by rubbing dung on the body, and these strategies likely played a vital role in attempts to fool prey in order to physically draw near for the kill. Another early deceptive technique might have consisted of breaking bushes or small trees that the hunter hid behind while approaching prey, and indeed this technique was used by the South African Bushmen (the period of observation was 1905–1931), or, alternatively, they would wear a fillet of grasses (Dunn 1931; Stow 1905). Numerous examples of hunting disguises were used by North American natives, i.e. wearing buffalo skins and scenting with dung. Indeed, disguises are still used by hunters today, i.e. duck blinds, camouflage clothing that imitates protective coloration, pheromone scents, hunting lures that imitate worms or insects, etc. Disguises against predators also sometimes take the form of concealment, or when this option is unavailable 'freezing' (i.e. remaining absolutely still, which is mediated by the amygdala), thereby helping to blend into the background.

Simultaneously with the development of deceptive techniques, the fundamental primate brain, already able to sort by categories, was evolving into a sophisticated system of neural structures that facilitated the perception, memory, imitation and prediction of animal behaviour. We can gain some insights into the evolution of these processes by studying the developing child's category knowledge of animals from the perspective of evolutionary psychology. Barrett (2005) has suggested that humans have a multi-faceted 'agency intelligence' (ability to detect animals that behave versus those that do not; as well as the capacity to distinguish living from inanimate objects by means of several variables; prey animals from predator animals; etc.) that allows them to predict and understand both human and non-human animal behaviour. This ability is observable in children two years of age and has had significant adaptive advantages over the course of hominin evolution as is evidenced in a number of ways. For example, infants as young as nine months are able to make inferences about intentional schemas that afford predictions about the behaviour of animals (Gergely et al. 1995; Csibra et al. 1999). By doing so they are in a better position to avoid and evade dangerous animals as soon as they are perceived. Young children the world over evince an unusual interest in animals, whether they live in rural areas or urban locales where they rarely ever come in contact with them. This motivation to learn and know about animals appears to be an innate predisposition whose survival value was of primary importance in early childhood for the acquisition of knowledge about the behaviour of predators and other dangerous fauna.

Thus, during our evolutionary history, hominins and finally *Homo sapiens* became biologically predisposed to certain kinds of learning that led to particular brain systems specialising in the detection of natural categories, such as knowledge of animal behaviour and assorted other biologically important information (Caramazza and Mahon 2003), and this systemic network of phylogenetically determined neurological categorical knowledge repositories is highly interconnected and complex (Damasio et al. 1996). Consequently, the greater the biological relevance of a feature, the easier it will be to recognise. The stimulus properties of these perceptual response patterns will have constituted the foundation upon which more sophisticated recognition and representation processes were subsequently built, a topic to which we will return.

Certainly, our hominid ancestors were highly interdependent with an array of faunal species. In this sense, as much as hominids were in competition with carnivores for the same animals, so carnivores preyed on hominids as a potential source of protein-rich meat. The fact that hominids, as well as being preyed upon, were also predators, had consequences for the evolutionary development of the primate limbic system because the same system in carnivores is structured so as to reward hunting behaviour, thus facilitating the necessary learning that promoted a predatory lifestyle (Guthrie 1984), particularly in males (Joseph 1992). The primate limbic system controls both the perception and expression of emotions and is intimately involved in learning and motivation. Moreover, it has been shown that the great ape and human facial expressions constitute a mode for the communication of highly nuanced non-emotional signals (Chevalier-Skolnikoff 1982). This finding provides a specific evolutionary mechanism for the development of an enlarged neural template concerned with information-communicating signals that convey non-emotional, factual information (i.e. one basic prototype for human language skills).

In hominids the amygdala (a structure that is a distinctive portion of the anterior temporal lobe) is crucial in mediating some aspects of emotionality including fear (Cahill et al 1996), and in humans it actually assigns emotional or motivational significance to that which is experienced (Aggleton 1992, 2000; Anderson and Phelps 2001). Moreover, it has been implicated in a variety of functions including modulation of memory and mediation of social communication. More generally, it appears to be a critical component of a system that evaluates the environment for potential dangers (Amaral 2003). Thus, the amygdala has a general role in directing attention to affectively salient stimuli and issuing a call for further processing of stimuli that have a major significance for the individual. It appears to be critical for recruiting and co-ordinating cortical arousal and vigilant attention for optimising sensory and perceptual processing of stimuli associated with novel, surprising, ambiguous or frightening events (Davidson 2003). Moreover, when visual emotional stimuli are compared with visual non-emotional stimuli, the visual cortex is more activated in response to the emotional compared with the non-emotional stimuli, suggesting projections from the amygdala to the primary visual cortex (Bradley 2003; Davidson et al. 2003: 64–75), and Amaral et al. (1992) have identified pathways in the macaque brain that connect the basolateral region of the amygdala to the primary visual cortex. This provides a mechanism whereby visual information processing can be modulated by affect-related signals from the amygdala. Over the course of hominin evolution the ability to develop voluntary control over emotional expression is evidenced by the interconnections between the visual cortices, the motor cortex and frontal lobes.

As LeDoux (1994) makes clear, certain key features may be enough to trigger an emotional response by way of the amygdala before an object, such as a dangerous animal, is consciously recognised. Thus, there seems to be an early warning system that proceeds directly from the retinal-thalamic visual pathway to the limbic system for the rapid discrimination of potentially threatening objects that primes conscious awareness for action if required, and over the course of hominin evolution these abilities would have been highly adaptive. Crucially, LeDoux (1998) has found that there are many more neural connections arising from the amygdala to the higher cortical centres than the reverse, thus suggesting the neural basis for emotional responses to influence, or even overcome, higher cognitive behaviours. The response engendered by those animals that populated the ecological niche of hominins is therefore likely to have been a highly-charged emotional one shaped by adaptive pressures. In other words, it seems that this type of visual-limbic response has certain in-built capacities that allow for early and rapid responses to particularly important stimuli crucial for survival.

Other limbic structures such as the septal nuclei (Heath 1964) and the nucleus accumbens have been known for many years to mediate pleasure and other emotions associated with rewards. The nucleus accumbens, adjacent to the caudate nucleus (both of which have extensive interconnections with the amygdala and the frontal lobes) appears to control feeding behaviour and affect in the rostral areas, and fear/defensive behaviour and emotions in the more posterior regions (Reynolds and Berridge 2000). It may, thus, be an important neural substrate in which affects associated with both feeding and hunting, or fear and defensive behaviour, with respect to predators or more dangerous prey, are mediated.

Neuroimaging studies with PET scans and functional magnetic resonance imaging (fMRI) have enhanced our knowledge of the functional neuroanatomy of emotion. A meta-analysis of 55 studies has demonstrated that common patterns of activation exist across various emotional tasks involving specific anatomical structures of the limbic system. For example, the medial prefrontal cortex has a general role in emotional processing; fear specifically engages the amygdala; sadness is associated with activity in the subcallosal cingulate; visual stimuli induced by emotion activate the occipital cortex and the amygdala; the induction of emotional recall/imagery involves the anterior cingulate gyrus and the insula, as did emotional tasks with cognitive demand (Phan et al. 2002).

As these data demonstrate, the exceptional developments of the primate limbic system were its evolving connections with limbic cortex, frontal cortex, and motor cortex, allowing for the greater role of learning and a more flexible array of cognitive, emotional and behavioural reactions, including responses to predator and prey. Emotional expression, including vocalisation in the chimpanzee, is essentially innate and involuntary (Goodall 1986: 125; Hayes and Hayes 1951; Menzel 1964), although we mentioned an example of some voluntary control above); whereas in humans much emotional expression is cortically-controlled and voluntary (an involuntary system is still present however, as manifested following specific types of brain injury), thus enabling humans to display emotional expressions when they are not directly under the influence of the actual affect.

This, of course, allows humans to deceive conspecifics. Presumably, early hominins were developing enhanced voluntary control over emotional displays, including postures, gestures, vocal calls and facial expressions. If this hypothesis is correct, we should be able to find evidence for the enlargement of brain structures involved in such behaviours, and there seems to be evidence for this. For example, primate evolution is marked by an elaboration of the mimetic facial muscles used for the production of facial expressions, resulting in greater variability in the form and number of expressions that are present in more recently evolved species (Anderson 1994; Huber 1931).

Moreover, it is well known that the facial nucleus, which transmits impulses to the specific muscles to contract or relax, receives impulses from many different parts of the brain. Areas of the forebrain such as the caudate, putamen and substantia nigra send impulses to the facial nucleus when emotions are aroused involuntarily and lesions in the extrapyramidal system (which carries axons from these nuclei to the facial nucleus) impair the ability to involuntarily respond, i.e. automatically smile when hearing a joke, but leave the voluntary system intact (Ekman 2003; Kahn 1966; Meihlke 1973; Myers 1976; Tschiassny 1953). A later evolutionary development is of an area of the motor cortex, which is the source of the impulses resulting from voluntary efforts to make a facial expression, and lesions in the pyramidal system (which carries the axons from the motor cortex to the face) impair the ability to perform a facial movement on request, yet leave involuntary emotional expression unimpaired. Thus, although chimpanzees have some ability for voluntary facial movements, early hominins evolved to expand such voluntary control as evidenced by the eventual evolution of a separate voluntary motor system (the pyramidal system) for the facial expression of emotion.

It is well-attested experimentally, both psychologically and physiologically, that arousal, by way of the limbic system and the autonomic sympathetic nervous system, leads to heightened awareness in the face of a potential threat (the fight, flight or freeze reaction), which would be especially activated during hunting expeditions. Such heightened awareness enables the hunter to focus on the object of concern with greater acumen, almost to the exclusion of neighbouring stimuli (some researchers also claim that the object under scrutiny appears to move as if in slow motion). The increased arousal also facilitates the memory storage of numerous details about the event and the slow motion effect would solidify the memory of the animal's specific behaviour and form, enhancing the ability to reproduce it in visual representations. If the arousal is too great, however, panic ensues and awareness is clouded by the effects of a cascade of noradrenergic transmitters and adrenocorticotropic hormones (LeDoux 1994). This response is controlled by the amygdala, which, when very highly stimulated, may over-ride the cortex, effectively suppressing it, resulting in the loss of behavioural control (Joseph 1996: 193). For example, in modern humans, anxiety disorders (fears over anticipated events in contrast to fear because of a direct threat) are associated with hyperactivity of the amygdala, and the negative emotion projecting from the amygdala appears to over-run rational judgements and behavioural control mediated by the frontal cortex, as evidenced by the fact that many anxious people 'know' that their emotional reactions are exaggerated or misplaced, and yet they respond to them as if they were 'real'.

Acute stress disorders, produced by exposure to traumatic events, include dissociative symptoms such as inability to experience pleasure, a subjective sense of numbing, detachment, lack of emotional responsiveness, a reduction in awareness of surroundings, derealisation, depersonalisation and amnesia for details of the event (American Psychological Association 1994: 429). Moreover, these symptoms appear to provide a subjective insight into the emotions accompanying the 'freezing' response mediated by the amygdala as seen commonly in mammals and primates exposed to potential dangerous predators.

Although the abject terror accompanying the experience of being the victim of a predator is not common among most people today, we can gain some insights into the reality of this experience for our ancestors through the example of two families of the Kalahari Ju/'hoan who, when camped out at night, were subject to the attentions of a marauding lion. Terrified, and holding their children close to them, the families attempted to keep the fire between themselves and the lion. The lion persisted until the morning, when it departed when one of the adults, Bo, fell into a trance (most likely incurred because of the prolonged terror), wherein he became non-responsive and behaviourally 'frozen.' The other members of the party attributed the lion's disappearance to the fact that while in trance, Bo's spirit had followed and chased the feline away (Biesele 1993: 112). Of note here is the fact that during popular 'healing dances', the individuals involved actually 'become' the lion, perhaps a compensatory strategy for gaining some 'control' over their most feared predator by means of ritual dancing and singing that deliberately induces a trance (for more on this see below). This example provides clear empirical evidence for the link between an emotional reaction to a predator and trance phenomena, both spontaneous and ritually induced.

Another significant aspect of the hominin limbic system was the enhanced capability of experiencing and expressing more nuanced emotional states. We realise that many archaeologists are uncomfortable with such a 'subjective' quality as emotion (Tarlow 2000). However, there is a vast body of research, [4] all of which provides a great

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[4] These data include comparative primate neuroanatomy; behavioural studies of facial expressions and vocal calls in chimpanzees and other monkey's and apes; visual scanning (Pet and fMRI scans) of the limbic system in humans and chimpanzees in response to the presentation of faces depicting a variety of emotional expressions; cross-cultural human studies of the subjective, physiological, and behavioural

deal of empirical data regarding emotion, its physiological correlates, behavioural expressions, subjective experiences, and neurological basis as mediated by the limbic system. For example, there are significant universals across cultures in the recognition of the facial expressions of sadness, anger, fear, disgust and other negative emotions (Ekman et al. 1987). There are highly specific facial expressions and autonomic nervous system correlates for the emotions of awe, amusement and pride (Shioto et al. 2003). Chimpanzees have a highly elaborate facial musculature and a hairless face, which, as we have seen, is specialised for the production of a variety of facial expressions. [5] One of these, the full closed grin is extremely dramatic and is manifest in response to an unexpected and frightening stimulus. Also, individual chimps may manifest idiosyncratic facial expressions not seen in other chimps (Goodall 1986: 119–21).

The limbic system is highly developed in the great apes, but the amygdaloid complex, a major structure in that system, is only one quarter to one half the absolute volume of the human limbic system (Barger et al. 2004). [6] Thus the absolute size of the limbic system has increased across hominin evolution. The same is true of the hippocampus, another limbic system structure involved with the maintenance of memory and subjective emotional feelings associated with specific events. The absolute volume of the human hippocampus is three times that of the great apes and shows a rightward asymmetry (Teffer 2004). Finally, although the frontal lobes in humans are about the size that would be predicted of an ape whose weight was equivalent to humans, the temporal lobes are larger than would be expected (Semendeferi and Schenker 2001) by about 20–30 % (Rilling and Seligman 2003). Part of this volume can no doubt be attributed to the increased size of the amygdala and the hippocampus, although the cortex of the temporal lobes is also highly involved with receptive language development.

As the human emotional repertoire is more nuanced and differentiated from that of the chimpanzee, we can assume that over time the hominin emotional experience of basic fear came to mediate the many subtle dimensions seen in modern humans, including expressions of terror, anxiety, awe and admiration. Accordingly, when disguised hominins began to be able to come closer and closer to their huge prey, they likely experienced a variety of emotions — veneration, wonder, dread, fright, horror, aesthetic appreciation, anticipation of reward (a tasty meal), all of which are reported by historical hunter-gathering peoples.

Part 2

Cognitive evolution and representation

Mimicry: from episodic to mimetic culture

Merlin Donald has proposed a complex model in which he posits three broad stages of human evolution from our common human/chimp ancestor (1991: 124–61). For example, he begins his discussion by referring to ape culture as episodic. This is characterised by complex, periodic event perception; improved self-awareness, including the ability to recognise oneself in a mirror, as chimpanzees do; and event-sensitivity with a sporadic and reactive cognitive style and a limited voluntary expressive morphology. Over the past 40 years it has been possible to observe various primate species in the wild on a continuous basis and there are some who believe that several species, including specific bands of macaques and chimpanzees, have rudimentary cultural traditions (Boesch and Tomasello 1998) that are transmitted by means of mimesis. These proto-cultural behaviours form a bridge leading from episodic culture to Donald's first stage of hominin evolution, mimetic culture, which he believes peaked with *Homo erectus* (this bridge of development stretches from about 3 Ma–0.5 Ma).

If mimetic culture was so crucial in the cultural development of hominins, we should find some biological basis for it among primates. During the past decade empirical research has explored the neuroanatomical substrate for imitation, a highly complex cognitive process, involving vision, perception, representation, memory and motor control, through numerous comparative primate studies and human imaging, neurophysiological and neuroanatomical studies. Chimpanzees may be the only primates, except of course for humans, able to recognise a reflection of themselves in a mirror as their own (Gallup 1970). This capability suggests a neuroanatomical substrate for imitation, a rudimentary ability for self-reflection and detachment that may be a precursor to representational competence. Interestingly, de Waal (de Waal et al. 2005) has found a more elementary kind of mirror recognition of self in capuchin monkeys that suggests a very gradual evolution that began well before apes and humans came along.

Further neuroanatomical evidence that chimps can envisage the viewpoints and intentions of others derives from the discovery of 'mirror' neurons in the ventral premotor cortex (F5) of monkeys (Rizzolatti and Fadiga 1988), which is considered the equivalent of Broca's expressive language area in humans. Motor neurons related to mouth and hand actions discharge when the monkey executes specific goal-directed hand actions such as grasping, holding, tearing and manipulating objects (Buccino et al. 2004). But the specialised 'mirror neurons' are also activated in an observer by merely viewing another individual make these gestures, thus the observed action seems to be 'reflected', like in a mirror, in the motor representation for the same action in the brain of the observer. More recently, mirror neurons have been found in the inferior parietal lobule of the monkey, area PF (Fogassi et al. 1998: 154; Gallese et al. 2002). In addition, there are neurons in the superior temporal sulcus region that respond to the presentation of goal-

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concomitants of emotion; neurological and neuropsychological studies of brain-injured humans and experimentally-induced lesion studies in lower primates.

