
Chapter 7

Did a Small but Significant Enhancement in Working-memory Capacity Power the Evolution of Modern Thinking?

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Introduction

Consider the following:

- complex goal-directed actions;
- flexibility in problem solving;
- innovative solutions to problems;
- analogical reasoning;
- planning over long distances or time.

If these abilities seem familiar it is because they often appear in the anthropological literature on the evolution of the modern human mind. But these are, in fact, a list of 'executive functions', a set of cognitive abilities that psychologists have long associated with the highest levels of human cognition, and which they have also linked to the frontal lobes of the brain. It should not be a surprise that palaeoanthropologists interested in the final stages of human cognitive evolution should refer to a set of abilities that psychologists have also identified as the highest levels of thinking. But what is a surprise is that palaeoanthropologists have rarely turned to this literature to help resolve puzzles in their quest. Since beginning collaboration in 2001, this is precisely the path we have taken, and it has led to a powerful, and also controversial, hypothesis that posits a relatively recent enhancement in human working memory capacity. We are not the first to have identified a potential role for working memory in human evolution (Russell 1996), but we believe that we are the first to give it serious consideration that includes examination of the palaeoanthropological record.

Working memory

Working memory is a theoretical construct initially proposed in 1974 by Alan Baddeley to explain certain kinds of experimental results in human memory research (Baddeley & Hitch 1974). A classic example of a working memory problem is the 'reading-span'

test. A subject is asked to read a series of 14–16 word sentences, and asked to remember the final word of each sentence. The maximum number of final words remembered is the subject's reading span. This test reveals several of the important components of working memory. First, there is a processing component (reading) and a memory component (terminal words); the test is not simply a short-term memory test. But performance on the reading-span test also requires an ability to perform in the presence of distraction, and this is clearly a matter of attention, not storage. The essence of working memory is the capacity an individual has to hold and manipulate information in active attention. Working memory is much more than recall. It is, in a real sense, what one can 'hold in mind' *and* process at the same time. This attentional component clearly distinguishes working memory from simple measures of recall. Indeed, Baddeley himself has recently opined that a better label would have been working attention (Baddeley 2001). The emphasis on attention is clear in all recent treatments of working memory.

To reiterate ... we argue that working memory reflects the capacity for attention control, which is critical for tasks that demand maintenance of task-relevant information (Hambrick *et al.* 2005).

As currently conceived, working memory is a multi-component cognitive system (see Fig. 7.1) made up of a central executive (with a processing sub-unit and a temporary store of information) and two 'slave' systems, an articulatory loop and a visuospatial sketchpad. Experimental results indicated that subjects could hold and process more information if it included spatial *and* verbal tasks, than if the test contained only multiple verbal tasks or multiple spatial tasks. The two domains appeared to tap separate cognitive resources that did not interfere with one another. One of the best-

