The effects of the tree-to-ground sleep transition in the evolution of cognition in early *Homo*

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Abstract

Just as the study of great apes aids in the understanding of early hominid evolution, so too can contemporary dream research help in the understanding of ancient hominid dream life and cognitive evolution. It has been proffered that a major leap forward in the cognitive evolution of hominoids may first have occurred in the building of nests, and a second major step may have been the full transition to ground sleep. These two changes may have begun a modification of the quality and quantity of hominid sleep, which in turn may have enhanced waking survival skills through priming, promoted creativity and innovation, and aided the consolidation of procedural memories. Current dream research with children, adults, animals and the dreams of modern hunter-gatherers, appears to support the hypothesis that these changes in sleep may have been important to the cognitive evolution of hominids from *Homo habilis* to *Homo erectus*.

The evolution of sleep and dreaming has recently received serious treatment in journals of psychology and cognitive science, but these efforts do not typically incorporate paleoanthropological evidence (eg, Franklin & Zyphur 2005; Revonsuo 2000; Walker 2005). However, just as the study of great apes aids in the understanding of early hominid evolution, so too can contemporary dream research help palaeo-anthropologists understand evolutionary developments in hominid sleep and perhaps even aspects of cognition. It has been previously proffered (Fruth & Hohmann 1996) that one major leap forward in the evolution of the cognitive abilities of hominoids may first have occurred in the building of nests. We intend to build on this argument and will suggest that the hominid switch from arboreal to ground sleep prompted selection for and against specific aspects of sleep and that features of *Homo erectus* niche selected for others. We will present evidence from contemporary sleep research and from the palaeoanthropological record that changes in the sleep of hominoids about 2 million years ago, during the tree-to-ground sleep transition, may have aided the evolution of cognition.

1 Characteristics of sleep

Researchers typically characterise sleep by five distinct EEG (electroencephalogram) stages. Stages 1 and 2 are considered light stages of sleep. Stage 1 is typically brief and usually occurs at the onset of sleep. Stage 2 accounts for about 50% of sleep and is distributed fairly evenly throughout a typical 8-hour sleep period. The brain waves during these stages are of lower amplitude than other stages but higher in frequency (ie, > 15 Hz). Stage 2 is also characterised by sleep spindles, which are periodic brief bursts of 12-16 Hz, occurring at a rate of about two per minute. Humans are typically awakened easily from these two stages and can report thoughts, ideas, and dreams after awakening from these stages. Stages 3 and 4 are considered deeper sleep stages, and are also referred to as slow-wave sleep (referring to its wave frequency). Slow-wave sleep has a frequency of 0.5 Hz to 3 Hz (called delta waves) and high amplitude (compared to other sleep stages). In humans, it is the stage in which it is least likely that coherent stories or vivid dreams are reported, and it diminishes sharply after the age of about 60. There appears to be an activation of the parasympathetic nervous system during slow-wave sleep and less activation of the cardiovascular system, with decreases of respiration, heart rate, and blood pressure. Activity of the gastrointestinal system accelerates, and there are increased movements of the gastrointestinal tract (Beatty 1995). The predominant amount of slow-wave sleep occurs during the first third of a human's eight-hour sleep period.

The fifth stage of sleep is not labelled as such. It is called rapid eye movement sleep or REM sleep, and it appears to be a newer evolutionary development compared to the other stages. Winson (1990) argues that it arose approximately 140 million years ago in a context of early mammalian evolution, whereas slow-wave sleep may date back as much as 60 million years earlier. The brain waves in REM sleep are similar to Stage 1 sleep with low amplitude and higher frequencies. However, there are periodic bursts of eye movements, and when human sleepers are awakened during REM, they often report vivid dreams and often see themselves actively participating in their dreams. These reports are usually qualitatively (or quantitatively) distinctive from the thoughts and snippets of ideas in Stages 1 and 2 (eg, Hobson 1988), although the issue is far from settled. REM sleep also predominates in the later third of a human's 8-hour sleep period (see Dement & Vaughn 1999 or Ellman & Antrobus 1991 for more elaborate descriptions of sleep and dream research).

There is a great deal of variability among mammals in the percentage of REM sleep. All great apes have slow-wave sleep, and their REM varies from about 7% to 15% of their total sleep (eg, Allison & Cicchetti 1976). Most monkeys, with whom we share a more distant common ancestor much further back in time than we do with the great apes, also spend about 5% to 15% of their sleep in REM. Human REM constitutes 25% of total sleep time. Interestingly, the onset of sleep in primates is often accompanied by a hypnic or hypnagogic jerk, which is a sudden muscle reflexive movement that frequently awakens the sleeper. Although the ultimate cause of the hypnic jerk is unknown, a common hypothesis is that it is an archaic reflex to the brain's misinterpreting the muscle relaxation accompanying the onset of sleep as a signal that the sleeping primate is falling out of a tree (eg, Coolidge 2006). The reflex may also have had selective value by having the sleeper readjust or review his or her sleeping position in a nest or on a branch in order to assure that a fall did not occur.

Muscle atonia (loss of muscle tone or muscle 'paralysis') is a physiological response that occurs with the onset of REM sleep. Jouvet (1980) explored the role of inhibitory neurons upon voluntary muscle systems in preventing these systems from acting out dreams. Morrison (1983) demonstrated that selective destruction of these inhibitory neurons allowed cats to act out predatory actions, presumably the content of their REM dreams. A similar disorder has been noted in humans, the REM sleep behaviour disorder (Sforza et al 1997). Also, some sleeping people can become aware of this muscle paralysis during REM sleep, and their accompanying dream themes often reflect the interpretation of muscle atonia, such as being paralysed by aliens or being crushed by ghosts (eg, Wing et al 1994). In their study of over 600 Chinese undergraduates, over 93% had heard of the ghost oppression dream and 37% claimed to have experienced it.

It has also been suggested that one of the most common themes of all adult dreams, falling, may in part occur because of the sleeper's interpretation of the complete muscle atonia that accompanies the onset of REM sleep (eg, Van De Castle 1994). The other suspicion, of course, is that the falling theme is connected to our arboreal hominid origins, as falling out of a tree was an event that an early hominid should not have taken lightly nor have easily forgotten (eg, Sagan 1977).

An evolutionary speculation for muscle atonia and the differentiation of slow-wave and REM sleep comes from the work of Kavanau (2002). He proposed that as ambient temperatures during twilight portions of primitive sleep rose above an animal's core temperature, the thermoregulatory need for muscle contractions became superfluous. With the absence of muscle tone, he proposed that selection may have favoured fast waves during nocturnal twilight sleep. These fast waves may have reinforced motor circuits of evolving warm-blooded organisms without the concomitant, sleep-disturbing muscle contractions. Through these and other mechanisms, twilight sleep may have become REM sleep, and the daylight sleep may have become slow-wave sleep and non-REM sleep.