[5] There are about eleven, which include a full play face, three expressions conveying fear and excitement, pouts, distress, relaxed face, and relaxed face with open mouth.

[6] The ratio of the limbic system to total brain size in the human is smaller than in the great apes, because of increased cortical development in the former.

directed hand actions, as well as to walking, turning the head, moving the hand and bending the torso (Carey et al. 1997).

Functional brain imaging studies and transcranial magnetic stimulation studies have revealed the presence of a 'mirror' neuron system in humans also (Fadiga et al. 2005). The human studies demonstrate that when we observe another individual acting, we strongly 'resonate' with that action. In other words, our motor system simulates 'underthreshold' the observed action in a strictly congruent fashion. The involved muscles are the same as those used in the observed action and their activation is strictly, but temporally, coupled with the dynamics of the observed action. Studies such as these demonstrate that 'actions are represented in the brain in a similar way to words in a vocabulary,' (Rizzolatti and Fadiga 1988) and provide a biological basis for mimesis, empathy, understanding and interindividual communication.

One of the greatest differences between episodic and mimetic cultures was the fact that in the latter, individuals were able to re-present a situation to reflect upon it, either individually or in groups, and thus hominins had now begun to acquire increasing abilities in the realm of representation. As Donald (1993: 746) points out, the ability of apes to recognise pictures, as per Bovet and Vauclair (2000), is processed through standard perceptual channels. Grill-Spector et al. (2001), for example, found that the lateral occipital complex in humans and monkeys is cue invariant — in other words, it responds the same to objects irrespective of the fact that they may be presented in the real situation, in photographs, or in the form of line drawings. This scenario is supported by the fact that various animals, from dolphins to chimps, are able to perceive pictures of different types produced by humans (Cabe 1980; Bovet and Vauclair 2000). Whether untrained animals are able to see these as pictorial representations, or mistake them, as human infants sometimes do for the real thing, remains to be established (Winner 1982). In the case of humans, we see the resemblance, and the difference, in a diverse range of instances and settings, whereas for most other animals, the response is usually linked more directly to a particular stimulus trigger. In fact, it has recently been established that different species react to pictures of objects according to their significance in terms of their own particular evolutionary niche (Bovet and Vauclair op. cit.). Not surprisingly, when predators or potential mates are portrayed, they are identified with more alacrity than other objects. The same may apply to *Homo sapiens* in that the universal portrayal of animals in profile during the Upper Palaeolithic, with the accentuation and obsession with the cervico-dorsal line and most salient features of animals, suggests that these were of particular significance, perhaps 'sign stimuli', in relation to the evolutionary niche of early humans (Hodgson 2003b). So, despite the greater flexibility of humans on one level, at the same time, certain innate constraints to do with enduring aspects of their evolutionary history continued to shape behaviour.

The ability to 're-present' appears to have been present in australopithecines about 3 Ma ago, as exemplified by a reddish cobble of ironstone discovered in Makapansgat, South Africa in 1925, which was carried over 20 miles from its place of origin. One explanation for this event suggests that the object had been carried because of its extraordinary resemblance to a hominin face (Bahn and Vertut 1997: 23). Carrying this stone for over 20 miles because of its resemblance to a face assumes that such an object was highly valued. If a positive response to an object that resembles a hominin face is assumed, then one obvious hypothesis suggests that there should be evidence of a deeply embedded preference and response to any semblance of such a visual cue in both chimpanzees and modern-day humans. Evidence for this comes from the fact that it has been known for some time that new-borns, only minutes old, can track an intact schematic face better than a scrambled (distorted) one, thus showing a preference for the more realistic abstraction (Johnson et al. 1991). In other words, a few minutes after birth a human infant shows preferential orienting towards face-like stimuli such as two round blobs over a horizontal line (two eyes over a mouth). Moreover, within a few hours after birth infants begin to imitate adults' smiles, frowns and other expressions, and, given a choice, babies will gaze longer at a picture of their mother's face than at an image of a female stranger (Johnson 2001). [7] Infant chimpanzees show similar preferences (Myowa-Hamakoshi et al. 2001). The fact that human infants can discriminate among chimpanzee faces at six months of age but not nine months, and a similar phenomenon and time frame has been demonstrated for chimpanzee infants in differentiating human faces, provides evidence that a general hominid facial preference is deeply embedded in the brains of chimps and human infants (Pascalis et al. 2002) which only disappears between six and nine months because of lack of exposure to the specific human or chimp faces necessary to retain the biologically-based skill through learning.

If the hominid facial preference is biologically determined, viewing the face should be 'rewarding' and thus accompanied by positive subjective feelings. For example, the reassuring quality of the mother's facial expressions and emotional vocalisations have a direct impact on how anxious an infant will become in a novel and challenging situation (Campos et al. 2003). Similarly, the chimpanzee emotional system appears to develop in interaction with the emotional responsiveness of social partners. The more responsive rearing environment results in a more positively expressive and less fussy infant, effects that are evident within the first weeks of life. Thus, early emotional interactions, as well as innate preferences, are important in the development of emotional expression (Bard 2003). Finally, when the human child begins to scribble, the most meaningful production it creates looks like a cephalopod (Kellogg 1969), i.e. a face with a long tail, again reinforcing the innate importance of the face for humans.

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[7] By two months of age face perception has developed so specific areas of the brain (fusiform facial area [FFA] in the fusiform cortex of the basal temporal lobes) are known to be activated by viewing faces (Nelson 2001: 3–18).

Donald emphasises that one of the greatest differences between ape and hominin abilities is that the latter have many more means of voluntary expression than the former, as discussed above. In other words, there is a large evolutionary gap between recognition and production. Drawing closely parallels iconic and metaphoric gesturing, such as when a simple picture is made in sand or mud. Donald therefore sees no a priori reason why intentionally made pictorial or representational artefacts should not have been made during the mimetic stage (more probably during the latter part of this phase and overlapping with the mythic stage during the reign of *Homo erectus* and/or early archaic *Homo sapiens*).

This hypothesis appears to be supported by the arrival in the archaeological record of natural objects that bear some similarity to human figures, i.e. Berekhat Ram. c. 233 000–800 000 BP (Marshack 1997: 327–37), which appears to have been slightly modified by engraving to bring out the resemblance to the human form. Bednarik suggests that the Tan-Tan figure from Morocco, c. 400 000 BP, also needs to be taken into account as a possible early example of an intentionally modified object (2003a); to our knowledge this interpretation has not yet been confirmed by other investigators. We suggest that Tan-Tan might be considered as another natural object in which intentional engraving by hominins enhanced the resemblance to the human form (see Pettit 2003 for a discussion of these and other similar figures). One hypothesis we would suggest is that any new finds of 'realistic' representational art from the Palaeolithic are likely to be in the forms of animals or humans. There is already some recent evidence to support this proposition. For example, the only Neanderthal representational artefact (yet to be confirmed by other researchers) takes the form of two stones intentionally fitted together to look like a human or feline face dating to about 32 000 BP (Marquet and Lorblanchet 2003). See also the finds of 33 000-year-old animal sculptures of Conard (2003) from south-western Germany.

Clearly, the development of visual representation would have included a number of refinements to the already advanced chimpanzee visual system during hominin evolution in conjunction with the evolution of other neural structures and the behaviour mediated by them, as discussed above. The discovery that a particular set of re-presented features can potentially trigger the same response as when the real object itself is encountered, may have been critical to human cognitive/cultural development and constituted a crucial shift from a largely reflexive predisposition towards the world to one of a more consciously purposeful engagement (this ability being enhanced by frontal lobe evolution).

Some of the other characteristics of mimetic culture involve such novel forms of representation as non-verbal action modelling. With this advance there is a revolution in skill development transmitted via mimesis, non-verbal communication becomes increasingly important, and there are more opportunities for shared attention and participation in specific events. Mimetic culture thus allows for increased variability of custom and cultural 'archetypes' (Donald 1998: 7–17). Donald suggests that this ancient mimetic system is still crucially important in human behaviour and remains rather separate from linguistic cognitive evolution. Mimetic abilities, especially perceptual recognition, vocalisations and facial expressions are largely mediated through the right hemisphere. Hunting and gathering techniques no doubt began to evolve in complexity, as they were more readily transmitted across generations by means of imitation. In such a cultural milieu it is entirely likely that hominins observed the various camouflaging devices utilised by both predators and prey and attempted to mimic them.

Together with acting-out the behaviour of predator and prey, it would not have gone unnoticed that the wearing of animal skins simulated the appearance of animals and early Homo species will have come to realise that this form of parody could be usefully employed in stalking and tracking. Taking into consideration the previous discussion, it seems more than likely that early Homo will have been aware of this correspondence. In this regard, *Homo erectus* and *Homo sapiens* were both highly migratory (Ciochon and Larick 2000; Vekua et al. 2002), originating in Africa (1.8 Ma BP) and travelling to south China, Indonesia and the Caucasus, suggesting an early spread throughout the Old World tropics and into the temperate zone, which is consistent with emerging archaeological data (see O'Connell et al. 1999 for a brief summary). During the past 700 000 years they had to adapt to periods of intense cold during the various Ice Ages, so one wonders if the cognitive abilities necessary in employing animal skins for both disguise and warmth may not have served complementary adaptive functions.

With the increased development of mimetic culture, shared aspects of the hunt could now be re-presented around the communal hearth. Enhanced voluntary control over emotional expression would have enabled hominins to recreate and re-present emotional hunting situations after the fact (with voluntarily produced vocalisations, gestures and facial expressions). Perhaps, as Bednarik (2003b) suggests, the successful hunter, on returning to the campsite, might have re-enacted how animals were stalked and despatched to the extent that the replication of the behaviour of quarry came to be a routine occurrence. Such presentations, accompanied by strong positive affective reactions, would have served to strengthen the social bonds of the participants. Furthermore, the enhanced connections of limbic and frontal cortex would have facilitated the initiation and representation of past hunts prior to an upcoming event, which likely resulted in the development of various hunting dances and rituals designed to foster success.

During the pursuit of game, to the targeted quarry a disguised hominin would seem to have become one of the herd; whereas, to members of the hunting party, the same individual would appear to have metamorphosed into an animal. A strategy of this kind might have been interpreted as 'magical' by those involved, as it would have seemed able to transport humans into the midst of the animal world with impunity. For much of hominin history, throughout mimetic culture and later mythic culture up until about

30 000 years BP, the social organisation underlying these groups most likely consisted of small band societies (Gamble 1999; Renfrew and Bahn 1996), which were characterised by egalitarianism, with leadership being informal and based upon natural ability. Earlier in the cultural development of animal disguises for hunting, many individuals were probably considered competent in this role. But, as the demands increased due to growing cultural complexity, one particular individual is likely to have been especially convincing at mimicking animals. This person therefore probably came to be seen as in possession of a special 'gift', in the sense of appearing to be able to pass, at will, from the human to the animal world.

Early visual representation in the mimetic and mythic stages

Early hominins, while re-creating the elements of a successful hunt, with all of the emotional expression entailed therein, may have begun to represent various animals by scratching images of their tracks in sand or mud with a stick or their fingers, a very early example of visually represented symbolic expression, perhaps accompanied by imitations of the vocal calls and behaviour of the animal being imitated. Though they appear to be incapable of producing anything representational, chimpanzees seem to enjoy drawing indiscriminate shapes with some sense of order and will pursue such activities for long periods of time (Morris 1962), so the rudiments of the motivation toward, and the emotive reaction experienced during the expression of representation were likely present in early hominins. As Hodgson (2000) and Davis (1986) have pointed out, the production of graphic primitives (repetitive lines, crosses, circles, grids etc.) may have been a necessary stage that will have predated iconic image making by a considerable period, as is increasingly being borne out by archaeological discoveries that predate the Upper Palaeolithic (Bednarik 1992).

Although most animals generally tend to mistakenly treat a representation as the real thing, early humans eventually came to realise that they could, to some extent, inhibit this automatic response as well as manipulate its heuristics to suit their own purposes. What separated hominins from hominids was the ability, enabled by increased encephalisation and brain reorganisation, to imitate a broader range of species with a more sophisticated assortment of mimicking skills, of which depictive visual representation may have been one further, but relatively late, development. As Bednarik (2003a) points out, the experience of perceiving a snake on a forest path when there is only an exposed tree root is an example of visual ambiguity that may have led early humans to an understanding of its potentialities. In other words, they came to realise that one thing, through resemblance, can iconically stand for something else. Once this had been grasped it was only a matter of successive approximation before fully-fledged 2D depictions came about.

Bednarik (2003b: 127) states that this capacity for iconicity, as manifest in the first representational depictions, is a "… *'managed', intentional use of visual ambiguity*" (Bednarik's emphasis). Representation, therefore, will have evolved from an ability of hominins to shift attention and action from an immediate reflexive response in the face of a deceptive stimulus to an alternative association. In brief, they began to consciously deploy camouflage, thereby imitating the mimicry initially evolved by various fauna to 'defeat' the hominin predator's own visual system. This was achieved by way of deceiving fauna through the use of disguise; later still, to perhaps improve recognition thresholds for detecting such fauna through their depiction in both 3D and 2D (Hodgson 2003a). This scenario suggests that iconic representation, as exemplified in the two latter cases, evolved incrementally out of an earlier phase where disguise (in the sense that one's appearance was deliberately modified to create a resemblance to an animal) will have played a significant role. The hominin visual system would therefore have been well prepared to apportion iconic status to marks when the time came. Davis (1986) agues that iconic representation emerged from the mistake of seeing a mark as an object but discounts Gombrich's (1961) theory of projection as having much to do with the process. These contrasting accounts, however, can be viewed as complementary. Davis makes the valid point that if Gombrich's theory were correct then there should be many different kinds of object portrayed in Upper Palaeolithic depictions, not just animals. We have shown that animals came to feature prominently in palaeoart because they played such a key role in our evolutionary history, especially in relation to the development of the brain. It was therefore inevitable that when a line came to be interpreted or reacted to as an object, the object was bound to be some kind of animal because the hominin visual/recognition system is especially equipped to be highly sensitive to such forms — even modern humans see animals in the Rorschach Ink Blot Test more than any other object and the same applies to hallucinatory experiences (Shanon 2002). As Bednarik (1986: 165) has proposed, the visual processes involved in visual misinterpretation would have favoured objects that dominated the taxonomic visual system of hominins, namely those that provoked desire and fear, i.e. large mammals. What the present account adds to this debate is to show how these processes are interlinked in complex ways with the evolution of the limbic system and the visual brain as well as ecological/ethological considerations.

In short, the propensity of early humans to imitate animals for the purpose of hunting was eventually accompanied by two-dimensional drawings in mud or sand and this resultant ability to depict animals ever more skilfully was likely accompanied by developing ideas of a mythic kind. Furthermore, this process constituted a valuable by-product that eventually facilitated a more highly tuned ability to discern animal profiles in degraded situations through helping to prime perceptual/ recognition systems (Hodgson 2003a; 2003b). By selectively abbreviating and obfuscating animal outlines palaeo-artists were both expressing their preferences and 'exercising' those parts of the brain, especially the right hemisphere, crucial for disambiguating camouflage and discerning obscured forms. Such representation, as a potentially enduring store of information, became a means of passing down accumulated knowledge and subsequently took on many functions and roles.

Scratching animal shapes and tracks in sand, while clearly representational, was a relatively ephemeral event, but pecking, engraving and painting them on rock surfaces yielded permanent historical documents. It is estimated that over 70 % of all known rock art was produced by hunting and gathering societies (Anati 1994: 32). There are further examples in Africa of the tracks of predators and prey that come from Namibia (Coulson and Campbell 2001: 105). Many examples can be cited from Australia of a similar or even older vintage (Taçon 2001), where innumerable drawings depict animal tracks, frequently those of the emu, often shown in stencil form along with stencilled human hand prints, animal limbs (butchered?) and hunting weapons (Lewis 1988: 199; Clegg 1983: 69). In fact, animal tracks are a common icon as depicted in rock art from most hunter-gatherer societies all over the world, as far south as Patagonia (Anati 1989: Pl. 4). Such drawings of animal tracks are extremely common throughout the American South West, usually in petroglyph form, where they have been produced by Native Americans for thousands of years in some cases.

These examples demonstrate how archaic humans, although probably on a more simplified scale (e.g. hand prints, simple outlines, collection of natural-occurring rocks with incidental likeness to animals or the human form etc.) were already commandeering 'representation' for a specific purpose in order to gain an advantage in the cut and thrust of survival. This is a proactive exploitation of representation, which we argue was originally found in nature in the form of deception and camouflage, for much broader functional purposes. The realisation that it was possible to subvert nature's capacity for representation in this way will have greatly facilitated the production of the first 2D representations in 'art'. The preoccupation with animals in palaeoart can, therefore, be traced back to the way the limbic system and its cortical connections, as well as the enhanced visual system of humans was fashioned out of the reciprocal interaction between predators and prey during hominin evolution (Hodgson 2003a, 2003b).