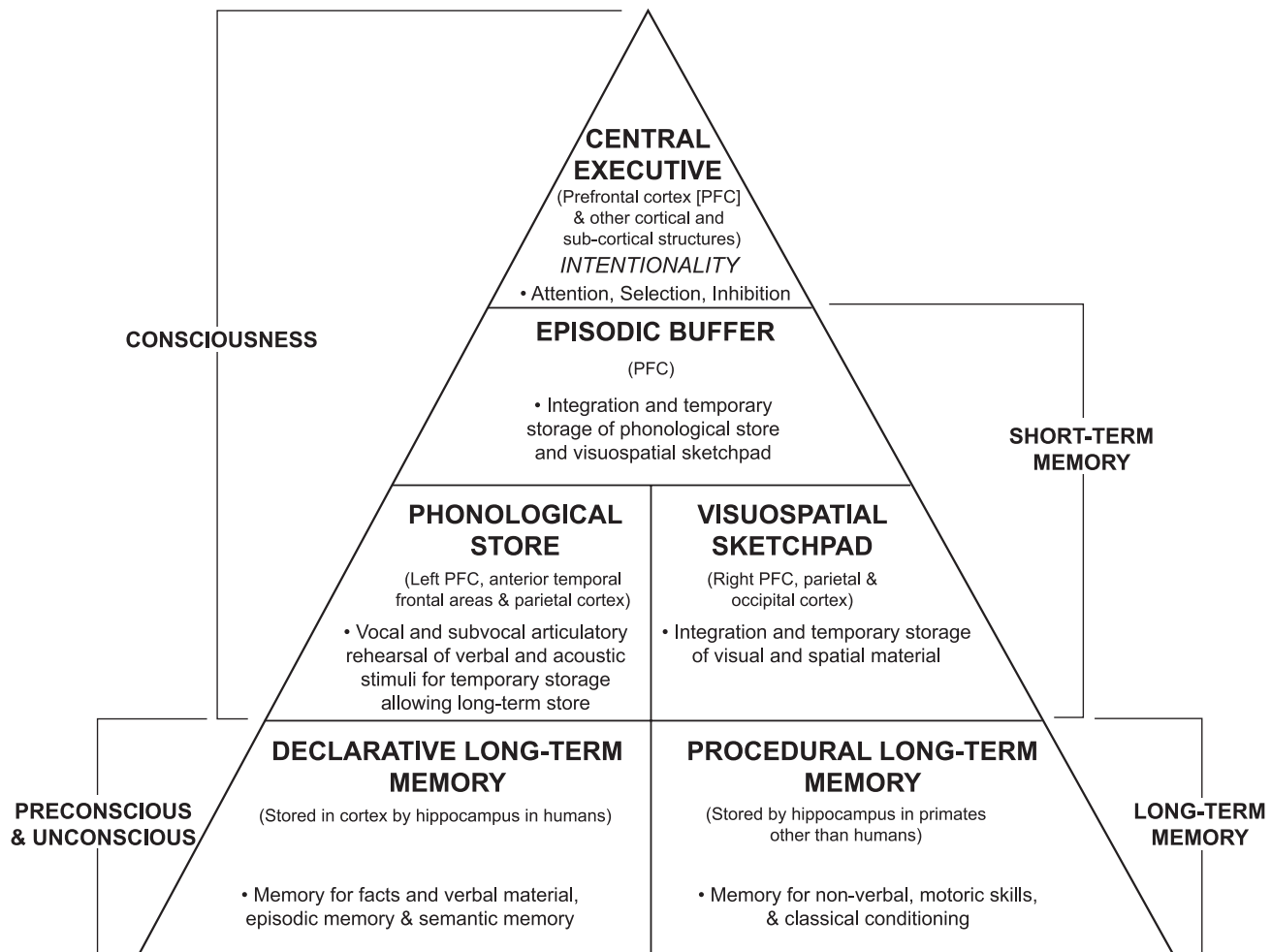


Figure 7.1. *Caption?*

documented sub-systems of working memory is the articulatory loop, which includes a short-term store for words and a rehearsal mechanism for maintaining a list of words in active attention. The existence of a comparable 'image' store in visuospatial sketchpad is not as clearly documented, and indeed the 'boundary' between visuospatial sketchpad and the central executive is not as well understood.

Neuropsychological and brain-imaging research indicates that working memory is largely a frontal-lobe neural network, with significant links to parietal and temporal lobes. The dorsolateral pre-frontal circuit is generally associated with the classic executive functions, i.e. complex problem-solving, decision-making, verbal fluency, and some of the operations of working memory. The orbito-frontal prefrontal region is more closely connected to the limbic system and is associated with the processing of emotions and the regulation of social behaviour and social interactions. Both systems are closely connected, and the pre-frontal cortex in general has extensive projections to almost all regions

of the temporal and parietal lobes, some projections to the occipital lobe, and to sub-cortical structures such as the basal ganglia, the cerebellum, and many brainstem nuclei. The gist of these interrelationships appears to be that the prefrontal cortex coordinates 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).

Modern humans express considerable within-population variability in working-memory performance. Kane & Engle (2002) and others (Kyllonen 1996) have provided support that individual differences in working memory capacity may be related to general intelligence (also known as Spearman's *g*) and more specifically, fluid intelligence (Cattell's *gF*). Citing the work of Kyllonen & Christal (1990), they note a strong positive correlation (.90) between working memory and *gF* (Hambrick *et al.* 2005). This latter aspect of intelligence is thought to be the ability to solve novel problems and depends less on schooling

and acculturation (than crystallized intelligence, *gC*, which is more dependent on formal schooling and acculturation). They also note that working-memory capacity (or central-executive attention) is a domain-free process or mechanism. This implies that any specific task would require the use of some domain-specific stimuli, processing, and skills in conjunction with working-memory capacity. Thus, no single neuropsychological measure can exclusively capture the executive component of working-memory capacity, and each test or battery of tests would tap both the domain-free working-memory capacity and the domain-specific skill required.

The evolution of working memory

Comparative research with non-human primates indicates that human working-memory capacity significantly exceeds that of even our nearest relative (Matsuzawa 2001). It is clearly one of the cognitive developments that accompanied human evolution. As palaeoanthropologists we are faced with three questions:

1. When did significant developments occur?
2. In what evolutionary context did they occur?
3. Why?

We suspect that working-memory capacity is a theme that could be followed through the course of human evolution. We have chosen, initially at least, to examine the palaeoanthropological evidence for the final step in that evolution — the enhancement of working memory that enabled modern thinking and problem solving. We do not think that this final enhancement need have been dramatic, or that more archaic varieties of *Homo sapiens* were simpletons (see our characterization of Neanderthals — for example Wynn & Coolidge 2004). Instead, we suggest that a small but significant enhancement of working memory yielded profound long-term advantages for populations that possessed this characteristic in significant frequencies.