It also appears that the motor paralysis during REM sleep is accompanied by specific deficits in the executive functions of the frontal lobes. The latter functions are thought to include planning and organising tasks to attain goals and decision-making (eg, Pennington & Ozonoff 1996). A distinction is often made between the executive functions of the dorsolateral prefrontal cortex (PFC) and the ventromedial PFC. The functions of the former include complex problem-solving, decision-making, and verbal fluency and are sometimes referred to as cognitive executive functions whereas functions of the latter are thought to include decisions regarding social and interpersonal interactions and are sometimes referred to as affective executive functions (eg, Sarazin et al 1998). Studies from fMRI research appears to demonstrate that the dorsolateral PFC is deactivated during REM sleep, however, there is activation of the ventromedial PFC, the amygdala, and the anterior cingulate gyrus (eg, Maquet et al 1996). The latter structure is also thought to mediate attention and some of the affective executive functions (eg, Gazzaniga et al 2002). In summary, it appears that some important functions of the PFC are deactivated during REM sleep and other parts are highly active. It is thought that these differential brain mechanisms allow the dreamer to remain in a quiescent physical state, unable to select and attend freely to particular internal and external stimuli, and yet accept often bizarre dream scenarios as reality. For example, interacting with long-dead people we have known or people we have not seen for years is not rationally challenged while we dream, nor are we readily able to become aware that we are dreaming when we encounter these improbable dream scenarios, eg, Franklin & Zyphur 2005. We shall return to the latter's additional speculations later in the paper.

As for the function of sleep, Lima, Rattenborg, Lesku, and Amlaner (2005) have noted that most evidence has supported an important restorative basis, although it has also been recently proffered (eg, Coolidge, 2006) that an overview of this literature also supports mnemonitive and innovative functions as well. Furthermore, it appears unlikely sleep would have a single function, as multiple and interactive reasons for sleep are most likely, given the latter's behavioural and physiological complexities (eg, Walker 2005).

Importantly, Lima et al (2005) also pointed out the anti-predator function of sleep elucidated in earlier theoretical models, ie, sleep serves a protective role when an organism cannot be useful in performing other activities. This 'immobilisation' hypothesis is not entirely consonant with models that propose that sleep is primarily restorative in function, as immobilisation simply keeps the organism out of harm's way. However, given the fact that all animals sleep and the history of the differentiation of slow-wave sleep and REM sleep has at least a 140 million year history, early hominids' predatory environments would have made sleeping a very risky proposition, Thus, Lima et al proposed that dynamic changes in sleep states may reflect a trade-off in reducing sleep debt with the costs of predation. In brief, they propose that slow-wave sleep is most cost effective by occurring early in a sleep period and periodic awakenings and more vigilant sleep stages (eg, Stage 2) may have evolved to reduce the risk of predation (see Lima et al for additional details).

2 Hominoid and early hominid nesting

As noted earlier, virtually all animals sleep, but the nature of sleep is best documented and understood for vertebrates, especially birds and mammals. Both spend a significant portion of the day asleep, and selection of sleeping sites is therefore a significant feature of adaptive niches. Various considerations come into play in selection or construction of sleeping sites, including thermoregulation, nearness to and/or protection of food sources, social interactions, parasite threat, and risk of predation. All of these come into play for primates, but there is considerable variability within the order in solutions to the sleeping site problem. Many prosimians nest, but most anthropoids do not (Kappeler 1998). Instead, monkeys and lesser apes select sleeping sites, but do not modify them. For monkeys such sites are often high in trees or on cliff faces, sites which present a real risk of falling, but which, for the same reason, reduce the risk of predation. One apparent effect that this has had for many monkeys is a predominance of early stage, light sleep (Anderson 1998).

Construction of sleeping nests appears to be a derived feature for the great apes. Orangutans, chimpanzees, and bonobos typically construct nests in trees, while gorillas typically build nests on the ground. Fruth and Hohman (1996) report an average above ground height of 10-20 metres for the arboreal nests, while Groves and Sabater Pi (1985) report a range of 3 to over 25 metres for chimpanzees. Chimpanzees construct individual nests in new locations every night (infants sleep with mothers), and rarely reuse earlier efforts. When constructing nests chimpanzees most often start at a fork in the branches and bend down and weave nearby branches into a stable platform. Chimpanzees build the nests before nightfall and stay in them the entire night. The members of a travelling party build nests near to one another, and often vocalise in the evening after settling down, and in the morning before rising. In contrast, gorillas nest on the ground, a fact probably linked to gorillas' size. Gorillas also construct a nest each night, usually by bending over leafy vegetation. Chimpanzees do occasionally nest on the ground (6.1% of the time in one study [Koops et al 2007]), and gorillas, usually females, do occasionally nest in trees, attesting the variability present even within communities. All great apes sleep in a horizontal position, because muscle relaxation is a general characteristic of the onset of sleep, and nests undoubtedly aid in both sleep comfort and the prevention of sleep mishaps (ie, falling out of a tree).

The same considerations appear to go into great ape nest construction as go into the selection of sleeping sites by other primates. Great apes often nest near food sources (Fruth & Hohman 1996), and occasionally in fruit bearing trees (Basabose & Yamagiwa 2002). Predation risk is also real for most studied groups of chimpanzees, with leopards being the major threat (Fruth & Hohman 1996; Koops et al 2007). However, it has proven very difficult to assess the role of predation risk (Anderson 1998), and there are no known cases of predation on chimpanzees from nests (McGrew personal communication May 2004). Social considerations are clearly important in selection of nesting sites; the number and propinquity of nest sites closely reflects the make up of foraging groups. Significant social interaction takes place after settling down for the night, often via vocalisation (Anderson 1998), enough so that Fruth and Hohman (1996) consider this as a potential evolutionary source for information exchange among hominids. It is less clear that thermoregulation considerations come into play for great apes (they do for monkeys). The one tested chimpanzee case found that selection of ground nests was not influenced by windy or rainy conditions (at this site there was no predation risk) (Koops et al 2007).

In part based on modern evidence of nest building in great apes, Sabater Pi, VeaÌ and Serrallonga (1997) proposed that early hominids probably also nested in trees. Additional support for arboreal nesting among early (pre-2.5 Ma) hominids rests on the evidence of hominid post-cranial anatomy. The hominid fossil record from Africa has yielded numerous examples of post-cranial bones. For many of these examples, it is possible to assign taxonomic status, and for some (eg, AL 288 [Lucy]) and WT 15000 [Nariokotome]) it is possible to attribute bones to single individuals. Several limb features are reliable indicators of the hominid locomotor profile. In particular, climbing selects for more robust front limb features, longer arms relative to legs, a higher brachial index (length of forearm relative to upper arm), a more cranially (headward) orientated glenoid cavity, and curved fingers (Stanley 1992). These features are clearly represented in the anatomy of our nearest relatives, the common chimpanzees and bonobos, who forage, sleep, and nest in trees, but who travel on the ground between food sources.