Mythic culture

According to Donald's evolutionary scheme, about 500 000 BP some basic advances upon the earlier mimetic cultural stage began to develop, culminating in mythic culture. This culture was characterised by high-speed phonology, oral language and oral social records. It is 'mythic' because it is governed by representations that consist of a shared oral-mythic tradition, which includes a public, standardised version of reality permeated by mythic archetypes and allegories that can exert direct control over the form of human thought and convention (Donald 1998: 14). This would also include enhanced visual representational abilities that would form a basis for the creation of artistic objects such as the Berekhat Ram and Tan-Tan figures mentioned earlier. This phase of cultural evolution peaks in *Homo sapiens sapiens*, and some of the visual records of that culture survive in the Palaeolithic cave painting of animals.

Clearly, the mythic cultural period suggests numerous enhanced cognitive capacities over that of the mimetic stage. Therefore, we should be able to find evidence in the fossil record and comparative primate neuroanatomy for significant changes in the brain beginning prior to this period, and there appears to be solid evidence for this. As a basis for our discussion of increased encephalisation around 0.5 Ma BP, it is important to re-iterate first that there was a major expansion of the hominin brain from about 2.5–1.8 Ma BP. This is the period of time in which cranial endocasts of *Australopithecus africanus* are characterised by more human-like frontal and temporal lobes (Falk et al. 2000) and a bulge at Broca's area, which mediates vocalisation in lower primates and expressive language in humans. *Homo habilis'* endocasts reveal a number of developments including bilateral transverse expansion of the cerebrum (especially frontal and parietal-occipital cortex, with heightening in the later areas), increased bulk of the frontal and parietal lobes, well-developed inferior parietal lobule, and prominent enlargements of Broca's and Wernicke's (receptive language) areas (Tobias 1988). The evidence for Broca and Wernicke enlargements in the endocasts suggests that language, although at a rudimentary level, might have been within the intellectual capacity of *Homo habilis* (Tobias 1983a, 1983b).

The increased encephalisation of the frontal lobes over the course of hominid and hominin evolution has led to the speculation that the types of activities seen in mythic culture may have resulted from an unusual enlargement of the frontal lobes in humans, but this has not proven to be the case. As Semendeferi has found, the frontal lobes in humans are about what would be expected from an ape of human body weight; however, area 10 of the frontal lobes is markedly enlarged in humans as compared to chimpanzees (Semendeferi 2001a, 2001b). In humans, lesions in the dorsolateral portion of the prefrontal cortex, including area 10, are associated with impairment in higher-cognitive abilities that facilitate extraction of meaning from ongoing experiences, the organisation of mental contents that control creative thinking and language, and the artistic expression, initiation of, and planning for future actions (Damasio 1985). The enhanced development of the parietal lobe, with its interconnections to the frontal lobe, has led some neuropsychologists to describe these areas as functioning like a single neurocortical unit, i.e. sensorimotor cortex (Luria 1980). The inferior parietal lobule is important in mediating tool making as well as the ability to construct more efficient weapons and hunting implements. The earliest simple tools appear to have been produced by *Homo habilis*, Australopithecus, or both from about 2.4 Ma ago (Hamrick and Inouye 1995; McGrew 1995; Susman 1995).

As these cortical areas continued to enlarge, weapons and tools associated with *Homo sapiens* became highly abundant, and by Crô-Magnon times had become an art form. The left inferior parietal lobule, and the angular gyrus within it, is associated with reading and writing, temporal sequences, grammar, gestural communication, and the production of signs (such as American Sign Language) in *Homo sapiens*. The right parietal lobe is more concerned with guiding the body as it moves through space, determining spatial relationships, and with the analysis, manipulation and depiction of spatial relations through drawing, carpentry, masonry, throwing, aiming, painting and art (Joseph 1996: 50–3). The synthesis of the 'what' inferior-temporal pathway for the recognition of objects with the 'where/how' parietal areas relating to visuo-spatial/manual guidance were also a decisive factor that promoted the practical application of expertise necessary to produce artefacts with greater control and accuracy (Hodgson 2005). Thus the increased encephalisation of these areas from *Homo habilis* to *Homo sapiens* provides some insight into the necessary neuroanatomical substrate for the development of mythic culture, with its enhanced use of oral myths and artistic expression.

Finally, there is increasing evidence that a marked period of encephalisation dates from 700 000 years ago, about 200 000 years before Donald estimates the beginning of mythic culture. Potts (2001) has shown through graphic plots of increased cranial capacity in hominins that most of the encephalisation, dated from 2.4 Ma ago, occurred during the past 700 000 years. This encephalisation is correlated with the largest recorded oscillations of climate and habitat during the late Cenozoic. He believes that functions of the primate brain unique to humans involve effective responses to diverse environmental contexts such as these, and that increased corticalisation served to enhance the human ability to 'learn to learn'. The anterior brain morphology has been stable over the last 300 000 years, a period of time when mythic culture would have been evolving (Bookstein et al. 1999).

Although the macroscopic appearance of the frontal lobes has remained stable, areas within the frontal lobes were differentiating, such as area 10 as mentioned. Moreover, the increase in the size of the cortex does not keep up with the increase in the size of the white matter (Hofman 1989; Ringo 1991). Interconnectivity within each cerebral hemisphere, as expressed by the amount of white matter, is larger in larger brains. This is especially true in area 10 of the human frontal lobes, as compared to those of apes, where there is increased space between neurons that enhances the potential for the elaboration of associative connections with other brain areas (Armstrong et al. 1986). Indeed, the final increase of human brain size appears to derive from the increased number of cortico-cortico association pathways, which also probably represent enhanced behavioural flexibility through cultural learning, one of Donald's major criteria for mythic culture which he believes reached an apex during the late Upper Palaeolithic.

Part 3

A reinterpretation of Upper Palaeolithic representation from the perspective of the evolution of the brain, specifically regarding cognition

The predominance of animals in palaeoart

We tend to agree with Chase that 'archaeologists cannot assume a priori that any given change in behaviour as reflected in the Upper Palaeolithic record, even a major one, necessarily indicates a genetic change in hominid "intelligence" ' (2001). It may rather be a point at which the expression of intelligence becomes materially manifest in 'art', tools, weapons etc. after a long period of cultural evolution, made possible by a given level of neurobiological evolution in hominins. For example, the fluorescence of mythic culture in the late Upper Palaeolithic may have gained impetus from the long life spans and late maturity that have been typical of most humans from 200 000–500 000 BP, during Donald's mythic cultural period (Leigh 1992; Ruff et al. 1997), thus enabling grandparents to help forage, hunt and watch the young, all activities that would have permitted more time for the development, transmission and material expression of cultural knowledge. If this is the case, the fluorescence of Upper Palaeolithic 'art' should be preceded by earlier and earlier attempts at 'artistic' representations. Therefore, we hypothesise that future recovery of the material remains of 'art' will continue to penetrate deeper into the Middle and early Palaeolithic. Indeed, some evidence for this already exists with the finding of engraved geometric zigzag patterns producing triangles on two small pieces of hard red ochre, dated to 77 000 BP, or the Middle Stone Age (Henshilwood et al. 2002).

We can get some sense of how hominins may have viewed animals by considering how they were represented in the Upper Palaeolithic. Imagine the mix of affect that would have been experienced when a hunter approached very close to felines, rhinos, horses or bison as depicted at Chauvet Cave, Pont-d'Arc (French Government 2005: end chamber, western wall); or a grazing mammoth, bison, aurochs and horses, as depicted in the 'black frieze' in the cave of Pech Merle; or upon encountering a giant cave bear as depicted in the cave of Ekain; or suddenly coming upon a big cat head-on as depicted at Trois Frères (Bahn and Vertut 1997: 122–3, 151, 152, respectively). Clearly, the actual hunting experience, imbued with powerful emotions and coupled with innate predispositions to attend to predator and prey, served to cement and fix images of animals in memory. This process was made more efficient by the expansion of the hippocampus and its cortical connections. This viewpoint is substantiated by the fact that animals, both fearsome and benign, constitute the commonest kind of hallucination experienced by those taking psychoactive substances, including Amerindians and individuals from industrial societies with little previous contact with animals (Shanon 2002).

Moreover, the experience of such emotions, coupled with keen observations of animal behaviour, probably contributed to the view that the large and powerful prey animals hunted during the Upper Palaeolithic were special, such that these animals came to symbolise traits venerated, admired and feared by humans, as well as providing a practical solution to hunger and a source of clothing and other goods. One result of the close interaction between hominins and their prey was the fact that each exerted a selection pressure on the other, with the result that they may be said to have co-evolved (Mayr 2001). Such interdependence would have led to deep emotional involvement of early hominin communities with fauna. In this respect, many present-day rural communities in Asia and Africa still display an extraordinary closeness with their domesticated animals as exemplified in the myths and stories that surround these animals.

If these conjectures are correct, we should be able to find evidence of such attachments and attitudes toward animals in the archaeological record. We should also be able to find evidence of the use of animal skins and similar accoutrements that are thought to take advantage of curiosity behaviour by encouraging an animal to walk within the range of weapons, or to alarm prey in order to encourage them to move towards traps etc.

Support for the veneration of animals comes from the fact that their depiction has been the primary subject represented during and since the Palaeolithic (Bahn and Vertut 1997). The most feared animals seem to have been depicted in the archaeological record earlier on. Hahn (1986) emphasises how the animal statuettes of lions and bears from south-west Germany are represented in an aggressive pre-attack posture in a way that evokes their power and strength. Clottes (1996) makes a similar point in the case of Chauvet. Images of animals were predominant in Mesolithic and Neolithic art from Saharan Africa, namely in the Tadrart Acacus and Tassili regions, the earliest of which are believed to have been painted by hunters, followed by animal depictions made by hunters who were developing pastoral strategies. The latter are believed to have created paintings in the so-called 'round heads' style (di Lernia 1999).

Evidence for the use of disguises comes mainly from hybrid human/animal figures, usually with animal-like heads and human bodies. They seem to be part of the earliest 'art' as is found in a therianthrope sculpture from Germany, dated to around 33 000 BP, with the head of a lion and the body/legs of a human (Conard 2003). There is a strange creature painted on a hanging rock at Chauvet Cave, which appears to be a bison standing upright on human legs. We also find depictions of therianthropic figures in Lascaux and Gabillou (the figure in the latter has obvious horns) or the 'wounded men' of Cougnac and Pech Merle. In addition to the sorcerer figure at Trois Frères, there is a bison-headed humanoid (Bahn and Vertut 1997: 165) that bears some resemblance to North American Indians disguised as bison for a dance or a hunt (Giedion 1965: 374). Some researchers believe the vertical bison of Castillo is also depicted with human legs (Bahn and Vertut op. cit.: 166). Leroi-Gourhan estimated that there are about 15 sites that have composite figures, with about six in each, some of which do not appear to be humanoid (Bahn and Vertut op. cit.). Given the number of Palaeolithic images of animals, these few therianthropes may be early examples of figures that might not only be associated with hunting disguises, but may also represent some of the earliest depictions of mythological supernatural spirits. The 'sorcerer' is a very strange beast; the upright position and the legs and hands are human, it has the back and ears of an herbivore, the antlers of a reindeer, the tail of a horse, and a phallus reminiscent of a feline. Such a creature suggests a more complex figure than a mere hunting disguise.

At least some of the figures may simply represent human hunting disguises that allowed the hunter to draw near to prey (Thackeray 1993; Guthrie 1984). Manaseryan (2003) has identified human figures wearing masks in the context of scenes portraying the hunting of animals in rock art from Armenia dated to 5000 years BP. Extraordinary evidence comes from a photograph taken by W. H. C. Taylor in 1934, of an individual from the San 'Bushmen' wearing the skin of an antelope (Thackeray 2005). The use of an animal skin costume and the adoption of a quadrupedal posture by a human figure bending forward with two sticks is strikingly similar to the imagery of more ancient Melikane rock art therianthropes of South Africa, considered to be disguised hunters. Further evidence derives from the semi-nomadic hunter/gatherer community of Starr Carr, Yorkshire, England, dating to around 10 000 BP, where antler 'frontlets' have been found which were probably worn during rituals and used as a disguise in the hunting of animals (Laing and Laing 1982; Conneller and Schadla-Hall 2003). Also, a triangular cobble from La Madeleine, France (c. 13 000 BP), has engraved upon it a human figure in upright position with two heads, one thought to be a human, the other an animal-like mask (White 2003).

As a 19th–20th century example, the Bushmen of South Africa employed various animal skins, most particularly the skin of an ostrich, and there are artistic depictions of such figures in Bushmen art (Vinnicombe 1976). By this period, however, a million or so years after our early ancestors presumably first used animal disguises, which the preceding discussion on brain and cognition suggests might have been the case, the therianthropes depicted in Bushmen art assumed a complex mythical status, above and beyond simply referring to actual hunting practices. Wearing buffalo skins during the hunt was a practice that was still carried out until quite recently by some North American Plains Indians. In addition to animal skins, other assorted disguises such as masks may have been employed. The 'sorcerer' figure found in the cave of Les Trois Frères in the French Pyrenees wears animal accoutrements with which he may have been hunting, or possibly re-enacting a myth, both of which would be consistent with Thackeray's findings discussed previously.

Rock paintings from the Drakensberg depict many scenes with human figures carrying weapons and hunting accoutrements, as well as numerous therianthropic figures (Vinnicombe 1976). Most of these paintings date to the last 600 years (Mazel and Watchman 1997), although some may be up to 2000 years old (Mitchell 2002). Therianthropes are highly significant in San mythology and their spirits, although long dead, can still mix with, and affect the living (Solomon 1997). This is an excellent example of exaptation (Skoyles 1999), wherein behaviour that had one use in ancestral forms, i.e. wearing hunting disguises, is adopted for a new and different use in a descendant form, i.e. the construction of mythological beings represented as therianthropic figures with supernatural powers that are now depicted in a permanent visual form. Indeed, this example encapsulates the core thesis of this paper, i.e. that hunting disguises eventually came to serve as an interface onto which other aspects of behaviour came to be projected. Furthermore, it is an example of the neural plasticity that is made possible by the hominin forebrain and cortical expansions.

The appearance of depicted animals during the Upper Palaeolithic may therefore have been one exapted outcome that sprang from a preceding spectrum of activities originally adapted to defeat the deceptive devices employed by predators and prey. From this perspective, it is safe to say that the original function of deceiving quarry became subverted to the extent that deception was exploited for purposes other than that to do with the fear, veneration or hunting of fauna. The Palaeolithic artists did not depict all of the animals upon which they preyed, but rather selected certain specific beasts that are depicted frequently, such as mammoth, bison, aurochs, deer, and horses. As Vinnicombe (1976) demonstrated, the Bushmen primarily depicted the animals that were sacred to them or which were associated with very unique and special powers, and some similar process may have been at work in determining which animals were depicted during the Upper Palaeolithic. Large predators and valued or especially large or dangerous animals, whether they were prey or not, were accorded very special, potent powers by the Kalahari /Kung. In fact, it was taboo to refer to these special animals by their proper names; rather, one had to use a culturally denoted, but disguised name that was supposed to convey special respect for the beast (Marshall 1962). Such ideas may have originated quite early in the history of *Homo sapiens*, who have been co-operatively hunting large beasts since at least 600 000 BP (Washburn and Lancaster 1968). That hunting very large animals is an adaptive strategy was shown by Bourlière (1963), who demonstrated that 75 % of the meat available to human hunters in the eastern Congo was provided by the elephant, buffalo and hippopotamus.

Conclusion

These deliberations show that the human relationship with animals is a deep-seated neuro-biopsychosocial contingency that often influences behaviour and culture in ways that are not always obvious (Shepard 1997). This is because the architecture of the human brain, particularly the visual association areas and limbic system as discussed in this paper, is a function of the evolutionary struggle that obtained between our distant ancestors and fauna viewed as predators or prey. 'Representation', as a means of promoting survival in nature through mimicry, eventually came to be exploited or exapted by archaic humans to suit their own purposes, thereby helping to gain a competitive advantage in the game of survival. The depictions of animals in palaeoart may have derived, in part at least, from this long-standing interaction, whereby the ability to exploit the heuristics of mimicry to facilitate the pursuit and bringing-down of quarry may have been a key predisposing factor. The relationship between these various components will have engendered a dynamic that fuelled an obsession with animals that led to increasingly complex and diverse ways of thinking about, interacting with, and finally re-presenting them in the material record.

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RAR 23-744

Final MS received 25 October 2005.

COMMENTS

There's more to art than animals

By JOHN BRADSHAW

The authors' core thesis, as they explicitly state, is that hunting disguises (e.g. wearing animal skins as cover or camouflage) eventually came to serve as an interface upon which other aspects of behaviour, such as palaeoart, came to be projected. The detection of animals in the Upper Palaeolithic may have sprung from a preceding spectrum of activities originally adapted to defeat the deceptive devices (disruptive patterning, camouflage) employed by predators and prey. Representation as a means of promoting survival through mimicry eventually came to be exploited by archaic humans to suit their own purposes, and the depiction of animals in palaeoart may have derived, in part, therefrom.