The major hurdles to applying a working-memory model to the palaeoanthropological record are methodological. Given working memory's basis in a reorganized neural network, it is unlikely that the fossil record will be much help. The enhancement of working memory was a change in degree; modern *Homo sapiens* exhibit a greater working-memory capacity than *Homo erectus*, and probably even archaic members of the species. However, there is no known connection between working memory and encephalization, and the neural changes associated with enhanced working memory leave no recognizable landmarks on the gross anatomy of the brain, so even a superbly-preserved endocast would fail to reveal enhanced working memory. This leaves the archaeologi-

cal record. Archaeological evidence for enhancement of working memory comes primarily from evidence of the executive functions it enables. The methodological task of the archaeologist is to identify patterns in the archaeological record that could not have been generated without enhanced working memory. This is a two-step task. It is first necessary to identify executive functions (the behavioural manifestations of enhanced working memory) that might yield tangible clues in the archaeological remains. The following strike us as the most likely candidates:

- group contingency planning;
- temporally and spatially remote action;
- innovative plans of action;
- cultural algorithms;
- analogical thinking;
- response inhibition.

The second step is to identify specific archaeological signatures of these executive functions. Unfortunately, the vast majority of the archaeological record documents mundane, everyday activities that rarely, if ever, taxed the working-memory capacity of our ancestors. Gathering food, making and maintaining tools, using fire, and so on, can all be accomplished with routine plans of action and procedural memory. But the record is not entirely mute. Some technologies, and some foraging systems, required modern executive functions. We have assembled the following list based on two requirements: 1) the pattern must have been generated by behaviour that required enhanced working memory; and 2) the pattern must be reliably documented in the archaeological record. The list is relatively short (see Table 7.1).

Note first that this list omits many of the items that have traditionally been used to document modern thinking (beads, for example). This is because the items do not meet the two requirements for membership (more on beads later). But more important, the list points to a very late date for the emergence of modern EWM; indeed, we cannot make a truly compelling case for EWM prior to about 28,000 years ago (Coolidge & Wynn 2005). As few discussions of the evolution of the modern mind invoke such a late date, we are left with a conundrum. There are three possible solutions:

1. Absence of evidence is not evidence of absence. The archaeological record is either too poor, or of the wrong things, to document enhanced working memory reliably, and its apparent late appearance reflects differential preservation more than evolutionary developments.
2. Enhanced working memory appeared with the first anatomically modern humans, and enabled progressive cultural change. Owing to the ratchet effect, innovative cultural developments were at

Table 7.1. *Caption?*

Archaeological signature	Executive function required	Strict standard less strict (?)
Facilities (Oswalt 1976)	<ul style="list-style-type: none"> • Spatially remote action • Group contingency planning 	European Mesolithic (10 kya) North American Archaic
Reliable technologies (Bleed 1986)	<ul style="list-style-type: none"> • Remote action • Group contingency planning (?) 	Magdalenian harpoons (17 kya) Katanda bone points (?)
Calculating devices (d'Errico 2001; Marshack 1991)	<ul style="list-style-type: none"> • Analogical thinking • Cultural algorithms 	Iberian Epipalaeolithic (14 kya) Aurignacian (?)
Storage (Soffer 1989)	<ul style="list-style-type: none"> • Temporally remote action • Response inhibition 	Late Upper Palaeolithic on Russian Plain (20 kya)
Managed (complex) foraging (Deacon 1993; Straus 1996)	<ul style="list-style-type: none"> • Group contingency planning • Response inhibition 	Late Upper Palaeolithic reindeer hunting (20 kya) Corm use in South African Late Stone Age (?)
Colonization of oceanic islands (Rabett & Barker this volume)	<ul style="list-style-type: none"> • Group contingency planning 	Buka (28 kya) Sahul (?)

first few and far between, but the pace quickened toward the end of the Pleistocene.

3. The archaeological record is accurate. Enhanced working memory evolved late in human in evolution, and powered the dramatic developments in human culture that emerge after 50,000 years ago.

It is possible that our standards are too strict. If we relax them only slightly to include all bone armatures as reliable technologies, and bead use as evidence of a kind of remote action (see below), then we can push the earliest evidence back to the time of Blombos cave. Note that this still does not allow us to choose confidently between options no. 2 and 3, though the increasingly early dates for modern anatomy (195,000 kya at Omo Kibish: see Shea this volume) still incline us toward option no. 3.

Advantages of the enhanced working-memory hypothesis

The current hypothesis of an enhancement of working memory has several advantages over alternative hypotheses concerning the emergence of the modern mind:

1. Working memory has been extensively investigated and has voluminous experimental support (e.g. Baddeley 1993; 2000; 2001; Baddeley & Logie 1999; Kane & Engle 2000; 2002; Miyake & Shah 1999).
2. Working memory has been shown to have a strong correlation with the 'g' of general intelligence as measured by intelligence tests (e.g. Kyllonen 1996).
3. Working memory has clearly established implications for language (more on this below) (e.g. Baddeley *et al.* 1998; Becker *et al.* 1999; Gathercole *et al.* 2004; Gupta 2003).
4. Working-memory capacity can be linked to innovation (Shepard 1997).
5. Working memory has integrated the vast literature on executive functions of the frontal lobes (e.g. Luria 1966; Lezak 1992; **Not in refs 1982?**; 1995) by subsuming these functions into the 'central executive' com-

ponent of Baddeley's working-memory model (e.g. Coolidge & Wynn 2001; 2005; Goldberg 2002).