All of the early hominids retain features of a climbing anatomy (McHenry & Coffing 2000). The earliest extensively-documented hominid was *Australopithecus afarensis* (ca 3.8 – 3.1 Ma) which, though clearly bipedal, retained robust fore limbs and long arms relative to femur length. Between 3.8 and 2.5 Ma, a variety of hominids evolved in Africa, including a robust group (generally assigned to genus *Paranthropus*) and a more gracile group (assigned to genus *Australopithecus*). All were clearly bipedal, but all also retained features of a climbing anatomy (McHenry & Coffing 2000; Stanley 1992; Wood & Collard 1999). Current hypotheses for the evolutionary advantage of bipedalism now focus on features of woodland niches, rather than the open grasslands favoured by earlier hypotheses, and a variety of proposed explanations remain tenable (Richmond et al 2001). What one can conclude with confidence is that these early hominids must have spent more time, and travelled longer distances, on the ground. But they all lived in habitats with trees, and do not appear to have exploited treeless savannas. Their teeth document an adaptation to heavy chewing, perhaps of small hard seeds, or buried, gritty foods, and they may have spent much of their foraging time on the ground. Their climbing anatomy would then have been linked to predator avoidance and nesting (Stanley 1992). In other respects these early hominids were ape-like. Their growth rates resemble those of chimpanzees (Wood & Collard 1999), and there is no evidence (prior to 2.5 Ma) for extensive tool use. Thus, because of their climbing anatomy and other evidence, it appears likely that these early hominids nested in trees and, by extension, retained an ape-like pattern of sleep.

3 Early *Homo* and *Homo erectus*

The earliest fossils assigned to the genus *Homo* are harder to assess, largely because the record of post-cranial anatomy is poor; there are few examples *in toto*, fewer still that can be reliably assigned to an individual, and few complete examples of individual bones, requiring that measures of relative limb proportions be made from estimated lengths (Haeusler & McHenry 2004; McHenry & Coffing 2000). Nevertheless, studies of early *Homo* indicate that its post-cranial anatomy was much like that of an *Australopithecus*. It, too, retained features of a climbing anatomy, though it may have been more human-like than the australopithecines (Haeusler & McHenry 2004). Complicating the picture is the likelihood that there were two species of early *Homo* in Africa between 2.5 and 1.8 Ma. One, *Homo rudolfensis*, may have had a more modern post-cranial anatomy, if an isolated and fragmentary humerus is a reliable indication (McHenry & Coffing 2000). Both forms continued to live in the wooded environments favoured by earlier hominids, though they may have occupied a wider range of specific habitats (Reed 1997). Early *Homo* had larger brains than australopithecines, and at least one of them made and used stone tools. However, neither the tool-making, nor the way the tools were used, required cognitive abilities not already possessed by apes (Wynn & McGrew 1989), and the specific adaptive reasons for encephalisation remain unknown. There is, however, no reason to conclude that *Homo habilis* and *rudolfensis* had given up sleeping in trees.

But *Homo erectus (sensu lato)* almost certainly had. This conjecture is supported by the post-cranial anatomy of Nariokotome. The remains of this individual include at least one example of all the major limb bones, excepting only the radius and small finger and toe bones, along with the majority of the axial skeleton, and the skull. From this virtually complete skeleton, palaeoanthropologists have been able to reconstruct a detailed picture of Nariokotome's biology and life history. This was a pre-adolescent male, who was 160 cm tall at the time of death, but who would have attained an adult stature of over 170 cm. He was tall and thin, with an ideal body type for heat dissipation, and had led a rigorous life (Walker & Leakey 1993). Otherwise, his limbs were little different from those of a modern human – he had the anatomy of modern bipedalism, and no remnants of climbing anatomy in his forelimbs (McHenry & Coffing 2000; Wood & Collard 1999). Moreover, his maturation pattern (tooth eruption sequence, etc) was more like that of modern humans than it was like that of apes and may have included secondary altriciality. Other *Homo erectus* post-cranial remains indicate another important step toward modernity. *Homo erectus* females were closer to males in size than was true for earlier hominids (Aiello & Key 2002; McHenry & Coffing 2000). The anatomical features of *Homo erectus* alone indicate that a profound shift in adaptation had occurred. It is the anatomy of a hominid adapted to hot, open environments, and to travelling longer distances on the ground. It was larger than earlier hominids, and had lost all remnants of climbing anatomy. The differences between *Homo erectus* and earlier *Homo*, including *Homo habilis* and *Homo rudolfensis*, and the similarities to modern humans, are so significant that Wood and Collard (1999) have suggested relegating *habilis* and *rudolfensis* to the genus *Australopithecus*. The advent of *Homo erectus* was clearly one of the most significant transitions in human evolution. We suggest that it almost certainly included a transition to ground sleep.

4 Ground sleep, fire, and tool production

The archaeological record supports this picture of a profound adaptive shift. A number of developments, almost certainly attributable to *Homo erectus*, made their first appearance. Perhaps the most significant was use of fire. The evidence for early use of fire is controversial, and a conservative stance recognises use of fire only after 500 Ka. However, there is some early evidence from Africa that is difficult to explain through natural processes alone. The most compelling evidence, in the form of burnt bone, comes from the South African site of Swartkrans, and dates to about 1.4 Ma, well after *Homo erectus* had appeared on the scene (Brain & Sillen 1988; James 1989). The possible benefits of fire for a ground sleeping hominid should be obvious. Whereas fire may have been used for protection, it is also possible that it signals an important nutritional change from exclusively uncooked foods to cooked ones, including foods that might otherwise be too tough to eat or digest (for a more complete description of cooking and its possible morphological and cultural *sequelae* see Wrangham et al 1999). Interestingly, Wrangham et al estimate the beginnings of cooking at about 1.9 million years ago and attribute the behaviour to early *Homo erectus*. A second development was that of deliberate tools, in the guise of large bifacial tools that were carried about and used for a variety of tasks. We use the term 'deliberate' tool intentionally. Earlier stone tools were *ad hoc* productions made for a specific task at hand (Toth 1985; Wynn 1981, 1985). Earlier *Homo* had perhaps carried raw material from place to place, but did not make tools that they carried around. This may strike one as splitting hairs, but we think it is quite important. *Ad hoc* tools result from a motor procedure tied to an immediate task. A deliberate tool results from a motor procedure tied *to the tool*, and a range of *potential, future tasks* (Wynn 1993). If nothing else, this suggests that tools had become an enduring and essential component of the niche. *Homo erectus* also employed a new cognitive ability when he or she made these tools – the ability to coordinate shape recognition (in this case symmetry) with spatial cognition (Wynn 2002). Indeed, Rossano (2003) has recently speculated that the repeated practice and comparison process of tool-making may have served as the incipient foundation for self-awareness and consciousness. Both of these developments – deliberate tools and coordination of shape and spatial cognition – are never found with modern apes or earlier hominids. They are, in fact, human characteristics, and indeed for the first time it is perhaps appropriate to speak of proto-humans.

Another feature of this period is that the stone tools start to show a more pronounced right hand preference of their makers (eg, Corballis 2003). Life in trees would have almost demanded ambidextrous hand and leg movements. With the transition to life on the ground, hand preference symmetry would no longer be a requirement of successful living. For example, it has been argued that bipedalism would have allowed the hands and arms to gesture. Corballis argued that the incorporation of gestures along with vocalisations might have served as a foundation of language. He also postulates that the left-hemisphere's predilection for vocalisation probably occurred much earlier in time. As a consequence of the incorporation of manual gestures with vocalisations, language could then evolve beyond simple manual gestures, although interestingly, modern humans often still gesture while speaking and show a right-hand preference for gesturing. Toth (1985) found a right-hand preference ratio (57:43) in stone tools from 1.9 to 1.4 million years ago that is not close to the modern ratio of 9:1 of right-handers to non-right-handers. This discrepancy and other factors led Corballis to suspect that true syntactic modern speech was not to evolve until a million or more years later.