My concern is what I regard as an excessive emphasis on the presumably male role of hunting large animals, in an almost exclusively European Upper Palaeolithic context. Carnivory was not a major driver in primate evolution, though in Ice Age Europe the nuts, roots, seeds and ripe fruits (which were of such early importance for the evolution of colour vision in supporting frugivory) certainly would have been far less abundant; indeed, meat has been (for higher primates and most 'primitive' human societies) a relatively rare delicacy, the stock staples being the vegetable materials largely gathered by females. Indeed in this (largely female) context, rather than in that of male hunting (where silence would usually be obligatory), the development of verbal communication (what, where, when, how …?) would have been particularly important, as also of course in rearing infants. Language is one form of symbolism, and iconic representation (manual gestures — which may also have contributed to the evolution of spoken language — and sketches in the sand or outright 'art') is another. In some contexts a picture is worth more than the proverbial thousand words; it is far easier to show some-one how to tie a knot, or shape or haft a stone axe, than to try to explain it.

The brain (human, primate or simply vertebrate) is primarily a modelling tool, be it of objects, actions, options or consequences; and drawings, sketches or art generally, palaeo- or modern, are external representations or concrete realisations of these models or of their consequences.

Palaeoart outside of (one-time) Ice Age Europe certainly was not limited to large and dangerous animals. Human figures engaged in a number of activities, ceremonial as well as hunting or warfare, are seen in rockshelters throughout southern Africa and Australia. In the latter instance the Gwion (formerly 'Bradshaw') paintings of the Kimberley region of north-western Australia are a prime counter-example, while throughout Australia small innocuous creatures, doubtless still a valuable food source, such as lizards, fish and turtles, are frequently encountered as paintings or petroglyphs. I do agree that the very frequent representation of animal spoor (footprints of macropods, birds etc.), especially in petroglyphs, may signify an important food source. However, during a recent visit by boat to the Kimberley coast, I often saw on dark basalt headlands, contrasting with the otherwise ubiquitous pinkish-white Kimberley quartzites, very old pecked representations of *human* feet, often, surprisingly, with six toes. Animal iconography is by no means the only or even the major manifestation of early art, and the authors' account, even if limited exclusively to that very particular class of representation, is I feel unlikely to be the only possible explanation.

Thus I am unhappy about developing an argument apparently based so disproportionately upon one part of the world — Ice Age Europe — and on predator/prey interactions with large, dangerous animals. Contrary to the authors' claims, while an 'advanced' visual system (with associated cognitive structures) certainly is helpful, if not obligatory (as indeed in successful frugivory) in an evolving, emerging or developing aesthetic sense, nothing more is needed in that department, for hunting or evading the predator, than is possessed by a mammalian herbivore or a parrot. I do not feel that such a hunting/evading scenario provided the necessary preconditions for a pre-adapted visual system to accommodate an emerging aesthetics. Sorting by categories, moreover, as the authors argue, is not a faculty unique to ourselves or even primates generally; the African Grey Parrot, as Pepperberg (1999) has shown, can with its tiny brain do very well indeed in that context.

There is in fact probably an excessive emphasis on a unifactorial approach to 'explaining' the emergence of palaeoart. In medicine, ecology and evolution generally, all regarded as complex, dynamic, interactive systems with multiple feed-back loops, we so often find that multifactorial explanations, models or accounts have to be invoked. The overemphasis on deception in interacting with large dangerous animals blinds us to the fact that in the higher primates generally, and in our own species in particular, an individual tends to face the gravest threats from *conspecifics*. Much of our time is spent in what has come to be known as 'Theory of Mind' activities, where we continually assess what we believe others know, believe or think we know, suspect, fear or intend (Happé and Frith 1999). Primates, and especially humans, are essentially *social* creatures, forever evaluating the knowledge, emotions and perspectives of our fellows. Theory of mind, together with the construction and deployment of tools, are surely better models for the evolution of intellect, abstract thought, and probably even aesthetics as a particular instance of symbolic behaviour (which more generally of course also includes language), than is interaction with large, dangerous animals at one time in pre-History and in one corner of a very large world. Unfortunately, I just cannot accept that 'the production of the earliest visual depictions arose out of a common primate adaptive heritage, the decoding of deception and subterfuge manifested by predators and the deciphering of such diversions when pursuing prey … and that pictorial representation … derived from a suite of interrelated activities concerning how distant human ancestors interacted with and felt about animals'. That said, I do accept the importance of the mirror-neuron system as a common link between perception, understanding and action, and while the authors mention very briefly indeed this whole new emerging concept, whose wider theoretical and explanatory potential and importance is almost certainly yet to be fully realised, I suspect it will also be found to underlie in a fundamental fashion the evolution and realisation of an aesthetic sense.

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Working forward from distant times; working backwards from recent times

By CHRISTOPHER CHIPPINDALE

After the weary whingeing (Helvenston and Bahn 2002; etc.), and worse, about the hopeless ideas of the deluded 'shamaniacs', it is good to see this school's discussion of Palaeolithic imagery turning to a positive mood, and amusing it has chosen an observation even older than supposing a possible connection between the pictures and visionary experience. Alongside — yet again — theories based on man the hunter, it might be fresher and instructive to think of gathering. Since gathered plant foods provide the bulk of the nourishing for gathering-and-hunting humans, and since gathering seems often to be woman's work, there are gender issues here (Dahlberg 1981): is it the males among non-human primates who do the hunting? Are we to conclude, if hunting is man's business, and if art concentrates on the animals, then early art was man's business?

Exceptions to the common pattern that plants have minimal representation in rock art seem to be few. The plants in Lower Pecos art, Texas, are persuasively linked to plants with medical and hallucinogenic properties (Boyd and Dering 1996; Boyd 1998). In the singular 'yam figures' in the rock art of western Arnhem Land, Australia — if their motifs *are* rightly identified as depicting yams, and therefore a vegetable domain — we seem to see hybrid figures, largely of human or quasi-human traits but with the human head replaced by a yam; and some of the singular traits of these root-headed beings appear also on quite other kinds of subjects (see Chaloupka 1993 for illustrations of some Yam figures).

The Makapansgat pebble (apparently natural), and the Berekhat Ram and Tan-Tan figures, again depended on here (p. 10–11) are slight and difficult evidence. We read them as having human form — or can read them so (even after publishing the paper on Berekhat Ram, and hearing all Marshack's advocacy of it, I struggle to make my eyes see it as taking as plainly human in form); but how do we know ancient hominins did? Sometimes a cigar, as Sigmund Freud never said, is just a cigar: is the Makapansgat pebble just a pebble? A small handful of ambiguous objects scattered across the last 3 million years is not evidence of a pattern in human behaviour.

I do not see why (p. 15) the Upper Palaeolithic hybrid human/animal figures are seen as likely to be humans disguised the better to hunt, rather than other kinds of beings, or why we can know that the modern use of animal skins to conceal the hunter 'presumably' follows a tradition that is a million years old. All the evidence directly relating to this which is adduced is either ambiguous or from very recent times or both.

In exploring the earlier forms which modern human culture has taken, a chronologically structured argument can start beforehand and move forward, or afterwards — even in the present — and move back. Starting beforehand, the researcher is pushed into the cultural mists of the deep Palaeolithic and beyond, where our knowledge of hominin or human thought — rather than descriptions of how they broke rock — is so very thin, and to depending on similarities with other primates' behaviour which seem culturally tenuous. That is one good reason why the other direction of timely movement, to work from modern knowledge back, may have a richer potential, and why I still find studies doing this (e.g. Clottes and Lewis-Williams 1998; Lewis-Williams 2002) a more rewarding kind of exploration. I would think deducing by analogy with beings of the same species living perhaps 30 000 later, who are likely descendants in a pretty continuous cultural tradition, is methodologically sounder than jumping back to other species and even genuses which are very much further removed in time from the cultures of the Upper Palaeolithic persons whose images we seek to grasp, and for which the behavioural evidence is vanishingly slight.

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The role of enhanced working memory in the production of animal and therianthropic art in the Upper Palaeolithic

By FREDERICK L. COOLIDGE and THOMAS WYNN

Hodgson and Helvenston have proposed that visual depiction of animals in the Upper Palaeolithic may be a signature of modern brains, although not necessarily of modern minds (Helvenston and Bahn 2004). They noted that inchoate palaeoart may have developed as consciously deployed camouflage to deceive the visual systems of hunted fauna. Although simple animal representations may have indeed had their roots in prey deception, the deception hypothesis fails miserably to account for such therianthropic figurines such as Hohlenstein-Stadel: it would be highly unlikely that Upper Palaeolithic people dressed as lions in order to hunt them. Hodgson and Helvenston also reviewed and rejected the more controversial hypothesis that such art was the product of exogenously or endogenously caused trance states (Lewis-Williams 1991, 2002). We have already suggested (Wynn and Coolidge 2006) that a much more prevalent and ubiquitous phenomenon, dreaming, could have served as a stimulus for animal representations in Upper Palaeolithic art, particularly therianthropic figures. However, as Hodgson and Helvenston duly noted such art would require highly advanced visual-spatial representational abilities and motor skills. Using Donald's (1991) three stages for the evolution of culture and cognition, Hodgson and Helvenston re-propose that the last stage, mythic culture, was characterised by 'high-speed phonology, oral language and oral culture … [requiring] enhanced representational abilities … [suggesting] enhanced cognitive capacities over that of the mimetic stage' (p. 13).

We believe Hodgson and Helvenston correctly implicate neuronal changes in the dorsolateral prefrontal cortex, interconnectivity between the frontal and parietal lobes, and cortico-cortico association pathways as the neuronal basis for these behaviours characteristic of mythic culture and its participants' apparent enhanced behavioural flexibility. We have already proposed that an additive genetic neural mutation 125–50 ka BP may have had a profound effect upon the prefrontal cortex and that the mutation may have affected non-domain specific working memory (WM) capacity (Coolidge and Wynn 2001, 2005; Wynn and Coolidge 2006).

WM is a theoretical construct initially proposed in 1974 by Baddeley and Hutch, reflecting a capacity to hold and manipulate information in active attention consistent with short- and long-term goals, in spite of task-irrelevant interference. As currently conceived (Baddeley 2000, 2001), WM is a multi-component cognitive system consisting of a central executive which manipulates two 'slave' systems, (a) phonological storage with an articulatory processor, and

(b) a visuospatial sketchpad. Baddeley's most recent addition to WM is an episodic buffer that integrates information from the two slave systems and serves as a temporary store for this information and other material at the behest of the central executive component. Two of the components of WM have received strong initial empirical support, the central executive and phonological storage (e.g. Miyake and Shah 1999) and more recently so has the visuospatial sketchpad (e.g. Shah and Miyake 2005).

The chief function of the central executive, the maintenance of task relevant material consonant with goals in spite of interference, has been well documented by nearly five decades of research in both normative neuropsychological studies and clinical studies of patients with documented brain dysfunction. This chief function and its other functions have heretofore been known as executive functions of the frontal lobes. These functions include decision making, complex and novel problem solving, action selection, maintenance of attention in spite of distractions, planning and response inhibition.

The other well-documented sub-system of WM is phonological storage, which serves as a short-term store for acoustic stimuli (primarily words). An important component of phonological storage is an articulatory loop, which includes an articulatory processor, which is a rehearsal mechanism for maintaining sounds or words in active attention. The articulatory processor can rehearse its temporarily stored material either vocally or sub-vocally. The existence of a comparable 'image' store in visuospatial sketchpad is not as clearly documented.

Neuropsychological and brain imaging research indicates that WM is largely a frontal lobe neural network, with significant links to parietal and temporal lobes. The dorsolateral prefrontal circuit is generally associated with the classic executive functions mentioned previously. The orbitofrontal prefrontal region is more closely connected to the limbic system and has been shown to be associated with the processing of emotions and the regulation of social behaviour and social interactions. Both systems are closely connected, and the prefrontal cortex in general has extensive projections to almost all regions of the temporal and parietal lobes, some projections to the occipital lobe, and to subcortical structures such as the basal ganglia, the cerebellum, and many brainstem nuclei. The gist of these interrelationships appears to be that the prefrontal cortex co-ordinates the processing of broad regions of the central nervous system. A third region of the prefrontal cortex is the anterior cingulate gyrus, and it is thought to mediate motivational systems and action selection (Pennington 2002). These findings are important to Hodgson and Helvenston's contention that the frontal lobes, in particular area 10 of the prefrontal cortex, and their connections to other lobes, may be critical to the ability of modern *Homo* to represent animals in Upper Palaeolithic art.

Our hypothesis is that an additive genetic mutation specific to working memory capacity, which we have labelled enhanced working memory (EWM), hinges critically upon evidence that WM and its components are heritable. Recent genetic studies are strongly supportive. In fact, it has been repeatedly shown that WM's various components have a highly heritable basis, even greater than for general intelligence, whose genetic contributions are now accepted as substantial (e.g. 45 % to 50 %). In a behavioural genetic study of child and adolescent twins (Coolidge et al. 2000), core functions of the central executive (e.g. planning, organising and goal attainment) were found to be exceptionally heritable (77 %), and attributable to a polygenic influence with as few as four pairs of alleles. The phonological storage component of working memory has also been shown to be strongly heritable, e.g. 35 % to 56 %, and polygenic (Rijsdijk et al. 2002; Ando et al. 2002). Ando et al. found their measures of the central executive and visuospatial sketchpad were also strongly heritable (37 % to 57 %). Hansell et al. (2001), using event-related potential slow wave measures of WM within a visuospatial sketchpad-related task showed similar polygenic heritability (35 % to 52 %). Although Hodgson and Helvenston (2006) do not address the timeframe for the expression of final features of 'enhanced behavioural flexibility' (p. 14), we presume that they believe it was long in place neurologically and only expressed itself through some cultural processes, of which they leave both the exact timeframe and the nature of the cultural processes vague and unspecified.

Our hypothesis is that the final neurological formation of the modern mind was far more abrupt, thus, accounting for the apparent explosion of culture in the Upper Palaeolithic. We have also speculated (Coolidge and Wynn 2005; Wynn and Coolidge 2006) that it may have been an additive genetic mutation that specifically affected WM capacity, which as noted earlier, is not only highly heritable but has been empirically demonstrated to be demonstrably measurable and varied in normative modern human populations. An alternative hypothesis is that the additive genetic mutation did not directly affect non-domain specific general WM capacity but occurred in one of its domain-specific subsystems. We have previously speculated that one likely culprit, because of its possible direct consequences for speech and language (and verbal fluency), is phonological storage. Baddeley and his colleagues (Baddeley and Logie 1999; Baddeley et al. 1998) have already proposed that phonological storage capacity could be a bottleneck for language production and comprehension, and indeed recent empirical studies support this contention (Gathercole et al. 2004). Furthermore and highly provocative are the findings that WM capacity and to a lesser extent phonological storage capacity are significantly related to general intelligence and fluid intelligence (i.e. novel problem solving; Kane and Engle 2002).

We believe the EWM hypothesis has much to offer to the arguments of Hodgson and Helvenston. Where they noted (p. 12) that 30 ka, small groups may have been organised by 'egalitarianism, with leadership being informal and *based on natural ability …*' (italics ours), we would counter that the highly heritable features of WM, particularly its demonstrated individual heritable basis, allows such differentiation and underlies 'natural' leadership abilities. Where Hodgson and Helvenston propose that mythic culture was characterised by 'high-speed phonology' (p. 13), we would purport that enhanced phonological storage capacity may have been a critical key to increased verbal fluency and its subsequent interpretation. What good would exceptional verbal fluency be if the speaker could not be understood? Increased phonological storage capacity would simultaneously allow for increased verbal fluency and increased comprehension of such productions. Hodgson and Helvenston's contention that modern minds had to have been characterised by enhanced visual representational abilities also fits well within our speculations, although it might support our first hypothesis (that the neural mutation affected general WM capacity), rather than our second (that the mutation was specific to phonological storage capacity). Their depiction of modern minds' 'numerous enhanced cognitive capacities' (p. 13) and 'enhanced behavioural flexibility' (p. 14) also fits nicely within our model of EWM. Finally, they speculate that actual hunting experiences 'imbued with powerful emotions and coupled with innate predispositions to attend to predator and prey, served to cement and fix images in memory' (p. 14) and further, they linked this process to more efficient connections of the cortex to the hippocampus. The latter neuronal structure is part of the limbic system, which itself is heavily involved in the processing of emotions and transfer of verbal memories to long-term storage. Earlier, we also noted the important role the orbitofrontal cortex in emotional processing, social regulation, and interpersonal decisions. Thus, their latter speculations not only fit well with the known neuropsychological functions of the limbic system but also with various constructs associated with WM.