6. The power of the theory, and the variety of experimental conditions in which it has been applied, make it a good source from which to generate archaeologically visible attributes (Wynn & Coolidge 2003; 2004).

Challenges

Reactions to the hypothesis have ranged from dismissive to lukewarm to enthusiastic. In anonymous reviews, two criticisms have been raised repeatedly. First, enhanced working memory could not possibly have resulted from a simple genetic change and, second, our hypothesis under-values the importance of language and symbol use. We address these issues below.

A simple genetic change

We have proposed that a relatively simple genetic mutation about 100,000 years ago (more or less), probably in general working-memory capacity or one of its subsystems, was the final evolutionary development that modernized the human mind. We are not the first to propose a genetic mutation as the cause of modern thinking. Mithen (1996) proposed that a genetic mutation may have led to a neural reorganization beginning about 100,000 years ago and ending about 30,000 years ago. This neural reorganization, whose substrate he did not specify, occurred without an increase in brain size yet resulted in 'cognitive fluidity', a seamless blending of various aspects of intelligence and knowledge. Klein & Edgar (2002) also proposed a sudden neural change about 50,000 years ago that promoted the modern human ability to innovate, and they also hinted that one essential aspect of this change might have been the ability to produce and comprehend rapidly spoken phonemic language. Yet the critics of the genetic change hypothesis have not been kind.

The essential argument against the genetic-change hypothesis is that a single gene mutation could not possibly result in a major reorganization of the brain. We too would argue vehemently against a single gene hypothesis. We believe that part of the problem with the popular understanding of genetic transmission and mutations is that for decades students have been introduced to genes and the processes of heredity through only two Mendelian forms, dominant and recessive gene transmission. The former involves a single dominant gene, usually mutated through a transcription error, which expresses itself without consequence of its allele on its paired chromosome. The second classically taught method of gene transmission involves a pair of genes, which can express themselves only when paired with a complimentary allele. Over 2000 diseases and syndromes, many associated with central nervous system dysfunction such as Huntington's chorea, have been identified as being caused by a single dominant gene. Over 1500 diseases and syndromes have been identified as being caused by a pair of recessive genes and many of these problems also affect the central nervous system. Inherent in these two Mendelian forms is the assumption that one gene codes only one protein but we will deal with that flawed hypothesis later. However, neglected in this introductory gene education is the fact that perhaps over 100,000 to perhaps 1,000,000 behavioural traits and complex behaviours such as intelligence and even political orientation, and behavioural disorders such as Attention-Deficit Hyperactivity Disorder, are caused by neither of these two forms but are caused by groups of genes. The latter form of genetic transmission is known as *polygenic* or *additive genetic transmission*.

Among modern behaviour geneticists, it is even standard thought to accept that perhaps little or no complex human behaviour is without some additive genetic influence (e.g. Pinker 2002; Turkheimer 2000). Thus, we are not arguing that some single dominant gene somehow miraculously reorganized the human brain. One possibility for our concept of enhanced working memory is that it was created through the very common process of genetic mutation, by which nearly all modern human and animal behaviour was created (at least indirectly, since natural selection acts on variations in behaviour as a result of genetic transcription errors). However, we are not arguing that it was single dominant genetic mutation but that it may have been a *single additive genetic mutation* that somehow influenced working-memory capacity.

For example, a plethora of genes is undoubtedly responsible for working memory and its subsystems, yet its *capacity* theoretically can be modified by a single *additive* genetic mutation. The human nose is undoubt-

edly created by a confluence of a number of genes; however, the length of one's nose can theoretically be controlled by a single additive genetic influence.

Our argument would be strengthened if (1) there was evidence for the polygenic basis of working memory (or its components), and (2) if there was any recent evidence of genetic influences, polygenic or otherwise, upon the central nervous system, and more specifically upon cognitive abilities or language. With regard to the first, there is strong evidence for the polygenic basis of working memory. Recent genetic studies have also shown that working memory's components have a highly heritable basis, even greater than for general intelligence (e.g. 45 per cent to 50 per cent) whose genetic contributions are now accepted as substantial. Coolidge *et al.* (2000), in a study of child and adolescent twins, found that a core of functions consisting of planning, organizing, and goal attainment of the central executive component of working memory, was highly heritable (77 per cent) and the core functions were found to be 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 per cent to 56 per cent, and polygenic (Rijsdijk *et al.* 2002; Ando *et al.* 2002). Additionally, Ando *et al.* found their measures of executive functions and visual spatial storage were also heritable (37 per cent to 57 per cent). Hansell *et al.* (2001), using event-related potential slow wave measures of working memory in a visual-spatial delayed-response task, showed strong heritability (35 per cent to 52 per cent) in a sample of 391 adolescent twin pairs.

Our argument would also be strengthened by evidence of a gene that would affect cognitive functioning. Certainly, there are dramatic and undeniable examples of genetic influences that profoundly affect cognitive functioning, such as Down's syndrome and Huntington's chorea. Alzheimer's disease also has been shown to have a polygenic basis, and schizophrenia is strongly suspected of having a complex genetic basis. However, there is tantalizing new evidence for a single gene basis (1) for speech and language production and discrimination, and for (2) rapid brain encephalization.