5 The weed hypothesis

The distribution of archaeological and palaeontological sites provides a final piece to the puzzle. *Homo erectus* had moved away from woodland habitats to occupy not only hot, open savannas, but also higher altitudes and latitudes. It moved out of Africa and away from the tropics. By 1.7 Ma there are *Homo erectus (sensu lato)* sites in the Caucasus (Dmanisi), and perhaps as far as Southeast Asia (Anton et al 2002; Cachel & Harris 1995). Indeed, *Homo erectus* became widespread so quickly (in an evolutionary sense), that some palaeoanthropologists now question whether it is justifiable to place its origins in Africa (Dennell & Roebroeks 2005).

This suite of adaptive developments (eg, the ground sleep transition, deliberate tool-making, the coordination of shape and spatial cognition, rapid dispersal, etc) has led several palaeoanthropologists to suggest that the evolution *Homo erectus* represented a significant break from previous, more ape-like, ways of life (Aiello & Key 2002; Wood & Collard 1999). Cachel and Harris (1995) have proposed a provocative hypothesis for the niche of *Homo erectus*, a hypothesis that dovetails nicely with our arguments for enhanced sleep. They suggest that *Homo erectus* was a 'weed' species, especially adept at invading disrupted environments, such as those common in the Pleistocene, and new locales. An essential element to this was the ability to learn new territories very rapidly.

> It is tempting to infer that, if relative brain size increase in genus *Homo* is associated with an enhanced ability to map important resources and predict their availability across a home range, this might explain the greater dispersal ability of this genus in comparison to the australopithecines' (Cachel & Harris 1995:59).

However, they also observe that there is no correlation between dispersal ability and brain size in other animals, and focus on the increase in body size and culture as the important factors. We think they abandoned the neurological factor too quickly. In addition to the increase in body size, *Homo erectus* demonstrated new spatial abilities unknown in any ape (Wynn 2002), and though the relationship between small scale spatial thinking (artefacts) and large scale spatial thinking (landscape) is not simple in a cognitive sense, there does appear to be a correlation (Silverman et al 2000). The increase in home range, and increased dispersal ability may have been the factors that selected for *Homo erectus'* spatial cognition. It is precisely these kinds of spatial tasks that may be related to changes in the quality of sleep during the tree-to-ground sleep transition.

To our knowledge, Fruth and Hohmann (1996) were the first to propose that nest building may have been a 'great leap forward' in the evolution of cognition. Specifically, they proposed not only that the proximate functions of nests may have aided the transfer of information but also that nests themselves may have help established memories through increases of slow-wave and REM sleep. We are proposing that the full ground sleep transition may have further aided increases in slow-wave and REM sleep and preserved the general integrity of the sleep period (eg, less fragmented sleep by being subjected less to the vagaries of tree sleep such as strong breezes, bad weather, etc). Furthermore, we hypothesise tripartite benefits from sleep on the ground:

1 threat simulation, social rehearsal, and priming
2 creativity and innovation, and
3 procedural memory consolidation and enhancement.

6 Threat simulation, social rehearsal, and priming

Dream reports of modern children may provide possible insights into the life and consciousness of early hominids. Van de Castle (1983) and Domhoff (1996), in large surveys of children's dream reports, found that animal characters made up the largest proportion of children's dreams (approximately 20%–45%). They noted that the animals in dreams tended to be those that were not often encountered in children's actual lives, eg, monsters, bears, wolves, snakes, gorillas, tigers, lions, and biting insects, although children do often dream of commonly encountered animals such as cats and dogs. The authors also noted that college students and older individuals, whose percentage of animal dreams was much lower, tended to dream of animals more likely to be encountered in real life, eg, horses, dogs, and cats. Children's dreams also had higher rates of aggression than adult dreams, and higher rates of aggression involving animals. Revonsuo (2000) interprets these findings in terms of a threat simulation theory, which states that the present dream-production system simulates threatening events in the ancestral environment.

The recurrent dreams of adults, in particular nightmares, may also present a glimpse of ancestral dream life. Robbins and Houshi (1983), in a study of college students, reported that the most common recurring dream theme was anxiety in the context of being pursued or threatened. The most common themes in nightmares, of course, contain high levels of anxiety but also appear similar to recurrent dream themes such as being threatened, chased, or attacked. Revonsuo (2000) argued that the waking lives of most of these dreamers were unlikely to have high levels of real daily threats, especially attacks by wild animals. He hypothesised that the dreamers were reliving archaic dream themes, particularly ones that would simulate the real dangers of the ancestral environment, including falling, violent encounters with natural disasters, and being threatened by strange people and wild animals. He reasoned that through natural selection, dreaming came to be a biological function that rehearsed threat perception and threat avoidance. The selective advantage would come from a dream theme repetition that would enhance and prepare waking threat-avoidance skills, which experimental psychologists call priming. A recent study (Malcolm-Smith & Solms 2004), in part designed to test Revonsuo's hypothesis, may provide weak support for it. University students were polled for threatening dreams and about 9% of the sample reported a realistic physical threat in a dream and about 3% reported a realistic escape response in the face of the threat. Stronger support for the threat simulation hypothesis comes from Revonsuo and Valli (2000) and Valli et al (2005).

We also argue that even Freud (1900/1956) provides evidence for Revonsuo's threat simulation hypothesis, albeit a weaker case. Freud noted at least two dreams that may have had ancient ancestral roots: (1) the examination dream, and (2) the embarrassment of being naked dream. In both instances, we would posit that the dreams serve to prime the dreamer to be prepared in his or her subsequent waking life. In the examination dream, the dreamer is unprepared for an examination about to be undertaken. Freud noted that the dream may appear years after any actual examinations may have been taken and that they may represent neurotic (anxiety) fears of being punished for being unprepared by our parents or schoolmasters.

Freud interpreted the dreams of being naked or partially clothed as repressed sexual wishes. We would posit that both dreams probably had their origins in the ancestral hominoid environment. Hunters who were improperly dressed for hunt might die in a sudden and harsh weather change. Hunters without proper stone tools or weapons might also regret their lack of preparedness. The replay of these themes may have served to prime the dreamers so they were less likely to actually commit these errors upon awakening.

Would regular confrontation with a threatening environment increase dream themes of danger and threat? There is evidence from the dream reports of contemporary hunter-gatherers that daily confrontations do increase dream themes of aggression and anxiety. Domhoff (1996) reported the results of dream studies conducted in the 1930s on Yir Yoront, a group of native Australian hunter-gatherers. The dreams of the adult males had significantly higher percentages of dreams with animals, aggression involving animals, and physical aggression than did those of male American dreamers. Gregor (1977) analysed the dreams of Mehinaku Indians of Central Brazil. He found significantly more aggression and animal-aggression themes than those of American dreamers. Gregor estimated that about 60% of the dreams of the Mehinaku males had threatening themes, while only 20% of their dreams involved non-threatening or non-aggressive activities. In a classic study of one adult woman of the contemporary !Kung hunters-and-gatherers of the Kalahari desert, Shostak (1981) recorded over 10 dreams with recurring and threatening themes of sexual infidelity, jealousy, omens and divinations, and falling (while climbing a tree and falling into a well). These findings are again consistent with Revonsuo's threat-simulation hypothesis, and it appears highly probable that threatening ancestral environments helped sustain threatening dream themes in early hominids.