Hodgson and Helvenston also mention oral language and oral social records as characteristics of mythic culture, with the implication that they also may be manifestations of modern thinking. We do not think that WM and language functions are synonymous, nor do they appear to involve identical neural structures. However, we believe WM capacity does affect how language is actuated. As an example of the effect of WM on sentence complexity, we cite recursion, a feature of grammar that many, including Chomsky (e.g. Hauser et al. 2002), argue is a key development in the evolution of language. Recursion is the mechanism in grammar that enables a speaker to use an entire phrase as an object of a higher level phrase, e.g. 'He said that she said'. It is this feature that supplies native speakers of a language with the ability to produce, in principle, an infinite number of meaningful sentences. In practice, the size of this 'infinity' is constrained by several practical limitations, one of which is WM capacity, and perhaps more specifically phonological storage capacity. The number of recursions must be held and processed in attention if they are to be understood not only by the speaker but also by the listener. 'He said that she said that they said that we said that I said that Hagrid wants to see you', is a grammatically correct sentence, but one that nearly exhausts the capacity of WM to analyse. Add two more levels of recursion and few native speakers could keep track. The syntactical rule (recursion) has not changed, but the sheer size of the task has. Perhaps the simplest interpretation of the effect EWM has on linguistic communication is to conclude that it enlarged the recursive capacity of language. An enhancement of WM would yield immediate results in the length and complexity of sentences, thus accounting for Hodgson and Helvenston's emphasis on oral language and oral traditions typical of the inhabitants of mythic culture.

We have also previously speculated (Coolidge and Wynn 2002) that EWM may have affected the nature of speech acts or the pragmatics of speech. A speech act refers to the act which is done or performed by speaking (e.g. Adams 2002). While the classification of speech acts is far from decisive, five modes or pragmatics of speech are often noted: declaratives, which are statements of facts; exclamatives, which are short bursts of speech usually associated with surprise, pain, or pleasure; imperatives, which are commands; interrogatives, which ask questions; and subjunctives, which state hypotheticals, conditionals, speculations, and statements that are not true. We have hypothesised that EWM may have had a particularly profound effect upon the latter category of speech. EWM may have allowed the speaker to 'hold in mind' a much greater number of options, and as such, given the speaker a greater range of behavioural flexibility and even creativity. We previously hypothesised (Coolidge and Wynn 2005) reflection upon a greater number of options allows the organism not only a choice among those options, perhaps based on previous successes or failures of each option, but also to choose a future option or actively create an alternative plan of action. Thus, we would tentatively speculate that the 'what if' capability of the subjunctive mode of speech, may have arisen as a function of EWM, and this mode of speech may have been required to produce therianthropic figurines. Certainly, monsters would have lurked in minds of ancient waking dreamers such as *Homo habilis*, but it may have taken truly modern minds, with a full complement of speech acts, to turn those monsters into tangible icons.

Finally, if we were to weigh in on Hodgson and Helvenston's claim that palaeoart is an indicator of modern brains but not necessarily modern minds, we would agree in part. As one of those authors already noted (Helvenston and Bahn 2004), rock art images produced by Palaeolithic people do not logically imply that their minds were *identical* to modern minds. However, we would throw our support to the *speculation* that the people who produced therianthropic figures such as the Hohlenstein-Stadel figurine did indeed not only have modern brains but also had modern minds. We would also reiterate that dreaming, a far more prevalent and ubiquitous phenomenon among all people may have been the more likely stimulus for animal representations in Upper Palaeolithic art, and we would argue that this is exceptionally true for therianthropic and chimeric figures, which have been frequently noted in the dream reports of contemporary populations of children and adults (Foulkes 1978; Van de Castle 1983, 1994). Furthermore, reports of 'things', monsters and animal predators may be even more prominent in the dreams of children than adults (e.g. Stevens 1995). Regardless, therianthropic and chimeric figures, such as monsters, are far from rare occurrences in modern dream reports.

In summary, we find that Hodgson and Helvenston's 'neuro-biopsychosocial' explanations for the emergence of animals in Palaeolithic art to be well explicated and provocative. As we have noted, however, we believe there is also much to be gained by grounding their speculations in Baddeley's model of WM and our EWM hypothesis.

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Hominin cognition and animal 'art': a comment on the Late Pleistocene evidence

By FRANCESCO G. FEDELE

This paper offers a brave attempt at unravelling the ultimate origins of hominin 'obsession with animals' (i.e. with *other* animals), including its late expression as depicted imagery in western Europe and elsewhere. Sometimes it is over-intricately written and, in my opinion, the last section, 'A reinterpretation of Upper Palaeolithic representation', may have been hastily completed. These blemishes, however, do not detract from the substance and value of an important paper, impeccably up-to-date and cogently argued. I add at once that I find myself in agreement with Hodgson and Helvenston's approach in Parts 1 and 2, particularly on the subject of deep-rooted precursors — neurological, behavioural, and for me ecosystemic — to more manifest and recent expressions. On the problem of the so-called Upper Palaeolithic and its endlessly emphasised 'art' (Part 3) I concur with the authors on a number of points, and share the exaptation model wholeheartedly (cf. Fedele and Giaccio in press); however, I believe that our understanding of what really happened is still very incomplete. It is precisely papers of this kind that may lead to a coming of age, characterised first of all by the rejection of diehard, uncritical notions.

What we have long called cultural evolution or plain old-fashioned 'prehistory' is *inter alia* the evolution of cognition. It is good to be reminded that, in us humans, cognition is in turn an evolutionary by-product of vision, as well as touch. In current debates sometimes it seems that humans ceased to be primates on entering the Late Pleistocene, and shed their primate mindset altogether. For humans as primates, being visual and tactile is integral to their ecological niche, otherwise they would not be a distinct animal clade. Although fossils of cognition still seem to be sparse, a probable product of researchers' bias, the available evidence suggests that a much greater time depth than 30 000 or 40 000 years should be admitted for the emergence of distinctly 'human' ideological artefacts (cf. Fedele 1994). This paper provides an excellent summary and discussion from the standpoint of palaeoart. The authors especially stress how long a span of evolutionary time must be involved in the full-fledged emergence of visual depictions. I agree with the premise that we have a built-in 'vocabulary' of actions and gestures. Image-making, regardless of any subsequent complexity, is little more than gesturing with a material correlate, i.e. a visual/pictorial outcome.

This much for the impressive canvas of the paper. In what follows I would like to single out just one topic for particular comment, or rather integration. That is the problem of hominin cognition and animal imagery during the so-called Middle to Upper Palaeolithic transition. Readers well know that this 'transition' is a popular interpretive construct for human evolution in parts of Eurasia, falling within the 40 000 ± 10 000 BP time bracket, but it is sometimes overlooked that popularity by itself does not mean veracity. The Upper Palaeolithic in particular has perhaps become the most obsolete and dangerous among the 'uncritical notions' alluded to above. Furthermore, concerning the 'transition', I hasten to add that, not surprisingly, it is now imperative to decouple the anatomical from the sociocultural (e.g. Brantingham et al. 2004).

Recent work (Fedele et al. 2002, 2003) has shown that an acute climatic deterioration caused by arctic ice discharge — Heinrich Event 4, starting at c. 40 050 cal BP — was soon followed by a very large volcanic eruption of the explosive kind. This Campanian Ignimbrite (CI) eruption occurred precisely in the 40 000 ± 100 cal BP time range, and possibly at '40 012 cal BP' according to a correlation with the GISP2 Greenland ice-core tephro- and chronostratigraphy (Fedele et al. in press: Fig. 7). The CI originated from southern Italy and its immediate impact was the cause of a super-regional crisis affecting human ecosystems throughout south-eastern Europe. A 'volcanic winter' was felt at least on a hemispheric scale. The occurrence of a major eruption of such scope and chronology brings a new and unexpected factor into the study of the 'transition' in question. Of interest here, in my opinion, are its potential implications for the emergence of the sociocultural expressions usually termed 'modern' behaviour, prominent among them being image-making or 'art' (Fedele and Giaccio in press; Fedele et al. in press; the information summarised below derives from these papers and unpublished working documents).

Through complicated feedback circuits, the CI is modelled as having produced a sudden shift in population density and distribution, with fringe effects far distant from the core area of impact. Concurrently, the CI is likely to have caused a disruption of the communal, cognitive balance of social groups. We would posit a critical interplay between an altered resource base, population ecology (not demography *per se*) and social configuration, with ideology and cognition as additional major players. Cognition as a component of the social fabric leaves traces in the material record, with image-making being a vital clue. At a date of 40 000 BP we are dealing with hunter-gatherer groups of enough complexity to organise life along socially constructed cognition, and with 'locales invested with association and meaning' (Gamble 1999: 425) — a condition that was a source of both social fragility and resilience. My theory is that the rapid elaboration and accentuated *visibility* of 'art' are to be understood against this backdrop and in connection with the demands of 'crowded', shifting social environments. In hunter-gatherers' lifeways image-making is best explained from an information-exchange perspective and taking into account its combined 'know-how' and emotional values (e.g. Gamble 1982; Conkey 2001).

I wish to object to singling out 'art' as a proxy for human 'modernity', not least because the latter is in the eye of the beholder, and art frequently as well. Following Donald (1991), Hodgson and Helvenston are careful to show how hominin behaviour cannot be easily phrased as modern *vs* non-modern, in view of the evolutionary timespan and multiple threads involved. They also show from what a broad and deep base the apparent booming of cognitive 'modernity' — including animal depiction — clearly sprang. The prevailing notion of modern behaviour is biased, indeed a *moderno-centric* construct; 'art' itself is no more than an arbitrarily overemphasised component of expressive culture. The naturalistic imagery of the European Palaeolithic, in particular, is only over-attractive because it is localised and 'exaggerated', thus exhibiting the hallmark of local invention. Southern Germany and the Don valley may have been seedbeds of a sort, the plausible context being provided by the regional, evolving Mousterian (e.g. Conard et al. 2004, after the re-dating of Vogelherd).

Like language or symboling in general, image-making appears to have evolved from simpler and less manifest antecedents, and have then subsequently exapted, i.e. it took on other functions. 'It clearly was a "process" (and not an "event"), and almost certainly had nothing to do with genetic superiority' (Clark 2003). Reorientation followed by rapid and successful expansion can easily look like a break or an explosion in the archaeological record and be accordingly misconstrued. Explanations of the c. 40 000 BP 'transition' in terms of demic migration and replacement appear at least simplistic and discourage the search for local roots. Symbolism and imagery do not qualify any more as necessary and sufficient attributes for the definition of a major new stage in human evolution round the 40 000 BP timeline, if only because they predate any such stage, along with stone blades or bone tools. It is in this context a recognition of the role of other animals in making us human (cf. Shepard's 1997 title), and *cognitively* human especially, is not only welcome but refreshingly plausible.

In conclusion, it is predicted that a number of already available and somewhat latent behavioural traits, including those related to the functional neuro-anatomy of emotion and imitation, became viable options under the exceptionally stressful conditions which affected western Eurasia — or the whole northern hemisphere? — at c. 40 000 BP. Such sudden conditions interfered with precursor traits or processes and may have acted on them as powerful catalytic (i.e. reinforcing) or selective agents, according to situations and regions, thus generating accelerated change. The hominin cognitive makeup that is implicit in visually represented symbolic expressions was crucially involved. To this evolving scene of human cognition in Late Pleistocene Eurasia the authors of this paper are now adding time depth and sound 'biopsychosocial' background.

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Syncretic research architecture

By DONALD MEYER

In this compilation of current theory and clinical work, each generally disparate in intent to the central subject of the others, Hodgson and Helvenston point the way to a type of syncresis implied but not articulated in a course of action.

Contemporary cognitive studies surely have developed clinical technologies, such as TMS, for the direct study of the architecture of the human neuroanatomical systems involved in tactile interaction with objects in the environment. Contemporary archaeological technologies regarding the precise, confirmable chronological sequence in the found artefacts create a second grounding of cognitive archaeology in a syncretic approach. Cognitive science and archaeological science now need a syncretic research architecture, Hodgson's and Helvenston's work seems to imply here.

The key to this I suggest is extending cognitive archaeological study toward current cognitive studies of metaphor in linguistics as the architecture of all human thought (based on the indentical neuroanatomic constructs discussed in this article) that is necessarily inferential of visual experience. I refer to the work of George Lakoff at Berkeley and Mark Johnson in this area.

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Mimicry, deception, mimesis

By YANN-PIERRE MONTELLE

As a cultural behaviourist, I can only applaud this brilliant effort. Indeed, the behavioural trajectory from ecological mimicry to ethological deception to iconographic depiction promises a lot more hermeneutic results than many of the approaches offered so far in rock art research. Merlin Donald's[8] model provides an adequate structure for this investigation. He writes: [9]

> The first transition introduced two fundamentally new cognitive features: a supramodal motor-modeling capacity called mimesis, which created representations that had the critical property of voluntary retrievability. The second transition added two more features: a capacity for lexical invention, and a high-speed phonological apparatus, the latter being specialized mimetic subsystem. The third transition introduced external memory storage and retrieval, and a new working memory architecture.

The three major cognitive transformations proposed are not only effective in terms of describing an evolutionary environment where selection pressures were determining agents in shaping the known socio-cultural morphs, but also entail a new field of investigation in behaviour which is concerned with the restoration of behavioural bits. This restoration of behaviour is taxonomised into four main categories: episodic, mimetic, mythic and theoretic. The idea is to provide a framework capable of handling the multi-level processes involved in assessing the paradigmatic and evolutionary stages between the non-symbolic cognitions of animals and the symbolic representations of humans. The authors' concerns with cognitive successions marks a paradigmatic shift from chronology-based concerns and iconocentrism to an empirical exploration of 'the neurological and behavioural precursors' that led to the production of iconographic re-presentation of the natural world in a constructed space. The questions about mimicry, deception (tactical or not), imitation and representation (even beyond the ecological or ethological concerns) had to be introduced, and it has been well illustrated by the author's piece; it might indeed hold a key to unlocking the 'mind in the cave'.

Mimicry. It is presented as the main cog in the behavioural mechanism responsible for the production of Upper Palaeolithic iconography and, by association, for the human use of caves in the Upper Palaeolithic. Mimicry, as defined by the authors, is a deceptive strategy to manipulate perception. In terms of parietal iconography, it could be defined as intentional markings on a salient feature resulting in morphological changes that resembles known anthropomorphous, zoomorphic or abstract features. The behavioural basis for this deceptive process is certainly 'old' and its emergence would have to be excavated from the behaviour of fossil hominids. However, ethology will provide a very effective field of investigation, and analogical reasoning between human behaviour and primates is here fully justified. Echoing Fiedler (2003: 114–5), the authors endorse the notion that 'the origin of representation is to be found in ethology rather than archaeology or anthropology' (p. 3). Admittedly, there is a lot of truth in this statement. Mimicry as a tactical response to the inevitable dyad prey/predator in nature is a very efficient departure point, and provides the field of rock art research with a new battery of inquiries.

Deception. At this point moths and twigs are left behind, and the dissection of the tactical mind begins. Tactic is synonymous with intention. Hence, a discussion about deception must begin with intentionality. Three obvious levels of intention are detectable in deception. There is the unmediated spontaneous deception that is an adaptive phenomenon as a by-product of the dyad prey/predator. There is the unintended deception leading to an assessment of results whereby the 'organism' readjusts its behaviour to reproduce the deceptive act and produced the desired result(s). And finally, the fully intended and mediated deception where tactics and subterfuges are used to create a deceptive environment where manipulations can be performed with expected outcomes. Deception, as defined, when applied to the cultural and socioeconomic environment of the Upper Palaeolithic societies introduces another set of fundamentals. Indeed, the questions of cohabitation, co-operation, dissemination of information, and effective maintenance of the status quo are best understood in the light of deception. Deceptive strategies to minimise potential tensions and conflicts within a nucleus of connected individuals have been precisely described by ethologists. The tactical deception of an ape is 'episodic' — it does not seem to be the result of a premeditated response but rather the result of an 'intelligent' response based on the reactivation of recollected bits of experiences. However, when segmented it displays most (if not all) the necessary requirements for maintaining the social pressures and hierarchies that are fundamental in the establishment of a working and cohesive collective. Internalisation of deception with premeditation of retaliation or exorcism of stress and tension through externalisation in applied media is potentially at the root of depiction. Deception then becomes a stabilising means using deceptive strategies to maintain the status quo — read: the production of iconographic re-presentation of the natural world in a constructed (and monitored) space. Obviously, the lexicon of deception would also follow an evolutionary pathway with increasing complexity and exponential economy of signalling devices. In other words, draw what you know until what you know becomes so voluminous that it cannot be drawn anymore

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[8] All things considered, when we consult Donald's writing on cave iconography, we are quickly reminded of the naiveté that often stains this particular subject. In a sub-section of the Third transition (pages 279 to 284) in his seminal work titled *Origins of the modern mind: three stages in the evolution of culture and cognition*, M. Donald provides an overview of Upper Palaeolithic cave iconography which is rather unsatisfying. In this section he provides four references, two of which are Frazer and Campbell on page 282. This unfortunately weakens his commentaries on Upper Palaeolithic iconography.

[9] Excerpts from an online draft for his 1993 article titled *Précis of the origins of the modern mind. Three stages in the evolution of culture and cognition*.

but needs to be written. In fact, writing is deceptive!