The single gene basis for speech and language comes from the work of Lai and colleagues (2000; 2001). Studies of twins have consistently demonstrated the heritable basis of many speech and language disorders (e.g. Bishop *et al.* 1995; Tomblin & Buckwalter 1998; Dale *et al.* 1998). Lai and colleagues have identified a single fork-head domain gene, known as *FOXP2*, which appears to affect the normal developmental processes in speech and language.

They identified the gene in a family who had severe disruptions in orofacial abilities related to articulation, phoneme production and discrimination, and grammatical problems such as word inflection difficulties and syntax. Their work is not definitive evidence for single gene influences upon speech, language, and grammar, as the gene may actually influence more general processes upon which speech and language are predicated. However, it may serve as preliminary if not tenuous evidence that specific cognitive abilities may not only be disrupted but perhaps enhanced by a single additive gene influence.

A single gene basis was also recently found for rapid brain encephalization. A single gene, *Microcephalin*, had already been known to cause microcephaly, which results in a dramatic reduction in brain size and concomitant mental retardation, although remarkably a preservation of normal but overt brain structures (Evans *et al.* 2004; Ferland *et al.* 2004). The latter observations have led to the hypothesis that the brains of microcephaly patients actually function normally except for their size (e.g. Dobyns 2002; Woods *et al.* 2005), although it does appear that the cerebral cortex in these patients may be smaller relative to other brain structures (e.g. Jackson *et al.* 2002). Following upon the hypothesis that *Microcephalin* may be a critical regulator of brain size in evolution, Evans *et al.* (2005) investigated whether positive selection has acted upon a high-frequency haplotype (49) for the *Microcephalin* locus on chromosome 8p23. Through gene sequencing and chromosomal analysis of 89 individuals broadly representing human diversity, it was concluded that haplotype 49 was found to emerge from a single copy to high frequency in a short period of time and that minor variants of the haplotype emerged through recombinations and rare mutations (haplotype 49 and its variants were then labelled haplogroup D). The estimated coalescence age for the haplogroup D was 37,000 years (95 per cent confidence interval: 4000 to 60,000 years). The authors concluded that it appears that positive selection has acted upon a specific function of *Microcephalin* in the evolution of brain development, and perhaps that it may act upon the proliferation of neurogenitor cells, 'which in turns leads to different phenotypic outcomes of the brain visible to selection' (Evans *et al.* 2005?, 1720). They also noted that there is still the possibility that there may be an unrecognized function of *Microcephalin* that is actually the substrate of selection. Among an array of possibilities for a brain-related phenotype of *Microcephalin* upon which selection could have acted, they suggested cognition and personality. Of course, we would propose that these two possibilities are probable and not necessarily mutually exclusive. For

example, it has been recently shown that a specific cognitive deficit (i.e. executive dysfunction of the frontal lobes) shares a bivariate heritability with specific personality disorders (Coolidge *et al.* 2004).

Another speculative basis for our genetic change hypothesis comes from another non-Mendelian method of genetic transmission and inheritance. When the human genome was finally sequenced, scientists were somewhat surprised to find that there as few as 25,000 genes instead of the suspected 100,000 to 150,000. How could the great complexity of human behaviour be controlled by a few as 25,000 genes? Recently the genome for rice was sequenced (International Rice Genome Sequencing Project 2005), and where as rice has only 12 chromosomes compared to our 23, rice appeared to have about 37,000 genes. A common variety of rice has more genes than humans? We already knew that behavioural complexity was not related to the number of chromosome pairs as chimpanzees have 24, alligators have 32, and dogs have 39. To make up for this superficial anomaly, it was suspected that human chromosomes simply carried more genetic information, in the form of a greater number of genes. With the sequencing of the human gene, however, it quickly became apparent that even this hypothesis was inadequate, and there have been two major new trends in genetics as a consequence: 1) one gene must code more than one protein; and 2) there must be non-Mendelian and non-DNA forms of genetic transmission.

Both of these conclusions have recently received strong empirical support. With regard to the failed 'one gene, one-protein' hypothesis, it was partially predicated on the backward reasoning that if humans coded about 90,000 different types of proteins, there must be at least that many unique genes. Geneticists soon recognized that through a well-known process called alternative splicing (e.g. Ast 2004; Graveley 2001; Nissim-Rafinia & Kerem 2002), human genes allow a minimal number of protein-coding genes to code a much larger number of different proteins. The process also explained how such great diversity can exist among organisms with very similar core gene sets. Alternative splicing had been considered a rare phenomenon and now is thought to be not only common but crucial to the evolution of behavioural complexity.