Franklin and Zyphur (2005) have recently broadened Revonsuo's hypothesis. As noted earlier, they contended that differential brain mechanisms during REM sleep consisting of activation and deactivation of the PFC, anterior cingulate cortex, and amygdala allow dreamers not only to remain asleep but also unaware that they are dreaming despite the often bizarre and illogical nature of dreams. They proposed that dreaming may not only serve to simulate threats, but may also serve as a more general rehearsal mechanism whose virtual variations in dreams of scenarios encountered in daily life subsequently and positively influence waking encounters. They noted that the common inability to remember dreams does not necessarily invalidate their hypothesis, as humans may not often be able to consciously recall dreams but dreams may shape their behaviour subconsciously, and through the priming effect (as we noted earlier), our waking decisions may be biased or primed by the mere prior exposure to dream stimuli. It is also interesting to speculate that such a mechanism would allow waking actions to be decided sometimes without a major conscious influence or language influence, and thus dreaming may have played a more major role in early *Homo* evolution when language facilities may not have been nearly as sophisticated as present day *Homo sapiens*. Finally, Franklin and Zyphur noted that this virtual rehearsal mechanism might have had its most profound effect in social situations, conferring greater survival value on those who could interact with others with minimal interpersonal conflict and confrontation, allowing them greater access to resources in their group (eg, food or mates). Physiological evidence for their hypothesis, as mentioned earlier in the paper, comes from the activation of the ventromedial PFC, amygdala, and anterior cingulate cortex which mediate some of the affective executive functions, which are thought to play a strong role in social and interpersonal decision-making and evaluations, eg, Gazzaniga, Ivry, & Mangun 2002.

7 Creativity and innovation

Clear evidence for the intimate relationship between creativity and dreaming is nearly as old as written records. A Sumerian king in 2200 BC preserved at least two of his dreams on clay tablets. They reveal that the king had a puzzling dream, and reported that he searched with a goddess for the meaning of his dream. This record serves as one of the first examples, in what was to be a rich history, that dreams may be divinely inspired and that answers to waking problems may be sought in dreams (for a more complete historical review of near east dreaming see Oppenheim 1956). Mesopotamians and ancient Egyptians had long traditions of dream incubation, where patrons would go to an incubation temple to sleep and dream and subsequently have their dreams interpreted by a practiced dream interpreter. Solutions to problems and even treatments for diseases were sought in dreams, and it was also believed that dreams could be used to prevent or change future misfortune. The Chester Beatty Egyptian papyrus, which dates to about 1500 BC, contains a glossary-like index of over 200 dreams, divided into two groups of good and bad dream omens. From about 1000 BC to 750 BC, it was apparently popular in Egypt to have scribes prepare small oracular amulets, which were to be worn about the neck. Two thirds of 21 known oracular papyri were commissioned by female patrons. Their contents frequently contain dream messages and decrees that appeal to gods and goddesses to protect the owner from diseases, and one of the most common forms was 'make every dream which [he or she] has seen good and make every dream which someone else has seen for [him or her] good'. The tradition that dreams contain important messages and answers, and the notion that they may be divinely inspired continues throughout later written history. The Jewish Talmud, roughly contemporary with the Christian Bible, about 300 BC to 200 AD contains over 200 references to dreams, and both old and new testaments of the Bible contain dream references along these same themes (for a more complete description of the history of dreaming see Coolidge 2006; Van De Castle 1994).

More modern evidence for creativity and dreams is largely anecdotal but replete throughout the arts and sciences. Artists who claimed their work was based on a dream include Durer, Goya, Blake, Rousseau, Dali, and Magritte among many others. Musicians who claimed a work was based on a dream include Mozart, Wagner, Keith Richards (the lead guitarist for the Rolling Stones claimed the musical riff to *[I Can't Get No] Satisfaction* came in a dream), and Billy Joel, again, among many others. The 18th century violinist Tartini reported his inspiration for his most famous violin work, *Trillo del Diavolo* (The Devil's Trill), came to him during a dream in which the devil played a particular violin riff. Upon awakening, he reported that he excitedly tried to duplicate the devil's trill.

A number of writers have claimed the inspiration for a work came in a dream. Robert Louis Stevenson wrote that while pondering a duality that exists in all humans, he dreamt the story for *The Strange Case of Dr. Jekyll and Mr. Hyde* in virtually a single dream. Samuel Taylor Coleridge claimed that his poem *Kubla Khan* came to him in a dream and that upon awakening he wrote down about 40 lines before he was interrupted by someone, and thus left the poem incomplete (in fairness, it is not known to what extent opium addictions may also have played a role in some anecdotal dream reports, see Hartmann 1998 for more complete descriptions of creativity, dreaming and critiques).

Two chemists have anecdotally reported their most famous discoveries resulted from dreams. In the 19th century, the Russian chemist Dmitri Mendeleyev said he conceived of the periodic table in a dream (Van de Castle 1994). Also in the 19th century, German born and later French chemist Friedrich Kekulé had been pondering the structure of the benzene molecule. He knew that it had six carbon atoms but neither a branching chain nor a straight alignment would account for its chemical properties. In a dream, he saw snake-like 'confirmations' writhing together. He reported that one of the snakes had seized its own tail and 'whirled mockingly' before his eyes. He said he awoke in a 'flash of lightning,' and began working out his famous solution to the problem, the benzene ring. It has been suggested, however, that Kekulé may have made this claim to avoid accusations that he has borrowed his idea from the work of others (see Hartmann 1998 for a more complete discussion). Again in the 1800s, American Elias Howe reported that he had worked for five years trying to create an automatic sewing machine. He said that he could not figure out how to get the machine to grab the thread once it had pierced the material. In his dream, he said he was a missionary captured by natives. They stood around him dancing with spears that had holes in their tips. Upon awakening, he said that he recognised that this was the solution to his problem, a needle with a hole in the tip.

There is also a plethora of anecdotal reports of creative ideas and solutions for problems arising from dreams. For example, Krippner and Hughes (1970) found, in a survey of contemporary mathematicians, over 50% reported that they had at least once solved a mathematical problem in a dream. The brilliant Indian mathematician Ramanujan (1887–1920) said that the goddess Kali gave him solutions to theorems in his dreams, although there was some suspicion he said so for politico-religious reasons. There is also the phenomenon of lucid dreaming, where dreamers can become aware that they are dreaming within a dream, and thus control the direction or outcome of the dream. This technique has been reportedly been used successfully as a psychotherapeutic technique as claimed by its proponents (eg, Cartwright & Lamberg 1992; LaBerge 1985). However, lucid dreams are very infrequent, and lucid dream control requires strong motivation for success (eg, Coolidge 2006).

Hartmann (1998) speculates that dreaming allows the dreamer to make connections between disparate and often contradictory ideas. These connections, he proposes, are often more broad and inclusive than during wakefulness. By the nature of cognition, some intent and coherence is imposed and guided by the emotions (and limbic structures) of the dreamer. Thus, Hartmann believes dreams contextualise emotions and, by using visual and spatial pathways, create an explanatory metaphor for the dreamer's emotional state. He offers, as evidence for his theory, dreams following traumatic events like the holocaust and other horrific tragedies.