Mimesis. Donald considers mimesis or the mimetic stage critical for the externalisation of cognition. Mimesis is often defined as a behavioural process whereby what is achieved is a close external resemblance of an animal to another that is distasteful or harmful to potential predators. Mimesis therefore is imitation (at least in terms of its etymological root). Imitation is a complex behavioural assemblage of mimicry and deception. Imitation is the most performed (and restored) behavioural bits across the ecological world. It is by imitating that most of our learning (conscious or not) is done. Exercising imitative behaviour will provide a welcomed reduction of the alterity of 'otherness' and by performing deceiving hermeneutic tactics the destabilising unknown will be framed. Needless to say the advantages of imitation are endless. As described by the authors, the imitation of a preyed animal through disguise allowed a proximity that triggered all sorts of economic, cultural, and emotional applications. But imitation has its limitations. To restore imitated behaviour, a stress is made on memory. Unless memory is externalised into intelligible segments that can be stored and restored, imitation cannot be always duplicated and remembered. So once the hunter has performed for a collective his emotions during a successful stalking and killing, and unless the narrative is inscribed in the cultural reservoir, the sequence will be lost. Arguably, oral tradition was instrumental in preserving these narratives in the form of myths, but according to Donald, the mimetic stage happened at a point where the lexical capacities were minimal. It does not take a lot of effort to see that it was an advantageous step for hominids to externalise the narratives in what Donald has called 'visuographics'. And what better subject for categorising knowledge than known images of hunted and encountered animals?

Hodgson and Helvenston have opened an inviting door. It is up to the community of rock art researchers to step in and start digging into what I believe is the most promising area of investigation for this new century. This work brings us one step closer to answering some of the epistemological questions about how we, as a species, construct(ed) our realities.

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Cognitive archaeology and cognitive sciences

By ROBERT G. BEDNARIK

This important paper demonstrates that the issues of human cognitive origins are the domain primarily of such disciplines as ethology, psychology, cognitive sciences and neurobiology. Archaeology has limited input here, and palaeoart provides at best the raw material. Cognitive archaeology is thus not a sub-discipline of archaeology; it needs to be quite deliberately interdisciplinary. Hodgson and Helvenston demonstrate this with authority in their well-crafted paper. I find it particularly impressive how they follow up early pointers, develop them and provide them with neurophysiological substantiation or depth, showing elegantly how questions of human evolution can be usefully addressed via the cognitive sciences. For instance they develop my proposal of twenty years ago, that 'visual misinterpretation would have favoured objects that dominated the taxonomic visual system of hominins, namely those that provoked desire and fear, i.e. large mammals'. Another such key statement in this paper that illustrates the kind of direction we need to take is this:

> As LeDoux (1994) makes clear, certain key features may be enough to trigger an emotional response by way of the amygdala before an object, such as a dangerous animal, is consciously recognised. Thus, there seems to be an early warning system that proceeds directly from the retinal-thalamic visual pathway to the limbic system for the rapid discrimination of potentially threatening objects that primes conscious awareness for action if required, and over the course of hominin evolution these abilities would have been highly adaptive (p. 7).

Clearly, the main strength of this paper is its use of what we have learned in recent years about the operation of the human brain. Another strong point is the emphasis on the role of animals (or, rather, the role of other animals) in the lives and preoccupations of people in pre-industrial societies. Whether these were hunters and gatherers or herders, the importance animals played in their lives is hard to comprehend from outside their cognitive realities. As an example one might consider the Nuer, the Nilotic people whose daily life revolves entirely around their cattle, who have deep psychological bonds with them, and whose language includes a huge vocabulary defining nuances of appearance and character in the cattle. They lavish more care on the appearance of their stock animals than a film actress does on her make-up. The many expressions of kinship hunters feel for their quarry have often been documented (and they are very tangible in totemic systems), as has been the universal ability of hunter-fisher-foragers to empathise with and mimic animals. It is therefore easy to agree with the authors of this fine paper that the importance of animals to the people who produced the world's rock art can hardly be overstated. This is obvious enough, surely, from the iconic content of much rock art. Moreover, large mammals have been the principal source of food in Pleistocene Europe since the times of *Homo heidelbergensis*, much in the same way as for modern-day Inuit. The cognitive reality of such peoples must be viewed from that perspective. The late 'Neanderthals' (and I use this term without endorsing it) need to be assumed to have had a preoccupation with 'dangerous animals' (cave bears and lions, pachyderms), expressed in several cultural forms, and their therianthropes may result from this (it should be noted, conversely, that there are now two Aurignacian lion-headed therianthropes from the Swabian Alb of south-western Germany: the possibly female, large specimen from Hohlenstein-Stadel (Schmid 1989) and the much smaller one from Hohle Fels (Conard et al. 2003).

A few minor points in the paper require clarification. It has not been demonstrated that the Makapansgat cobble (which is of jasperite, not ironstone; Bednarik 1998) was carried 'over 20 miles from its place of origin'. Certainly it was carried into the dolomite cave for some kilometres and is clearly a manuport, but Dart's original claim of 32 km is not valid. If the cobble were of ironstone, as has been said incorrectly, it could come from 4.8 km away, but it eroded in fact from an ancient conglomerate and could be from any fluvial deposit.

Concerning the Tan-Tan proto-figurine, I am not sure what Hodgson and Helvenston mean when they say that my 'interpretation' has not yet been confirmed by other investigators. After all, my paper (2003a) avoids simplistic interpretation quite explicitly. If they mean that the object's significance has not been appreciated by archaeologists who have examined it, they are certainly wrong. It was discovered by Professor Lutz Fiedler, a specialist of the Acheulian tradition, and it was examined by Martin Kuckenburg, among others. These scholars agree with me concerning its significance.

I have several problems with the statement that 'the only Neanderthal representational artefact (yet to be confirmed by other researchers) takes the form of two stones intentionally fitted together to look like a human or feline face dating to about 32 000 BP'. First, my unimportant objection: I do not think Marquet and Lorblanchet (2003) have presented a credible case that this is an iconic 'artefact'. There is no indication of any modification, nor is intentionality apparent or even demonstrable. Literally thousands of such supposedly early stone 'sculptures' of purported Lower and Middle Palaeolithic ages have been reported from France to northern Germany, a massive amount of literature exists about them, and archaeologists consistently reject this material. Many of these stones bear more obvious resemblances to objects (usually animals and human faces) than does the stone from Le Roche-Cotard, hence I fail to see its relevance.

My more important objections, however, are more complex. The cited comment suggests that the authors believe no other iconic material is the work of 'Neanderthals'. This is firstly false, and secondly a premature assumption. It is almost certainly false because one of the three Micoquian engravings from Oldisleben appears to be iconic (Bednarik 2006a), and it is premature because the authors cannot know which of the indisputably iconic artefacts of the Early Upper Palaeolithic (EUP) were made or not made by Neanderthals. Unless they have proof, one way or the other, they need to withdraw this point.

This is not a pedantic observation on my part, it is a very deliberate measure to demonstrate that the archaeological paradigm within which we conduct debates of this nature is itself largely false. For instance, we have no evidence whatsoever that Aurignacian art was not made by 'Neanderthals'. All the unambiguous human fossil evidence we do have from EUP sites is that these occupations were by 'Neanderthals' (currently four instances). We have no unambiguous 'Graciles' from any clear Aurignacian context, and there is no evidence of gracile trends before the Peºtera cu Oase mandible. All the known European hominins between 35 ka and 25 ka are either 'Neanderthals', or what should be called 'post-Neanderthals' or 'Robusts' — people of distinctive sexual dimorphism, whose males were almost as robust as 'Neanderthals', while the females were far more gracile, preceding in physical evolution the males by many millennia. In other words, there is rapid gracilisation, which is a global trend at about that time, emphasising continuity and uniform evolutionary processes from Europe to Australia. Moreover, precisely the same applies to all tool traditions ever identified in the EUP of Europe, such as the Aurignacian, Châtelperronian, Uluzzian, Uluzzo-Aurignacian, Proto-Aurignacian, Olschewian, Bachokirian, Bohunician, Spitsyn culture, Szeletian, Jankovician, Streletsian, Altmühlian, Lincombian or Jerzmanovician. All of them evolved locally, and to the best of our current knowledge they were all the work of robust people, including those usually pigeonholed as 'Neanderthals'. Fully gracile humans do not occur in Europe until the Late Upper Palaeolithic, and even they are still considerably more robust than those of the early Holocene, which in turn are more robust than those of the late Holocene. In short, there is no apparent intrusion of either a new tool industry from elsewhere, or of a sudden change in human morphology. The change from Robusts to Graciles is gradual and simply mirrors a universal development in all human populations of the second half of the Late Pleistocene. The 'replacement hypothesis' is a farce, based on the fake datings by R. Protsch and others, and on a long series of mistakes (e.g. concerning the four Stetten specimens, Hahnöfersand, Velika Peæina, or the Crô-Magnon and Mladeè samples; see Bednarik 2006b and work in press).

What concerns me is not just how the African Eve advocates overlooked all of this, but the fact that their fervour has discouraged the consideration of more important issues. For instance, there is the question: why would human evolution tolerate the unprecedented developments of the last fifty millennia? That period has witnessed humans evolving into inferior forms. Their brains shrank (despite increased demands made on them), as did their muscles, while their bone architecture became significantly more fragile. None of this makes any evolutionary sense. There is a rational explanation but it attracts no interest whatsoever. This is a result of the African Eve fad. Now that we face the very real possibility that Aurignacian palaeoart is the work of Neanderthaloids (Bednarik in prep.), it is high time to start considering much more likely scenarios than the replacement dogma. In particular, the model offered by Fedele and colleagues not only provides a realistic explanation of demography, it has the complete support of the archaeological evidence, which the replacement dogma has always lacked (Fedele et al. 2002, 2003). I have been warning for many years that we have no evidence of what kind of people the 'Aurignacians' were (e.g. Bednarik 1995), and now that so many fake datings of European hominin finds have been exposed we have discovered that I merely understated the problem.

Archaeology is based on beliefs, science operates by falsification. The proposition that is currently on the table for falsification is that the EUP traditions *are not the work of 'fully modern' people*. Until it is falsified by presenting fully modern human remains (not intermediate or 'post-Neanderthal' Robusts) from a clear EUP context, the replacement model remains devoid of any archaeological or palaeoanthropological evidence. It is based purely on unresolved and dubious genetic claims (see Barinaga 1992; Templeton 1996; Brookfield 1997; Gyllensten et al. 1991; Kidd et al. 1996; Gutierrez et al. 2002; Strauss 1999 for some clarifications), i.e. it is without credible evidence. It never had any archaeological evidence to begin with, and all the palaeoanthropological evidence cited in its support is now exposed as either fake or mistake.

None of this has much effect on the authors' hypothesis, but it shows the inadequacies of the archaeological paradigm we start from: it should be assumed to be largely false. One of the many errors made by the 'short range' lobby has been its claim that to demonstrate symboling the evidence must be very numerous, because only often repeated use of symbols can demonstrate their use (Chase and Dibble 1987; Davidson and Noble 1998 and subsequent debates). This has been that lobby's standard response whenever I confronted it with pre-Aurignacian palaeoart evidence (e.g. Bednarik 1992) — as if a pre-Aurignacian status even mattered if the Aurignacian is by Robusts, as it apparently is. The work of Merlin Donald, mentioned by Hodgson and Helvenston, demonstrates the falsity of the cited belief: it is impossible for symbol use to exist in isolation, or as a 'running ahead of time' (Vishnyatsky 1994). One of the several reasons for this is that symbols are a form of memory storage external to the brain. Not only do they indicate cognitive 'modernity', a single instance suffices to demonstrate such 'modernity'. In that sense, Donald's work is invaluable, even if the lack of relevant data available to him has limited the utility of his sequence, and particularly its timing. If Donald had had the benefit of a catalogue of relevant material (Bednarik 2003b), his chronology would have been somewhat different. This may detract from the details of his model, but it does not affect the validity of his central thesis of external storage. Hodgson and Helvenston have made good use of this idea, and they have made equally good use of neurophysiology. The result is a superb paper pointing the discipline in what I have long regarded as the right direction.

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REPLY

Hunting disguises, ritual and animals in Palaeolithic art: a response to critics

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First we would like to thank all of the respondents for their thoughtful and insightful commentaries on our current paper, which has been adapted from a much longer work that will subsequently be published as a book. Both Bradshaw and Chippindale raise the issue of gender, apparently presuming that males did the hunting, while females did the gathering and, because of this, they interpret our focus on hunting as short-changing the contributions that presumably female gatherers made to hominin survival. Because we are dealing with the possible connection between hunting and representation of animals, our paper is limited to those activities but we are fully appreciative of the enormous contributions of gathering, likely by both sexes, to the hominin diet. We make no presumption as to which activities were performed by males or females in our paper. Having said this, Deacon (1997) has proposed that the procurement of meat from *Homo habilis* onwards would have led to crucial changes in the social fabric of foraging and scavenging communities. This involved a change in psycho-sexual bonding contingencies to do with the reciprocal negotiation between males and females, concerning the finding and sharing of meat, in the context of increasing demands coming from offspring relating to a prolonged childhood. According to this scenario, males would have been involved in the hunting of large game whereas females would tend to have been more concerned with the procurement of smaller animals as well as foraging. In the process of this 'negotiation' a nascent symbolic competence would have been essential, most notably in relation to language. In response to Chippindale, this is not to say that males rather than females will have been responsible for making images, as the above psycho-sexual dynamic suggests that both parties will have been involved.

In chimpanzee societies males do most of the hunting, i.e. at Gombe about 90 % of kills are made by adolescent and adult males, but dominant females have also been observed to hunt (Stanford 1995). Similar observations have been made at Ngogo (Mitani and Watts 1999). In most hunter-gathering societies world-wide, males also are dominant in the actual hunt for large game, while females are active in processing the carcasses, preparing the food, the hide etc., and may in fact have invented many of the tools which begin to show up in the archaeological record about 2.5 million years ago. In hunter-gathering societies such as the Kalahari Bushmen, males gather when they are not hunting, and females opportunistically hunt many smaller animals, so these activities are not as rigidly gendered as some would have us believe. However, our focus has been upon the relationship between complex hunting disguises, rituals, and representation in the European Upper Palaeolithic rather than these wider issues.

Just because we focus upon the emotional states that may be associated with the stalking and killing of large animals, along with the importance of ritual re-creation of the hunt and later re-presentation of the hunt in cave paintings, does not mean that we think only large prey are exploited. However, the meat of certain animals is special, far beyond its percentage of the total diet, in most hunter-gathering communities (Kusimba 2005) and is treated with more ritualistic importance than other foods (Vinnicombe 1972: 192–204; 1975; 1976). We are certainly aware that many kills are of smaller animals, including lizards, snakes, turtles, rabbits and other small mammals, and insects.

We confess to committing the crime of 'Eurocentrism' but one must begin someplace and we deliberately chose to focus on the art of the European Upper Palaeolithic because we were both more familiar with it than other areas. There may be other sites in Africa and Australia that contain just as many examples of this 'art' but, due to more intense archaeological scrutiny, Europe tends to figure more prominently in these discussions. We also chose Europe because the remains of *Homo erectus* and archaic *Homo sapiens* (*Homo heidelbergensis)* have been discovered there, dating back to about 800 000 years ago (Manzi 2004) which is within the initial time frame that we are mostly concerned with as our paper is based upon Donald's theoretical model, specifically mimetic and mythic culture. Moreover, due to the extreme climate shifts in Europe over the past 700 000 years of glacial and interglacial periods, hunting appears to have become increasingly important as plant foods became scarcer during the colder glacial periods. In Britain, both *Homo erectus* and *Homo heidelbergensis* are believed to have hunted large prey such as elephants, rhinoceroses and hippopotamuses. These animals were driven over cliffs and into bogs to facilitate the kill. This has been substantiated at the 500 000-year-old site of Boxgrove (England) where cut-marks made by tools have been found on de-fleshed bones of large animals that are situated *beneath* the teeth marks of carnivores (McKie 2000). The butchered animals included four 675 kg rhinoceroses. [10] Only hunters in full command of their territory with sophisticated and complex skills could have achieved this, which suggests *Homo heidelbergensis* did not rely on scavenging but was actively hunting and finding prey ahead of carnivores. It seems that a reversal of roles had occurred where now it was the carnivores who scavenged the kills made by *Homo* rather than the other way around. As Manzi points out, the African fossil record between 1 million–600 000 is very poor, in contrast to European data around the Matuyama-Brunhes boundary. A similar situation applies to remains in India (James and Petraglia 2005).

Animals are one of the major subjects for the Palaeolithic artists in Europe, plants are not depicted, at least not in any recognisable form. The fact that plant heads (yams?) with human bodies are depicted in Australia is most interesting and we thank Chippindale for pointing this out. We addressed questions regarding the depiction of plants in rock art in our original paper, but the space limitations required by a journal meant we had to cut that discussion. Russia, Siberia, China and Southeast Asia may prove to be very fruitful areas for future investigation of our hypotheses. The point made by Bradshaw, in connection to the Gwion paintings of humans with little evidence of animals being depicted, was addressed by one of us in a previous paper (Hodgson 2003b), where it was indicated that there are some 100 000 sites relating to these depictions of which only a few have been researched and documented. In fact, a recent paper (Taçon et al. 2003) has found that there are a significant number of animals in this art, some dating back to perhaps 17 000 years, including dangerous species such as crocodiles.