Geneticists also turned their attention to the previous thought to be 'silent' or 'junk' DNA. These were the long strands of DNA that did not appear to code proteins. However, it is now recognized that these silent strands do give rise to active RNA, which can also profoundly affect the behaviour of normal genes. However, a third form of genetic inheritance became even more compelling: a separate genetic code was

being transcribed outside a DNA sequence. This new field of interest, called *epigenetics*, may help to explain why some genetic diseases skip generations and why identical twins can have different characteristics and vulnerabilities. The epigenetic forms are themselves just being understood but it now appears that just as protein-encoding genes matter, so do non-coding DNA, RNA that lies outside non-coding DNA strands, and chromatin, a filament-like structure that supports DNA but also controls access to it. Even the shape of the chromatin appears to have a role in genetic transmission (e.g. Beck & Olek 2003; Felsenfeld & Groudine 2003; Georges *et al.* 2003).

Thus, the old tired mantra, 'modern human behaviour cannot be due to a single *dominant* gene mutation' has some grain of truth to it. However, there are still many vaguely understood patterns and forms of genetic transmission that could support our enhanced working-memory hypothesis. At some point, genetic transmission critics must also own up to the fact that at some place in time, there were demonstrable behavioural and neural substrate differences between ancient human types and moderns. The likelihood that some form of genetic transmission changed human potential now appears not only possible but highly probable. Also, it is important to recognize that all complex human behaviour has arisen as a result of positive selection upon a background of genetic mutations. There would be no evolutionary change without them.

Symbolic ability

There appears to be a general consensus among palaeo-anthropologists that the ascendancy of modern human behaviour was somehow tied to symbol use. And many, perhaps most, now think that symbol use was a cognitive development as much as, or even instead of, a cultural development. However, advocates of a cognitive/symbolic root to modern behaviour rarely specify exactly what cognitive ability is responsible. To be sure, there are references to language, symbolic mediation, and social marking, but these are little more than assertions that modern minds generate modern behaviour. They are cognitive arguments in only a very general sense.

We aver that it is not only possible, but necessary, for palaeoanthropologists to apply more sophisticated models. Our particular approach has been to explore the implications of a working-memory model for modern thinking. We do not pretend that working memory is the only component of modern thinking. However, we do maintain that it is a very important component and, moreover, that it can explain much that has often been loosely attributed to symbol use. Of course, it will

not do simply to reject or ignore the symbolic argument. Instead, the working-memory model must be explicit about its implications for symbolic systems, language, and social interaction.

Davidson and Noble

At the outset, it is necessary to critique the best developed archaeologically-based theory for the evolution of symbolic behaviour — that of Iain Davidson and William Noble (D&N) (Davidson 2002; Davidson & Noble 1989; 1993; Noble & Davidson 1996). Unlike most archaeological discussions of symbol use, D&N derive specific predictions about archaeological evidence from an explicit theoretical stance. Their understanding of the nature of symbols and cognition is derived primarily from the ecological psychology of James Gibson and the social constructionism of Wittgenstein. In a nutshell (and we risk caricaturing a lengthy argument) D&N argue that true symbol use cannot occur unless the sign can be the subject of reflection, that is, the user must be aware of the arbitrariness and meaningfulness of the sign-referent link (from this perspective vervet calls do not qualify as symbols). However, such awareness can only come from interaction with the environment, natural and social; the mind does not come structured in this way. Though D&N acknowledge the necessity of a neural substrate, they do not consider its structure, if any, to be relevant. For true arbitrary symbol use to arise, it must develop from iconicity. This has important implications for archaeology. Iconicity, in the form of depiction, must precede true symbol use. Moreover, any intentional imposition of shape requires the same kind of minded reflection that is the basis of symbol use. From this perspective the intentional markings from Blombos cave are the earliest direct evidence of true symbolic mindedness.

D&N's argument is a strong one because it lays out an explicit theory of mind and symbol use, from which it derives testable predictions about the palaeo-anthropological record. As such, it is refreshingly open to criticism. We believe their argument fails on two levels — theoretical and evidential. Detailed exegesis of D&N's theoretical position is beyond the scope of this paper, but one basic philosophical point is relevant. Their conception of cognition is very much a minority position in cognitive science (which of course does not mean it is wrong). Rather than embrace the huge strides in the understanding of the structure and organization of the brain that have occurred over the last thirty years, they eschew the topic almost entirely. Instead, they favour a position close to that of the empiricism of Locke and the behaviourists. However, recent research in the brain sciences has clearly docu-

mented that the mind is not a blank slate; the brain has a structure, and this structure limits and organizes behaviour. Yes, cognitive neuroscience has a long way to go before this structure is fully understood, but only a minority of practitioners continues to maintain that experience is paramount and neural structure irrelevant. D&N also fall down when it comes to the archaeological record. They specifically exclude any possibility that prehistoric artisans could impose form on artefacts prior to the appearance of mindedness and symbolic thought, the earliest evidence of which they now place at Blombos. Accordingly, no earlier artefacts can possess an intended shape, including Acheulean hand axes. Although they continue to go to great lengths to argue that hand-axe shapes were accidental, the evidence from refitting, replication studies, and site frequency and distribution analyses is against them. While it is not necessary that handaxe makers had ‘mental templates’, it is necessary that they attended to shape. If we accept D&N’s theoretical position, then the hand-axe makers must have had symbolic thought, and few palaeoanthropologists appear willing to extend modern symbolic thinking back one million years. It is to their credit that D&N developed a theory that produced falsifiable predictions; few archaeological treatments of symbolism are so blessed. In their case, it seems to us, the evidence has effectively falsified their position.