Whereas there exists a plethora of anecdotal evidence and personal speculation for the general claim that dreaming, problem solving, and creativity are linked, there have been few experimental attempts. Dement (1972) gave 500 undergraduates a problem to solve 15 minutes before sleeping. In the morning, they reported their dreams and any solution to the problem. Of 1148 attempts, it was reported that the solution came in a dream on only seven occasions (less than 1%). Blagrove (1992) presented a critique of problem solving in the dream literature and concluded that there is little empirical evidence that new and useful solutions to waking problems are created in dream sleep. He did propose that psychological solutions may be correlated with dreaming, but it did not imply a causative relationship. He counter-argued that solutions may more often occur while awake, and subsequent dreaming merely reflects the solution. In summary, there is no wealth of compelling experimental evidence for the link between creativity and dreams; however, the preponderance of anecdotal and other sources of evidence makes it a difficult hypothesis to dismiss completely, and a recent empirical study has revived the idea.

In that study of sleep and creative problem solving, Wagner, Gais, Haider, Verleger and Born (2004) gave 106 human participants a cognitive task that required learning stimulus-response sequences (which they deemed an implicit procedural memory task) where improvement, as measured by reaction time, was evident over trials. Participants could improve abruptly if they gained insight into a hidden abstract rule. After initial training, participants either slept for eight hours or stayed awake (at night or during the day) for a similar period. Twice as many participants who slept became aware of the hidden rule than those who stayed awake, regardless of time of day. Based on a slowing of reaction times in the sleep group, the authors postulated that the participants' greater insight was not a strengthening of the procedural memory itself but involved a novel restructuring of the original representations. They speculated that the restructuring was mediated by the hippocampus, related medial temporal lobe structures, and prefrontal cortex. These structures have been previously shown to play an important role in generating awareness in memory. Wagner et al suspected that cell assemblies representing newly learned tasks were reactivated by the hippocampal structures during sleep and incorporated by the neocortex into pre-existing long-term memories. They hypothesised that this process of incorporation into long-term storage formed the basis for the remodelling and qualitatively different restructuring of representations in memory. Thus, in their opinion, sleep may serve as a catalyst for insight (for a more complete discussion of the role of the prefrontal cortex, memory, and novel problem-solving *vis-à-vis* the archaeological record, see Coolidge & Wynn 2001, 2005).

8 Procedural memory consolidation and enhancement

Consciousness is a continuum from awake to asleep. Wakefulness obviously varies from very aware to semi-aware (some freshmen in lectures), but sleep also varies in levels of awareness. Vivid and elaborate dream reports are nearly entirely absent in the slow-wave sleep, but REM sleep often includes 'paradoxical awareness', which is the state of being selectively aware of some aspects of our external sleeping environment (for example, muscle atonia, or strange sounds or our names), yet sleeping through most other sounds and stimuli. Furthermore, we can become aware that we are dreaming, but more often than not, we accept our dream and our awareness of it as reality. Because learning and memory formation are aspects of consciousness (although there is some evidence for some types of learning without awareness), there is reason to suspect that memories are stabilised and consolidated during sleep, both slow-wave and REM. Indeed, it would not be reasonable to suspect that these activities would stop altogether during sleep, although it also seems plausible that these activities might be reduced during sleep (particularly active learning).

The first strong empirical research for REM's role in memory consolidation comes from the work of Winson (1990). He demonstrated in animals that a theta rhythm (6 Hz) arises from the hippocampus associated with specific and important functions such as exploratory behaviour of rats, predation in cats, and rigidity in rabbits. In research on sleeping rats, Winson found that theta rhythms in hippocampal neurons fired in similar patterns to their awake firing while learning mazes. Because exploratory behaviour in rats appears critical to their survival, Winson reasoned one purpose of REM sleep might be the strengthening and consolidation of these visual-spatial (procedural) memories. Thus, in arboreal nesting hominoids, including early hominids, the increases in REM sleep that were associated with nesting may have strengthened waking memories critical to survival, such as memories for sites of food, safety, resources, and predators and other dangers. In arboreal hominoids, as with other mammals, the hippocampus would also have played a dominant role in the consolidation of procedural skills such as nest building, and also any tool making and tool use (as it does with modern apes).

General support for Winson's hypothesis comes from a gene study by Ribeiro, Goyal, Mello and Pavlides (1999). They studied the expression of a plasticity-associated gene zif-268 during slow-wave and REM sleep of rats that had been exposed to an enriched sensorimotor experience in a preceding waking period. In this context, plasticity refers an ability of neurons, under the control of genes, to make lasting structural and functional changes in responses to a stimulus or an experience. They found that non-exposed control rats showed a reduced zif-268 gene expression during slow-wave and REM sleep, whereas the exposed rats showed upregulation in zif-268 during REM sleep in the hippocampus and cerebral cortex. They interpreted this finding as evidence that REM sleep opens a window of increased neural plasticity, presumably enhancing and/or consolidating the memory of the enriched experience.

The evidence for the enhancement (or even acquisition) of declarative memories (ie, the memories for facts and verbal material) during the sleep of humans is less persuasive. For example, there is only minimal evidence for the ability to learn verbal material during sleep, and in any case, it appears to be a highly inefficient method of learning (eg, Levy et al 1972). Most studies that have found any positive effect of slow-wave or REM sleep upon declarative memories (primarily semantic memories or the memory for facts and verbal material) have used a sleep-stage deprivation paradigm, and thus, the confound of sleep deprivation exists in nearly all of these studies. Reviews of these and other studies of declarative memory enhancement during sleep in humans tend, on the whole, to be sceptical that there is any acceptable evidence at present (eg, Coolidge 1974; Siegel 2001; Vertes & Eastman 2000; Walker 2005). However, episodic memory (also known as autobiographical memory), that is, memory that is recalled like a written story of a time, place, and emotional state, is considered to be a type of declarative memory, and it may be affected by dreaming (eg, Franklin & Zyphur 2005; Wagner et al 2001; Walker & Stickgold 2004). Indeed, one critical variable in the paucity of evidence for REM and/or slow-wave sleep affecting declarative memories may be the emotional valence of the stimuli. Wagner, Gais, and Born (2001) found that memories with a strong emotional valence were retained better than emotionally neutral memories across periods of REM sleep but not for slow-wave sleep.

However, there appears to be mounting empirical evidence for the enhancement of various kinds of procedural memories in human sleep. Walker (2005) argues that the initial acquisition phase of learning and memory does not appear to rely fundamentally on sleep. This initial stabilisation stage (which itself follows acquisition) is characterised by the formation of durable memory representations, resistance to interference, and like acquisition, develops as time passes. But there is a second stage, consolidation-based enhancement that may show additional learning benefits without further rehearsal. Walker proposes that consolidation-based enhancement may fundamentally rely on several specific sleep stages (but presently, only for procedural memories). The specific stages involved may themselves depend on the type of procedural memory, and slow-wave sleep, REM, and Stage 2 have all been implicated (Walker 2005).