We are certainly aware of the disdain that earlier versions of the model 'Man the hunter' (Ardrey 1961; Washburn and Lancaster 1968) have engendered in archaeology, for placing too much emphasis on male hunting, but surely it is just as misguided to deny the importance of meat to hunting and gathering societies when the documentation for it is worldwide. We are not claiming that hunting is the only activity that is important in human evolution, but we are alleging that it is highly significant. Indeed, the find of 400 000-year-old wooden spears in Germany, believed by their discoverer to have been used to kill horses, whose bones were found in the same site, raises the question as to whether Ardrey was that far off the mark (Thieme 1997). It has become fashionable to claim that early *Homo* species mainly scavenged their kills, or that gathering is much more important than hunting because it provides a larger percentage of the diet. Entire books have been written about 'Man the hunted', which attempt to refute the idea the hunting of big game was of major significance (Hart and Sussman 2005) and focus instead upon the large number of *Australopithecines* who made up the diet of huge predators. Indeed, these authors would seriously dispute Bradshaw's contention that hominins faced greater danger from conspecifics than they did from great predators like the sabre-tooth cat. Anyone who would like to gain a more concrete idea of the predators which earlier *Homo* species had to contend with would do well to read this book. The descriptions of huge wolves, bears and cats are truly terrifying.

We suggest that over the course of human evolution, hunting and meat eating have assumed great importance in traditional hunter-gatherer societies as is revealed by rituals, myths and artwork. Indeed, among the Kalahari Ju/'hoan meat is a great treat and valued over all other foods, as evidenced by the ethnographic data presented in the book *Women like meat* by Biesele (1993). That certain animals, who are hunted for their meat and fat, can become associated with complex ritual activities and ideas is exemplified by the fact that the /Xam Bushmen of the northern Cape believed that their creator was unhappy with them if they

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[10] Editorial note: the remains of large mammals dominate at numerous Lower Palaeolithic butchering sites across Europe. A better example is Bilzingsleben, where the rhinoceros accounts for 26.6 % of mammalian individuals.

killed an eland, and it may be that their numerous paintings of eland were some type of purification ceremony to regain the good graces of their creator. In this respect, it is interesting to note that the fat and blood of a freshly killed eland was used in the paintings of eland on rock surfaces. Vinnicombe speculated that painting eland was in some way concerned with the re-creation of eland, and that in this physical act of re-creation the conflict of restoring to nature that which had been destroyed in the hunt was ritually resolved (1972: 192–204). Although we cannot assume that hunter-gatherer hominins had such rituals, it seems reasonable to propose that some elements like this may have begun to form an important part of the cultural repertoire, probably later in the mythic cultural period.

Although it is speculative, we believe that special valuation of meat reaches far back into hominin history. For example, some observers have noted that there are specific behavioural patterns associated with the distribution of meat in chimpanzee societies (Harrod 2004), and we would go so far as to label these behaviours *proto-ritualistic*. Furthermore, if there are female chimps in heat and a number of males present, hunting parties are more likely to be formed and the meat is distributed not only to the males of the party, but to the females in estrus. Moreover, a begging female often receives no share of the meat until after the male has copulated with her. These observations suggest that males appear to gain access to receptive females by means of meat and in turn the females gain access to dominant males for mating (Stanford 1995). Although it has become popular to assume that large animals were scavenged by early hominins, chimpanzees primarily ignore dead animals, and it seems likely that the earliest hominins did also. It has been suggested that when the earliest tools still extant in the material record were produced, hominins began to eat scavenged kills because they could process them, but this seems unlikely because their competitors for this meat would have been large predators against which they may not have been able to defend themselves without paying too high a price in dead or wounded kin or associates (Hart and Sussman 2005). After all, most predators have a much more highly developed olfactory sense than hominins and could have detected and tracked the odour of a dead animal from a significant distance.

Finally, although hunting small prey and gathering fruits, vegetables, tubers, grasses etc. no doubt provided the staple of one type of hominin diet, there is empirical evidence that hunting very large animals is an adaptive strategy as was shown by Bourlière (1963: 43–55), who demonstrated that 75 % of the meat available to human hunters in the eastern Congo was provided by the elephant, buffalo and hippopotamus. Also, *Homo* species [11] have been successfully hunting very large beasts for at least 600 000 years BP (Washburn and Lancaster 1968: 293–302), and as mentioned earlier, there is evidence that suggests *Homo erectus* was killing big game in Britain, from about 700 000 BP. Also in modern-day Germany, either *Homo erectus* or archaic *Homo sapiens* were hunting horses and probably other large game from 400 000 years BP.

Our focus upon chimpanzee behavioural characteristics is a methodological choice based upon the assumption that our earliest hominin ancestors would have most of the same characteristics evidenced by chimpanzees. Just such an assumption is shared by the various biologically-oriented specialities involved in studying primate evolution. Of course, chimpanzees have continued to evolve just as *Homo sapiens* have, but the basic behavioural repertoires between chimpanzees 6–7 million years ago and the earliest hominins were probably similar, given the enormous similarities between the chimp and human brain and genome. Indeed, new genetic research reveals that humans and chimps are even closer genetically than has been previously thought and that chimps are closer to humans than to any of the great apes. Moreover, both humans and chimps have a slow 'molecular clock' or rate of evolutionary change and large brains probably only evolved about one million years ago, a conclusion based solely upon genetic evidence (Elango et al. 2006: 1370–5), although subsequent studies are needed to confirm these findings. Of course, palaeontologists document a slightly different sequence, and we have cited Holloway in this regard in our paper. Still, the greater part of hominin encephalisation dates from the past 700 000 years, so the genetic data are not that inconsistent with the palaeontological data we have presented.

As our closest living relatives, chimpanzees evidence behaviours that may very well have a major significance in the evolution of our own species. In this regard we are convinced that a knowledge of comparative vertebrate neuroanatomy, primatology, biology and fossil endocasts is crucial to the investigator who would study and speculate upon the evolution of *Homo sapiens'* brain and behaviour as it may be manifested in the material record. We completely disagree with Chippindale's assertion that an acceptable methodology for studying ancient behaviour is to assume that humans circa 30 000 years ago had a thoroughly modern brain — they may have, but they did not have a modern mind and to project such an assumption that far back in time greatly distorts the understanding of what sort of mind they did have, as has been addressed previously (Helvenston and Bahn 2004). In fact, this opinion, certainly not confined to Chippindale, represents a troubling trend among those archaeologists who claim to use neuropsychology without possessing more knowledge of that field, as well as evolutionary neurobiological processes and other related fields like neuroanatomy.

This debate needs to be seen against the fact that some recent hunter-gatherer groups (e.g the Songe of New Guinea) do not have any pictorial culture involving the representation of objects yet are quickly able to assimilate these if required. This suggests that the ability to produce representational depictions, although latent in modern humans, is not always expressed. The guiding principle seems

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[11] At times we will use the term *Homo* species rather than designating *Homo erectus*, *archaic humans*, *Homo neanderthaensis*, *Homo heidelbergensis* etc. rather than list all these possibilities because there is currently so much disagreement over the taxonomic classifications of these assorted *Homo* species in the literature.

to be that 'absence of proof is not proof of absence', implying that the archaeological record provides only a minimum index of cognitive ability. Deacon (1997) gives the example of African Pygmies whereby the simplicity of their tools compared to technological societies might suggest to some future archaeologist that an enormous mental gulf separated this group from contemporary people. Of course, such a conclusion would be totally unwarranted, as we know that African Pygmies are intellectually equal to other modern humans. This suggests that representation may or may not have been employed before the Upper Palaeolithic, depending on circumstances and inclinations of the particular groups concerned. The Franco-Cantabrian depictions of animals could have been either unique to this period or invented much earlier and not taken up or else existed in a perishable form. And, as we have stressed, representation was most likely expressed in alternative ways such as disguises and in the context of ceremonial activities. In fact, because most hunter-gatherer communities tend to be highly mobile, the 'art' produced is usually in the form of temporary materials and therefore remains invisible to the archaeologist. In this regard, the increasing number of finds of pigments, such as ochre, from 300 000 years onwards in various parts of the world (Bednarik 1992, 2003b; Hovers et al. 2003; Barham 2002) point to the fact that hominins had begun to utilise colour for, as yet, unspecified reasons. Power and Aiello (1997) speculate that one reason concerned non-menstruating females faking menstruation in order to attract and gain the support of males. This coincides with our hypothesis that deception was within the capacity of hominins during this period and suggests that pigment was being used to change physical appearance for specific reasons.

As far as the significance of the Makapansgat pebble and the Berekhat Ram and Tan-Tan figures are concerned, we agree with Henshilwood and Marean (2003) that those who favour a major biologically determined evolutionary leap in human cognition about 30 000 years ago tend to deny the existence or relevance of Middle and Lower Palaeolithic evidence to the contrary. Chippindale, we note, chooses to ignore d'Errico and Nowell's (2000) findings concerning the Berekhat Ram object. In fact, one of us (Helvenston) is amazed that archaeologists would assume personal ornamentation is evidence of modern human symbolic activity. For example, chimpanzees clearly have a sense of self as exemplified by the fact that they recognise themselves in a mirror, but the use of ornamental beads etc. is viewed as a sign of *modern human symbolic behaviour* because it evidences a *recognition of the self.*

From a neuropsychological perspective any sort of personal ornamentation most likely derives from some rudimentary sense of aesthetics and/or a desire to enhance one's appearance and status, which can be documented from contemporary chimpanzee behaviour, thus illustrating the time depth of these forms of human behaviour. Two observational examples come to mind here. The first is that Adriaan Kortlandt reported that 'once I saw a chimpanzee gaze at a particularly beautiful sunset for a full 15 minutes, watching changing colours [and then] retire to the forest without picking up a paw paw for supper' (1962: 128–38). Indeed there is a deep affiliation between aesthetic sensibilities and religious phenomena, a relationship whose biological depth has been thoroughly explored by Dissanayake (1995). The second example documents that in 1996 a group of chimpanzees at Mahale killed and ate a red colobus monkey in the afternoon. The next morning, observers noted that one of the juvenile females was playing with, and grooming a strip of colobus skin which was 'stolen' from her by a juvenile male. The next morning a young adult female was observed wearing the skin draped around her neck. When she discarded it later that day the investigators found that the skin was tied in a single overhand knot, creating a 'necklace' (McGrew and Marchant 2006). There have not been other similar examples reported in the literature that we know of, but perhaps as more and more scientists study chimpanzees in the wild, this sort of behaviour will be more frequently observed. While this example could be some sort of 'fluke' and somehow the skin got accidentally twisted into a knot, on the other hand, it might represent an attempt on the part of the young adult female to enhance her appearance and/or status by adorning herself with the remains of a highly valued kill. Only further research can distinguish between these possibilities.

Although we do not elaborate upon the discovery of the mirror neuron systems in specific terms like 'theory of mind,' all of our discussion about the ability of primates to categorise between animate and inanimate objects, recognise animal behavioural characteristics, and distinguish between predator and prey, presupposes such abilities. Thus, we agree with Bradshaw's comments on the importance of the mirror neuron systems and believe they likely have not only enormous significance for social interactions, but also they may facilitate increasingly effective hominin hunting behaviour. Bradshaw speculates the mirror neuron systems will ultimately be found to relate to hominin aesthetic perceptions and artistic production. If he were correct, that would be another confirmation of the linked hypotheses we present in our paper. There is no question that hunters are intimately familiar with the behaviour and spoor of their prey and their strategies and myths indicate that they have theories about each animal's mind. Simultaneous with the development of deceptive techniques, the fundamental primate brain, already able to sort by categories, was evolving into a sophisticated system of neural structures that facilitated the perception, memory, imitation and prediction of animal behaviour.

One example from the 19th century provides some insight into how an understanding of animal behaviour may ensure a successful hunt. The Drakensberg Bushmen, after having wounded an animal with a bow and arrow, and waiting for the poison used in hunting large game like the eland, gemsbok and buffalo to take effect, followed the spoor and interpreted all the details such as where the animal had rested, urinated or rubbed itself, with uncanny accuracy. They could tell from the signs when the quarry began to weaken and could judge when to close in for the kill before a scavenger seized the animal, as they knew when it would collapse (Silberbauer 1960: 49). The animal's death was then visually represented, as depictions of animals that appear to be incapacitated in some way, with splayed legs, heads hanging low, lying down etc., are common in that area (Vinnicombe 1976: 298).

We are not certain that Bradshaw intended his comments about parrots, hunting, and categorisation to be taken seriously, but indeed parrots can categorise and we never suggested that this ability was exclusive to primates, as Bradshaw maintains. Parrots hunt prey much smaller than themselves and most of their actions are instinctive, whereas humans hunt both small prey and animals who are many times larger than themselves and who possess formidable physical advantages which are only offset by the superior intellectual capabilities of hominins. Few would dispute the fact that intellectual superiority is the major reason why *Homo sapiens* as a species is such an awesome predator. The human has the advantage of more than instinctive stimulus-response behaviour, rather, relying upon the greater development of the ability to 'learn to learn' which is only made possible by enhanced encephalisation and multiplying interneuronal connections such as exemplify the latest hominin brain.

Bradshaw's statement that 'carnivory was not a major driver in human evolution' overlooks the evidence for what is often referred to as 'the expensive tissue hypothesis'. This model holds that one of the major factors associated with increased encephalisation in hominins was a higher quality diet that included increased exploitation of animal protein (Aiello and Wells 2002; Aiello 1997; Aiello and Wheeler 1995; Leonard and Robertson 1994; 1996). Aiello (1997) views increased meat consumption as a 'prime releaser' for brain evolution. Leonard and Robertson (1996) using some different measuring techniques, concluded that the evolution of the human hunting-and-gathering economy with increased consumption of meat may have both necessitated and allowed for a higher quality diet (i.e. animal protein).

We wish that Coolidge and Wynn had spent more time addressing our paper and less time writing their own. However, we find their discussion regarding what they refer to as *enhanced working memory* to be interesting and thought provoking, but think they may be relying too heavily upon the importance of this one significant skill and its associated neuroanatomical substrates to the exclusion of some other neurobiological systems that we view as more crucial to our argument, namely the limbic system and somatosensory cortices. Thus, we do not agree that our linked hypotheses could fit into the model first proposed by Baddeley and Hutch (1974). Rather, we view our larger, multi-system model as encompassing not only working memory but all augmentations to it that may have occurred with the increased development of area 10 after the human/chimpanzee split seven million years or so ago. Because of this, we cannot completely agree with them with respect to *working memory* (which neuropsychologists formerly referred to as 'recent memory'). While we agree that the evolution of area 10 appears to be critical to the ability to maintain enhanced focused attention, this area is already well-developed in the chimpanzee brain and cannot be viewed as unique in *Homo sapiens*. Moreover, Donald recognised this when he referred to ape cultures as episodic because that is what *working memory* regulates — episodes. Area 10 has become much larger in the human brain and may be involved in more functional abilities, including *augmented working memory*, than its precursor in the chimp brain but no special mutation is needed to account for its expansion in the hominin brain. In this respect, Todd and Marois (2004) found that the capacity limit of visual short-term memory (VSTM) in humans may be a function of the posterior parietal and superior occipital cortex, whereas the frontal/prefrontal cortex may serve to maintain task-specific goals or assist VSTM-related processes at high loads and/or long duration intervals (René and Ivaoff 2005). The obvious advantages of a being that possessed more working memory and 'executive' ability than his conspecifics would be sorted by natural selection and these traits are clearly heritable as they document. In this regard we wish to emphasise that working memory, while important, is but one of numerous other skills that were necessary in hunting, mimetic re-creation of the hunt in ritual, and re-presentation of the hunt on media such as cave walls. A slow gradual increase in the size and connections of area 10 seems more likely to us than an abrupt change in a suite of traits that might be viewed as 'modern behaviour'.

Of course, one of the great debates in archaeology concerns the criteria for 'modern behaviour', and the other is, did the neural capacity necessary for the expression of that behaviour evolve slowly over eons of time or was there a punctuated event in which modern human behaviour originated as a package, and if so, when was it — Upper Palaeolithic, Middle Palaeolithic etc. (Henshilwood 2003)? We favour the long, slow evolutionary model as expressed best by Chase and Dibble (1990: 58). These authors refuse to assume a link between the behavioural changes documented in the material record and the biological capacity for that behaviour, a stance that we follow also. Moreover, Chase and Dibble note that

> given that the model of mosaic evolution has been well documented in biological evolution, it would be foolish to assume the evolution in tandem of the set of biological and behavioral traits that anthropologists see as characteristic of modern humans. It seems more likely that different biological and behavioral traits, even though they may be linked today, had functionally and temporally separate origins (1990: 58).

Thus, we do not agree with Coolidge and Wynn that characteristics of the modern brain involve an abrupt mutation around 120 000 years ago. Our view, based upon neuroanatomical studies and fossil endocasts, as well as the increasing number of material remains, is that these characteristics are much more accurately understood as gradual enhancements of the hominin brain. Although we think that the neurobiological substrate for these abilities was probably completed about 300 000 years ago, as represented by the macrosopic appearance of the frontal lobes, area 10 may have still been evolving. Even as it did so, we agree with Donald that a gradual accretion of cultural adaptations was likely crucial to the expression of modern human behaviour.