Language

Cognitive scientists and linguists are now in general agreement that language is a complex communication system that is based in multiple neural systems or networks. There is considerable disagreement about how many discrete components there are, which is most important, and how they relate structurally, functionally, and developmentally to other neural systems but, despite identification of genes such as the *FOXP*, few if any neuro-linguists believe that language as a whole is simply inherited. However, individual components may be simply inherited, and we contend that working memory is one of these. But how does working memory relate to other neuro-linguistic components, and what effect would enhancement of working memory have on language as a whole?

Even the lumpiest neural models for language distinguish between a lexical component and a grammar component. The lexicon is the store of words, words being the primary components in the sound-meaning linkage in linguistic communication. The linkage of an arbitrary sound to a referent is not a particularly difficult cognitive task. Psychologists have successfully taught arbitrary reference to a range of non-humans, the most well-known being those of the

ape language experiments. Of course, human words are more than simply arbitrary names for things or actions. They are generated by rules of morphology and phonology, and indeed often act as grammatical markers rather than straight forward symbols (e.g. determinants such as ‘the’). Chimpanzees can acquire some of this, but very far from all of it (they don’t use determinants, for example). Much of this complexity arises from the overlap between words and grammar. Non-humans are best at the simple word part, though even here there is a big difference in degree. Human adults master 30–60,000 words; the best chimpanzee uses maybe 300. This expanded lexical capacity almost certainly has a neural substrate. Most neuropsychological and brain-imaging data point to the long-term memory structures of the parietal and temporal lobes as the primary loci of the lexical store. Because of this, an expansion of the lexical store is not a good candidate for the source of the modern brain, which seems largely to be a frontal lobe phenomenon.

Enhancement of working memory would have little effect on lexical capacity. Working-memory processes chunks from the lexical store, but is not itself part of the store. The phonological store of working memory is, instead, the number of words that can be held in attention. But even this is affected by other components of the language faculty. The phonological store has a greater capacity for meaningful words than nonsense words, and a greater capacity for grammatically correct sentences than random strings of words. Interestingly, this phenomenon is similar to expert performance in other cognitive domains. In expert performance, working memory accesses ‘cue structures’ that organize long chunks of content. These cue structures are stored in long-term memory, and this link between working memory and long-term memory has interesting implications for archaic language. We know that archaic humans, including Neanderthals, deployed expert performance systems as complex as any used by palaeotechnic modern humans. The cognitive bases of such expert performance almost certainly lay in the same long-term memory structures that underpin the lexical store. Archaic language may well have been based on a large corpus of words and phrases, held in long-term memory like the cue structures of expert performance. They would have been flexible, but not innovative; they would have lacked the generativity of grammatical language. They could have referred to the past and the future, but in a limited way. This account resembles, of course, Bickerton’s (1998) description of proto-language.

An enhancement of working memory would have had a significant impact on the grammatical component of the language faculty. Indeed, the im-

pact of an expanded working memory on grammar and syntax is far easier to specify than the impact of grammar on problem solving. Recall that at the behavioural level working memory is the amount of information held in and manipulated by attention. An enhancement of working memory would increase the sheer number of words, or phrases if the phrases could be remembered and held as chunks, available for processing. This alone would provide the potential for increased complexity in communication, a fact appreciated by most linguists. Hauser and colleagues (2002) agree with this general conclusion, even though they do not include working memory within their umbrella group of cognitive processes the term 'faculty of language — broad sense'.

For example, lung capacity imposes limits on the length of actual spoken sentences, whereas working memory imposes limits on the complexity of sentences if they are to be understandable (Hauser *et al.* 2002, 1571).

But what about the 'faculty of language — narrow sense' (FLN), to use Hauser *et al.*'s term? We do not think that working memory and FLN are the same, or even draw on the same neural structures. However, working memory will affect how the FLN is actuated. As an example of the effect of working memory on the complexity of utterances produced by FLN, we cite recursion, a feature of grammar that many, including Chomsky, argue is the key development in the evolution of grammar. 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 working memory. The number of recursions must be held and processed in attention if they are to be understood. 'He said that she said that they said that we said that I said that George W. Bush is a true Texan', is a grammatically-correct sentence, but one that just about exhausts the capacity of working memory to analyse. Add two more levels of recursion and few native speakers could keep track. The syntactical rule, the FLN feature, has not changed, but the sheer size of the task has. Perhaps the simplest interpretation of the effect enhanced working memory had on linguistic communication is to conclude that it enlarged the recursive capacity of language. An enhancement of working memory would yield immediate results in the length and complexity of sentences.