Karni, Tanne, Rubenstein, Askenasy and Sagi (1994) first demonstrated consolidation-based enhancement in humans on a procedural visual-spatial discrimination task. Learning was enhanced after a night of sleep but not after 4 – 12 hours of wakefulness. They also established that selective disruption of REM sleep, but not non-REM, resulted in a loss of these memory gains. Stickgold, James, and Hobson (2000) used the same task as Karni et al and found that the consolidation enhancement was dependent only on the first night of sleep following acquisition. They also found that learning enhancement was correlated with both the amount of slow-wave sleep and the amount of REM sleep. Again using the same task, Gais, Plihal, Wagner and Born (2000) deprived participants of sleep early in the night (presumably of predominately slow-wave sleep) and later in the night (presumably REM and Stage 2). They concluded that consolidation-based enhancement might be instigated by slow-wave sleep, whereas REM and Stage 2 may solidify and add to the enhancement effect, but that slow-wave sleep was a necessary component. If the latter conclusions are true, then the presently proposed further increases in both slow-wave and REM sleep and the general integrity of a sleep period, as a result of the ground sleep transition, would have been advantageous for the consolidation-based enhancement of the procedural memories.

In the first of two studies of a procedural motor skills task (sequential finger-tapping), Walker, Brakefield, Morgan, Hobson and Stickgold (2002) again found consolidation-based enhancement for normal length periods of sleep immediately following acquisition, or after a period of wakefulness after acquisition then followed by sleep. They found no enhancement effect during a 12-hour awake period following acquisition. When sleep-stage amounts were correlated with enhanced learning, they found that Stage 2 amounts were most strongly and positively correlated with learning. In a second study, Walker, Brakefield, Seidman, Hobson and Stickgold (2003) found that a majority of the consolidation-based enhancement occurred after the first night of sleep following acquisition, but that additional delayed learning did occur on subsequent nights. They also speculated that acquisition learning and delayed learning during sleep were regulated by different mechanisms. Fischer, Hallschmid, Elsner and Born (2002) replicated these findings and supported the conclusion that a full night's sleep after acquisition is critical to the delayed enhancement effect. However, they found that learning was positively correlated to REM sleep, but not for Stage 2.

In a procedural visual-motor task, Smith and MacNeill (1994) found that selective deprivation of late night sleep, particularly Stage 2, impaired retention. Maquet, Schwartz, Passingham and Frith (2003) used a similar task and again demonstrated the sleep-dependent enhancement of memory, and the effect was present after three nights of sleep following acquisition.

Aubrey, Smith, Tweed and Nader (1999) proposed that the degree of task complexity may be one determining factor in whether slow-wave, REM, or Stage 2 sleep are critical to the enhancement of memory. They suggested REM might be more critical to procedural tasks of greater complexity, such as visual discrimination, whereas Stage 2 might be more critical to more simple procedural tasks like motor skills. Walker (2005) surmised that if memory enhancement were one of the critical functions of sleep then evolutionarily it would make sense that the different sleep stages were exploited for their differential advantages for various tasks.

Peigneux et al (2004) trained 36 adult males on an episodic/spatial procedural memory task, that is, the subjects were trained to find meaningful targets (eg, a Buddha medallion) in a computer-generated virtual town. The authors used positron emission tomography to estimate regional cerebral blood flow in the subjects' hippocampal neurons and found that the amplitude of hippocampal reactivation in slow-wave sleep correlated significantly with their performance the next day on route retrieval measures. Peigneux et al concluded that enhanced hippocampal activation after a spatial memory task during post-training slow-wave sleep reflected the sleep processing of spatial memory traces, which led to enhanced performance upon awakening.

A summary of the research on the relationship between sleep and memory leads to the following conclusions:

1 there is little evidence that neutral semantic declarative memories are consolidated or improved by sleep or any of its stages, although episodic, affectively-charged declarative memories may be consolidated and/or enhanced by dreaming and/or sleep

2 there is increasing evidence that some types of procedural memories may be consolidated and/or enhanced by stages of sleep or the sequences of stages of sleep, however, it is not definitively clear which stages or stage sequences are critical to which tasks, and

3 the most recent research suggests that spatial procedural tasks may be enhanced by slow-wave sleep and hippocampal reactivation post-training.

Thus far we have proposed that the ground sleep transition may have aided the general integrity of an extended and less fragmented sleep period, enhanced REM sleep and perhaps Stage 4 sleep, and it may have aided the integrity of the sequence of Stage 4 and REM.

As a function of these sleep changes, and by means of the phenomenological contents of sleep (dreaming):

1. early *Homo* may have been primed to escape and avoid threatening events in their waking environments, and early *Homo* may have rehearsed social scenarios thus becoming more efficient in their waking endeavours in obtaining food or mates and/or interacting with others with less confrontation
2. REM and/or dreaming may have promoted creativity and innovation (the notion that REM and dreaming are synonymous is contentious, and our arguments do not hinge on their equivalence, for greater detail on the debate see Antrobus et al 1995; Cicogna et al 1998; Hobson et al 2000; Solms 2000), and
3. these sleep changes may have aided procedural memories, including memories for motor skills, visual-spatial discriminations, and episodic (personal)/spatial locations, without any further acquisition or practice.

Walker and Stickgold (2004) have recently proposed a homeostatic hypothesis for the relationship between sleep and learning that helps further to reinforce our arguments. In a review of numerous human and animal studies, they proposed that not only is there strong evidence that sleep consolidates and/or enhances learning but also that learning may enhance sleep. They noted that daytime learning of both declarative (emotionally valent) and procedural memories can trigger subsequent increases in particular sleep stages, suggesting a homeostatically driven demand on sleep-dependent memory consolidation (eg, Peigneux et al 2004). Thus, in the transition to ground sleep, ie, better sleep, visual-motor procedural memories and episodic memories may have been enhanced. The latter ability may have included greater success in subsequent waking behaviours in harm avoidance, better mate selection, acquisition of resources, enhanced exploration abilities, greater diversity of experience, and even creativity. These enhanced learning experiences, according to Walker and Stickgold's homeostatic hypothesis, reciprocally enhanced sleep (see Walker & Stickgold 2004 for a more complete review of their evidence).

9 Discussion

In sum, we believe that the palaeoanthropological evidence supports one strong conclusion and one weaker conclusion concerning the evolution of sleep. The strong conclusion is that selective pressure *against* lengthened Stage 4 and REM sleep was released with the transition to ground sleep by early *Homo erectus (sensu lato)*. An extended period of muscle atonia during sleep would no longer have been a handicap. Of course, gorillas also nest on the ground, and do not demonstrate lengthened REM sleep. It is therefore also necessary to account for some selection pressure *for* lengthened Stage 4 and REM sleep, and this is the more difficult of the two pieces of the puzzle to identify. Our admittedly weaker argument concludes that features of the *Homo erectus* adaptive niche selected for lengthened Stage 4 and REM sleep, and perhaps other stages as well. Our reasons are both general and specific. In general, *Homo erectus* represented a new evolutionary grade, with profound changes in anatomy, sexual dimorphism, life history, behaviour, and cognition. Such a profound shift may have included selection for lengthened sleep stages. More specifically, *Homo erectus'* behavioural repertoire included more complex technical procedures, movement within larger territories, and perhaps the ability to learn new landscapes very rapidly, all of which might have benefited from the memory consolidation and enhancement that may have accompanied an extended sleep period. Furthermore, if Lima et al (2005) are correct in their assumption that dynamic changes in sleep states reflect trade-offs in reducing sleep debt with costs of predation, then the role of Stage 2 sleep as a more vigilant state of rest becomes more prominent. As we noted earlier, Stage 2 is considered a lighter stage of sleep, constitutes 50% of all sleep stages, and is fairly evenly distributed throughout a full sleep period.