Furthermore, we are highly sceptical of models that seem to imply the brain can be likened to a computer module, with 'executive centres' and 'slaves'. The analogy of the nervous system to a group of computer modules, a viewpoint popularised by Mithen (1996, 2004), is far too simplistic to be useful beyond a very elementary level, in understanding the neurobiological evolution of the primate brain. Comparative neuroanatomists can discern that the hallmark of the vertebrate brain is its unbelievable inner- (within nuclei) and interconnectivity among associated nuclei, systems and cortical areas. Even in the lowly rat brain, the interconnectivity of neural systems is incredible (Chase et al. 1969; Chase and Moore 1968). Multiply this by the documented interconnectivity of the *Homo sapiens* brain and it is impossible to believe in separate 'modules' based upon computer science and not on comparative primate neuroanatomy. Modularity in the human, or indeed the hominin brain, is not an apt metaphor, rather one should think of large, complex, interacting systems with amazingly flexible functional abilities, rather than closed off, specialised compartments. Bradshaw, perhaps because of a hasty reading, fails to realise that we are speaking of multiple dynamic, interacting systems throughout our paper and nowhere do we propose a unifactorial approach to understanding the relationship between hunting disguises, ritual and re-presentation. These are all complex activities requiring the co-operation of many nuclei and cortical areas in assorted larger systems within the brain.

Although some areas of the brain are comparatively more specialised for one function than another, the neuroplasticity of the hominin brain is its *sin qua non*, not its relative specialisations. Even in areas of the sensory cortices that have traditionally been thought of as more highly specialised, plasticity is the norm. For example, the brains of people who were congenitally blind, or lost their vision very early in life and could read Braille, were scanned with fMRI and it was found that their visual cortex was processing touch, that is their brains showed 'cross modal' neural plasticity. Healthy sighted individuals were blindfolded for a week and every day they studied Braille. After only a few days, their visual cortex was processing touch, i.e. Braille (Hamilton and Pascual-Leone 1998). Over the past decade many other examples of such 'cross modal' plasticity involving auditory, visual and tactile sensory areas have been reported; although, of course, there has to be a limit to this plasticity, especially in adults, in order for the brain to function as a coherent and efficient unit (Pinker 2002).

We have no doubt that the so-called 'executive abilities' and *augmented working memory* are heritable, as amply documented by Coolidge and Wynn. Indeed, these abilities as a package may account for what psychologists who specialise in the construction of IQ tests refer to as 'g' or general intelligence. Certainly in any egalitarian band of hominins a natural leader might have a relative abundance of *augmented working memory*, as well as all the other traits characteristic of an enlarging area 10 and surrounding frontal lobe structures. We certainly agree that dreams could have contributed to animal representations in Palaeolithic art and perhaps early hunters re-created the hunt once again during sleep. Dreams contribute much of the imagery reported by San-Bushmen according to Keeney (2003), and Eliade reported that Siberian shamans often communed with their spirit animals in dreams (1964), which he classified as one form of ecstasy.

We do not believe that Upper Palaeolithic cave art is necessarily a sign of modern human behaviour — and a modern human brain. Helvenston and Bahn (2004) cited the fact that many others have considered it to be so, without discussing the issue any further. This is one of the great debates in archaeology as we mentioned above. The fact that more and more art objects are being discovered that date to the Middle Palaeolithic as reported by Henshilwood and colleagues, Bednarik and others as discussed in our paper, raises a serious challenge to the assumption that the Upper Palaeolithic cave art was produced by people with a newly acquired modern brain. We tend to agree with those who suggest the modern brain dates further into the past than has been widely believed because more and more the archaeological record points in that direction, as does comparative primate neuroanatomy.

We find Coolidge and Wynn's discussion of the contributions of *augmented working memory* to language development interesting and plausible, but this is not an area upon which we have focused our research, so we will not comment more upon it here. We do not believe that mythic culture presupposes a modern brain — we believe that oral language became increasingly important during this cultural phase and that it eventually included complex language and many oral myths such as came to characterise the Greek warriors of Homer, but again, we favour a gradual accumulation of culture upon a neural substrate that may not have changed all that much over the past few hundred thousand years.

Finally, we question Wynn and Coolidge's contention that the people who produced the Hohlenstein-Stadel figure had modern minds. Rather, a modern mind depends upon the extensive cultural evolution of the past 5000 years when writing first becomes obvious in the material record. A literate culture produces major changes in the human mind as compared to an oral culture, because of written documents and the ability to reflect upon what has been previously written, as well as to store it as part of a cultural heritage (Ong 1982). The therianthropic lion figure produced by the Hohlenstein-Stadel people need not presuppose that these individuals hunted lions, although they probably did. If the people who produced the Hohlenstein-Stadel figures were utilising hunting disguises, they could easily generalise from hunting deer by means of deer skin and antler disguises to theoretically hunting lions from lion-skin disguises, or, alternatively, they may have been using such disguises to frighten and herd animals in the direction of cliffs or traps etc. The natural categorical divisions that divide humans from animals will have become blurred due to the fact a disguise seemed to turn a person into an animal and vice versa. This will have been reinforced by the fact that the consumption of meat leads to the intake of animal parts with obvious implications with regard to animism. It is this apparent fluidity, wherein different aspects of animals and humans seemed to be interchangeable, that is the most likely explanation for the occurrence of therianthropes. In this sense, we noted in our paper that therianthropic figures may depict mythological creatures worshipped as divinities; an exaptation property we believe is adapted from pure hunting disguises.

We recommend Hart and Sussman's book as it discusses evidence of contemporary predation by large cats, wolves etc. and is a fascinating reminder of the importance of hominins in the diet of these animals. It also discusses various disguises that people use to 'fool' predators even in modern India and Pakistan. For example in the Sunderban Preserve, a mangrove swamp and forest preserve on the India-Pakistan border, local villagers looking for honey or timber, along with fishermen, sometimes enter into the territory of the Royal Bengal Tiger (*Panthera tigris*). It has been observed that these huge predators tend to attack humans from the rear, and so locals are advised by the government to wear a rubber mask in the form of a human face to cover the back of their head. This has been demonstrated to be a relatively effective strategy in preventing attack (India Profile 2004).

In pre-Historic eras, huge predatory cats were widespread across Europe and Asia during the relevant time periods and were no doubt acutely noticed by the *Homo* species of the time. It is simply not credible that these glorious animals were not hunted, because their very existence in an area posed a serious threat. Any of the species of sabre-tooth cats discussed by Hart and Sussman, preying upon early *Homo* species, would have been sought out and killed because they could literally decimate a small band of individuals had they been left to roam and stalk at will. Finally, we find these magnificent beasts graphically illustrated in the Upper Palaeolithic cave paintings, which must signify that they possessed some type of important attribute(s) to the creator of the painting, although we will probably never know precisely what it or they were. The point needs to be re-emphasised that the case we put forward, however, is *not* just about large carnivores and hunting, but rather the close relationship that would have existed between *Homo* and the fauna, whether predatory, useful or benign, populating the same evolutionary niche.

Critical comments are always valuable in refining one's viewpoint, but a response appreciative of the fact that our main contention is the long evolution of cognition from more basic primate attributes such as a highly specialised visual system is most welcome and Fedele's discourse clearly shows that he resonates with our viewpoint. Indeed, in contrast to Bradshaw's view that nothing more is required of the hominin brain to successfully hunt than the behaviours mediated by the mammalian or parrot brain, we view the visual system as highly evolved in hominins. This view is shared by specialists in the evolution of the primate visual system as evidenced in the publication of two excellent compendia in the past few years (Kremer 2005; Ross and Kay 2004). Indeed the advanced visual system of primates, especially colour vision, is one of their distinctive attributes and it is specialised for many forms of food retrieval, including the hunt, and in detecting predators partially hidden from view, a subject that Hodgson has explored in great detail. Crucially, because of its dual nature, the representation of animals in pictures etc. activates the same parts of the visual brain as when a real animal is seen, which has important implications for understanding palaeoart.

One area that we did not address in any depth is of course the detailed discussion of eco-systems and climates and the incredible effect these factors can have on human survival and the expression of what may have been previously latent abilities. We agree completely with Fedele that as we continue to refine our hypothetical model we need to become increasingly aware of micro and macro-climactic events such as the arctic ice discharge and the Campanian Ignimbrite eruption. Thankfully, we have his large corpus to point the way. We also agree completely that hominin interactions with other animals, both as predators and prey, have played an important role in the long evolution of *Homo sapiens.* Unfortunately, we had to cut much of our evidence documenting just how important hominin and other animal interactions were but our original title may say it all; it was *Wild Thing, I Think I Love You: the veneration of animals in palaeoart and the long evolution of religious experience and re-presentation from hunting strategies.*

In our response we have suggested that cognitive archaeologists need to become more familiar with biology, neuropsychology, neuroanatomy and primatology if they are going to discuss the cognitive evolution of the brain with any perspicacity and depth. Meyer has succinctly rephrased and translated our argument into a call for syncretic research, and of course this captures in a nutshell what we are recommending. Undoubtedly we will continue to search for documentary evidence related to our linked hypotheses, whether the evidence confirms or disputes our speculations. In this respect we did not address the huge role that the evolution of language skills play in the development of advanced cognition, beginning most probably with Donald's mythic culture stage — but we plan to explore evolution of language in the future and we welcome Meyer's comments and his referral to those who have already been exploring this rich area before us.

We welcome the comments by Montelle, who shares our enthusiasm for the overall theoretical model Donald presented in terms of recovering 'behavioural bits', a most ingenious description for the process of examining the material record in order to infer assorted past behaviours. Although there are specific aspects of Donald's model that are deficient, as Montelle points out, it has had remarkable predictive value as evidenced by the fact that 'behavioural bits' confirming his theory are recovered from an ever more distant past, as Bednarik and others have provided extensive documentation for. We thank Montelle for reminding us that the social consequences of using deceptive behaviour in close-knit groups has obvious survival value and can shed light onto issues of 'cohabitations, co-operation, dissemination of information, and effective maintenance of the status quo', topics which we did not consider other than in a superficial manner. These are clearly areas that we, and others of like mind, can fruitfully pursue in the future. For example, as Montelle suggests, ethology, i.e. the study of animal behaviour, clearly documents how such deceptive strategies can serve to 'minimise potential tensions and conflicts within a nucleus of connected individuals', all crucial mechanisms for hominin survival, where small groups were probably confined to limited cave spaces, trying to prosper in ice-coated Europe.

We are intrigued by Montelle's suggestion that deceptive strategies can serve the purpose of maintaining the necessary hierarchy in the ever increasing size of social groups and had not thought of this aspect of re-presentation of hunting escapades as a means of 'media-mediated' social control, but no doubt, this may well be one clear function of re-presentation, whether intended at that time or not. Certainly the massive statues in Pharonic Egypt were deliberately designed as a form of social control and art historians could supply many other similar examples from more recent periods. Finally, we completely agree with Montelle's cogent discussion of the evolutionary significance of mimetic behaviour. While in the early stages of mimetic culture, there may have been little use of language, the importance of mimicking successful hunts, preserved in some sort of external storage media, was undoubtedly crucial to, and overlapped with, the continued evolution of hominin language capabilities and cultural evolution. No matter how crucial mimesis is in learning (and it is still more effective than language in transmitting many skills that rely on implicit memory), language skills and written records provide a means of cultural transmission with a historically-documented and escalating pay-off, not the least of which was providing the cultural impetus for the development of the 'modern mind'.

The importance of mimesis to hunting societies is clearly illustrated by the activities of hunter-gatherers in the 1930s who imitated animal and human behaviour in dances and ritual. Pygmies of the African rain forest performed a chimpanzee dance in which men and boys proceeded through the entire camp with slow, serpentine movements, their facial expressions all the while consisting of weird grimaces. The eldest of the group, who represented the hunter lurking behind a bush or a tree, took aim at the revellers with a bow and arrow, and when the arrow was launched the participants all rolled around on the ground, grinning and roaring to the accompaniment of thundering drums (Schebesta 1933: 200). It appears that the group was portraying chimpanzees who have terrifying facial grimaces referred to as 'grins' that express fear and/or excitement, and which are accompanied with vocalisations such as 'Wraa' and roar pant-hoot, the second of which is accompanied by aggressive displays (Goodall 1986: 119–36). Dances, mimes and singing games of many kinds were still prominent in the life of the Kalahari Bushmen of the 1970s and many dances were 'based upon episodes in the lives of animals, when the hunter's inborn talent for mimicry and imitation is vividly displayed' (Vinnicombe 1976: 307). Moreover, there are numerous elaborate artistic depictions of similar dance scenes at many rock art sites in Lesotho.

In responding to Bednarik's comments we want to first acknowledge our indebtedness to him for agreeing to publish a shortened version of our original paper, and pointing out what he views as the strengths of our discourse. As many of his papers indicate, Bednarik has been instrumental in pushing the evidence for hominin brain capacities further back into the evolutionary past and we fully acknowledge the importance of his work.

We appreciate his discussion of the enormous importance that the attachments of humans to hunted or herded animals have in many areas of the modern world as it underscored both the veneration and affection that we believe highlights hominin evolution. The extremely close connection between humans and other animals can be seen in specific examples from contemporary hunter-gatherer cultures. For example, in a significant creation myth of the Maluti Bushmen of south Africa it was believed that men and animals had once been brothers during primal time; that is, they were one and the same creature, not animals, not men, and these creatures were depicted in San art as therianthropic figures, long before the world of the civilised modern San was created by their creator God, Cagn (Orpen 1874: 1–13). One myth tells how Cagn told his son to collect sticks for bows. The baboons killed this youth and hung his body in a tree because they thought the bows would be used against them. Cagn tracked the baboons and found them singing and dancing of their triumph. He was enraged and collected a bag of wooden pegs and drove them into the back of each dancer, thus giving baboons their characteristic posture. Then he banished them to the mountains to live on roots, beetles and scorpions. The Bushmen enjoyed enacting a baboon dance in which 'the performers imitated all the actions and droll grimaces of rival baboons, springing, gambolling and running on all fours' (Stow 1905: 117). There is a rock art painting of an animated dance showing human figures carrying weapons, leaping and somersaulting, with one participant wearing what appears to be a baboon tail, located in the Drakensberg Mountains in South Africa. Another painting in the same locale shows armed human figures and therianthropic figures dancing around a large, centrally positioned baboon (Vinnicombe 1976: 309–9a). All of these rituals, dances, stories and artistic depictions present many visual details based upon the keen observation of baboon behaviour and evidence an appreciation, perhaps a bit grudgingly at times, for the animal itself.

We were unaware of the fact that the Makapansgat cobble may not have been carried 20 miles, but we still maintain its significance to our arguments. As far as the Tan-Tan proto-figurine is concerned we believe it is a significant find and welcome the added information about its provenance and authentication that Bednarik provides. We tend to disagree with him on the point of whether or not the 'Neanderthal representational artefact' (Marquet and Lorblanchet 2003) does symbolise a human or feline face although we appreciate the points he makes on the subject.

Bednarik appears to read too much into our comment of 'the only Neanderthal artefact'. We cited it as being one with which we were familiar but welcome references to other Neanderthal artefacts and will most certainly include them in upcoming papers. We agree that there is often little credible evidence which can distinguish whether or not Neanderthals were responsible for some or most Aurignacian art or tools. We also agree that for too long the possible achievements of Neanderthals have been underestimated due to their characterisation as unfortunate stereotypes. While we believe they had a brain different in some significant ways from *Homo sapiens*, because of less well-developed frontal lobes, but more highly developed parietal and occipital lobes, as well as large temporal lobes, these later characteristics may in fact have made them superior in producing tools and art objects that required a high degree of visuospatial ability and constructive skills, or perhaps in hunting which may have relied upon visual memory advantages that they as a species possessed in Europe during the more extreme glacial periods. Indeed, their remarkable survival for over 200 000 years in the most extreme climatic conditions suggests that they must have had more cognitive adaptive advantages than have been determined at present. Perhaps being adapted to severe cold conditions had resulted in the development of social skills that reduced inner-group competition and facilitated co-operation along the lines that Montelle suggests. It could well be that the skills Neanderthals possessed were unique, highly specialised to severe environments (Fedele could no doubt elaborate on the importance of specific eco-systems), and perhaps somewhat less adaptable in milder climes. For example, if co-operative skills were relatively more valuable in extreme conditions, perhaps competitive skills were less well developed, which could have had repercussions when competing with another species that may have evolved more highly competitive behaviours in less demanding environments. Over perhaps a hundred thousand years of co-existence with early modern humans in some areas, these sorts of differences may have become significant. Of course, this is pure speculation at the moment and we have not done the necessary research to offer a really informed opinion at this time.

As far as the 'Out of Africa' model, or the 'replacement' hypothesis go, we think that the jury is still out, although one of us (Helvenston) tends to favour the multiple site evolution of modern *Homo sapiens* for many reasons, but as Bednarik says, this debate does not impact the linked hypotheses we present in this paper. The genetic studies, we think, suffer from many methodological problems and in some cases faulty assumptions. Only over the course of the next several years will these be corrected to such an extent that a consensus opinion based upon such studies will likely emerge with respect to either of these theories. After all, as Bednarik suggests, there is a century or more of archaeological and palaeontological data that seems at odds with some of the more popularised current genetic research. We appreciate Bednarik's vision of the likely deep-time evolution of human capabilities and, as our paper demonstrates, we certainly share it.

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RAR 23-752

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