There are at least two other possible evolutionary timings. The first places selection for enhanced sleep at the time of the transition from *Homo erectus* to *Homo sapiens*, well over a million years after the release of pressure against it. This transition was accompanied by two behaviours that would have benefited from memory consolidation, strengthening, and insight – complex lithic reduction procedures such as Levallois, and effective hunting of large mammals, such as the horses at Schöningen (Thieme 1997). The *chaînes opératoires* used by early *Homo sapiens* in lithic reduction were longer and more complex than those of *Homo erectus*; indeed, the technical complexity of Levallois rivals or exceeds that of any later lithic reduction procedures (Wynn & Coolidge 2004). The technique, with all of its flexibility and variations, is difficult to learn, and memory enhancement of sleep would have certainly helped. Our knowledge of hunting techniques is less clear, but if they used intimate knowledge of landscapes, as sites such as Saltzgitter Lebenstedt suggest (Gaudzinski & Roebroeks 2000; Munson & Marean 2003), then enhanced sleep would have been useful here as well, and the empirical evidence by Peigneux et al (2004) supports our contention. This scenario, however, runs afoul of the complex nature of hominid phylogeny in this time period. The best evidence for complex lithic reduction procedures is associated with Neanderthals and their ancestors, who now appear not to have contributed to modern gene pools (eg, Serre et al 2004). Of course, they too could have evolved enhanced sleep. The African evidence does include prepared core techniques of equal complexity, and also evidence for equally complex hunting (Marean 1997), so similar selective pressures would have prevailed for the presumed ancestors of modern humans.

A final possibility is that enhanced sleep only emerged with the appearance of anatomically and behaviourally modern humans sometime after 100,000 years ago. Certainly modern voyaging abilities, as suggested by the early colonisation of Australia, would take advantage of spatial memory consolidation and enhancement, as would the long technical action chains involved in manufacture of bone and antler armatures. Moreover, it is not until very late (30 Ka or so) that the archaeological record supplies examples of representations of super-natural or dream creatures, such as the lion-headed figurines from Hohlenstein Stadel and Hohle Fels cave. Lewis-Williams (2002) recently proposed that parietal art and artistic abilities of the Upper Palaeolithic might have been stimulated by trances and hallucinatory visions that were induced by hallucinogens in plants. There is a complete lack of evidence for those particular plants (those containing mescaline, lysergic diethylamid acid, or psilocybine) in areas containing cave art (Helvenston & Bahn 2003), so it seems to be a more reasonable hypothesis that the geometric and other figures of cave art could have been inspired by other more mundane states of consciousness, including hypnotic states, sensory deprivation, extreme boredom (freshmen in lectures again), deep relaxation, auras preceding migraine headaches and epileptic seizures, day-dreaming, and, of course, dreams during sleep. However, this latter development probably does not represent a development in the sleep cycle *per se*. Rather, it more likely represents a development in consciousness and self-reflection that allowed the content of REM images to become available to conscious thought and to be conserved and transmitted across generations.

10 Can this hypothesis be tested?

Our hypothesis is vulnerable to falsification through both sleep research and palaeoanthropological research. If research into sleep and dreaming demonstrates that consolidation of procedural memories is not, in fact, a significant function of slow-wave and REM sleep, then our specific hypothesis concerning a selective advantage *for* ground sleep in *Homo erectus* would be weakened. Similarly, if effective quantitative research on dreaming and creativity reveals that there is no real link, then this part of our argument would be rendered untenable. The palaeoanthropological basis of our argument rests heavily on the evolutionary coincidence of a non-climbing upper body, increase in body size, invasion of new (often treeless) habitats, a significant development in spatial cognition, and the use of fire. If this coincidence turns out not to have been true, eg if new fossil evidence places non-climbing anatomy much earlier than the changes in niche, then our hypothesis will suffer accordingly. Our hypotheses could be strengthened should evidence of managed fire be found closer to the earliest evidence for *Homo erectus*. It might also be strengthened if there was evidence of tools or tool use for the clear purposes of protection and hunting (hafting, spears, etc). Evidence for permanent or semi-permanent shelters and increased group size (both anti-predator adaptations) might also help our arguments, albeit weaker cases.

11 Conclusions

After the transition to complete ground sleep, hominids may have spent up to 33% of their total existence in sleep, about 9% of their total lives in REM sleep, and about 13% in slow-wave and REM sleep. If problem-solving, learning, and memory consolidation persist throughout waking and sleep (which appears likely), and dreaming provides for novel connections between ideas (for which there is overwhelming anecdotal evidence and some empirical evidence), it is possible that some sleep-linked innovative developments appeared as early as the period between 2 million and 1.5 million years ago. For example, Wynn (2002) noted that there is little evidence for transitional forms between Oldowan and Acheulean stone tools. Mode 2 tools (bifaces) appear rather suddenly as if in a punctuated event. In fact, there are some indications that they may have occurred as the result of a creative burst. Could it be that the idea for the imposition of symmetry came as the result of a dream in a sleeping hominid? Could it be that the neural mechanisms and structures were already in place by the time of the creation of Mode 2 tools and all that was required was the right dream? Could an expert *Homo erectus* stone tool knapper have been perplexed by the lack of large, sharp cutting tools? Did his or her answer come in a dream? It is more difficult to imagine that Mode 2 technology was not aided by sleep and dreams and was restricted to wakeful states alone.

In summary, enhanced sleep, and perhaps Stage 2, 4, and REM, may have played important roles in hominid evolution. First, changes in the quantity and/or quality of dream sleep, which may have included simulated threatening waking experiences and virtual interpersonal interactions, may have better prepared individuals for the actual events. Indeed, with the transition to ground sleep, incipient dynamic sleep changes may have been consolidated and enhanced as a response to increased risks of predation, thus, the value of threat rehearsal in REM sleep and the greater vigilance during Stage 2 may have cemented the evolution of the present sleep architecture. Second, abundant anecdotal evidence – and recent empirical evidence – suggests that sleep and dreams may provide unique and creative solutions that might otherwise not be provided, or aid the solutions to problems that arise while waking and are better reflected during sleep by dreams. Third, the neurochemical nature of the sleep stages and their sequences may have aided the consolidation and/or enhancement of procedural memories, and there is currently strong empirical evidence for the enhancement by sleep of visual-spatial and motoric procedural memories. The sudden appearance of Mode 2 tools and the clear ability of *Homo erectus* to explore and invade new territories undoubtedly were instigated by some biological, genetic, or environmental factors. Why could it not be that some might have occurred as a direct consequence of the enhancement of sleep and dreams during the tree-to-ground sleep transition?

Author Note

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