It is, of course, also possible to argue that many of the short-hand mechanisms of grammar — e.g.

gender or case marking — arose as a way to bypass the natural limits of working memory. Grammar enables speakers to encode more information in fewer words; indeed in many languages verb inflections can carry a tremendous amount of relevant information — person, tense, mode, transitivity, etc. It is this productivity and efficiency that has always made language such a unique and powerful communication system. So isn't it rash to claim that working memory, which has clear antecedents in mammalian cognition, should have equal billing in our understanding of the evolution of the modern mind? We think that it is not rash, and indeed contend that an enhancement of working memory is a better hypothesis than an enhancement of grammar for understanding the final step to modern cognition. Our major reason for this conclusion is that working memory encompasses more than just the production and decoding of utterances. It is the cognitive locus of immediate problem-solving, and much of this is non-verbal. Perhaps the most important non-verbal component is visuospatial, where shape and location information is held for processing. Much that we term 'creative' thought is based on the processing of images. And it is the central executive that processes all of this information, enabling such critical analytical procedures as analogy and thought experiment. These are not functions of the FLN, or even the phonological store. They are functions of the central executive alone. In sum, the implications of an expanded working memory for language are fairly clear. The effects of an enhanced grammatical ability would not be nearly as far reaching.

There is more to symbolism than language. In fact, many of the arguments for the evolution of modernity cite symbolism in general, or symbolic culture, as being the important factor. These arguments tend to be less specific than the arguments for language or speech simply because linguistics is a more formally developed discipline than symbolic anthropology, which is the source, acknowledged or not, of much of this argument. Modern human culture is based on symbols. All human action is mediated by symbols to one degree or another, to the extent that it is fair to conclude that human lives are immersed in symbols. The essential role of symbols in human life has been the focus of anthropological research for almost a century, and dominated socio-cultural anthropology in the 1970s and 1980s, when it was eclipsed by the hyper-relativism of post-modernism (which itself was seriously committed to the power of symbols). Beginning in the late 1970s archaeology came to a realization of the critical role that symbols play in directing action, and more important, the symbolic role of material culture. Modern people invest their artefacts with

symbolic meaning beyond their functional roles, and one cannot use artefacts as evidence of past behaviour without taking this into account.

As an extension of this realization Palaeolithic archaeologists began to look for evidence of the evolution of this component of modern life. This research remains today a robust and controversy-filled topic in Palaeolithic studies, especially in regard to the status of Neanderthals, Anatomically Modern Humans, and Behaviourally Modern Humans. Indeed, the emergence of symbolically mediated culture has become the *sine qua non* of modernity. However, this is not itself a *cognitive* argument. With few exceptions, archaeologists who advocate symbolic culture as the litmus test for modernity either do not invoke cognition or do not specify the cognitive structures that enable symbolic culture. Archaeologists remain very muddled about this point, and all too often fall back on assertion rather than argument:

Since syntactical language is the only means of communication bearing a built-in meta-language that permits creation and transmission of other symbolic codes (Aiello 1998), beadwork represents a reliable proxy for the acquisition of language *and fully cognitive abilities* by southern African populations 75,000 years ago (d'Errico *et al.* 2005, 19) [emphasis ours]

The form of this argument comes perilously close to tautology. In modern linguistic culture personal ornaments carry information about the status of the wearer. We have good evidence for beads at Blombos dating to 75,000 years ago. Therefore, fully modern cognition was in place in southern Africa long before the European Upper Palaeolithic. There is a problem here; this argument only works *if* the people at Blombos were modern, which unfortunately is what we want to establish. Of course, much archaeological reasoning suffers from this logical weakness, but this is not really the point we want to make. The presence of beads at Blombos does carry the possibility of symbolic culture (though there are alternative interpretations that do not require a symbolic component: Hodgson 2000; 2003), but one cannot then use this as evidence for modern cognition unless one can specify the cognitive component required. As we have seen, symbolic reference itself is not difficult. So what cognitive ability is required for the invention and maintenance of symbolic culture?

As much as we would like to conclude that enhanced working memory is the answer, we cannot. Certainly the ability to hold more things in mind would open up possibilities for symbolic life, but would not in and of itself force the issue. Yes, enhanced working memory underpins innovation, analogical thinking, and abstraction, but none of these appears sufficient to explain the emergence of symbolic cul-

ture. However, they may account for the appearance in the archaeological record of cultural components often attributed to symbolic culture. The use of beads at Blombos suggests attention to personal identity. At a minimum it suggests that individuals attended to how others saw and understood them. This is true theory of mind ('I know that you know who I am' or possibly even 'I know that you know that I know who I am') and, like recursion in language, depends on attentional capacity and working memory. Note that this does not require that the beads stand for anything at all, but it does require a level of intentionality typical of modern human social interaction. And if these beads did in fact play a role in social marking that was intended for socially remote groups, then it would require enhanced working memory. However, if they simply marked within group status, then it would not. Without greater resolution about spatial and temporal distribution (such as that available for Gravettian figurines, for example), it is impossible yet to eliminate the 'internal marking' possibility for Blombos.

We do not mean to suggest that beads, or ochre, or engraved bones, might not be acceptable bits of evidence for modern behaviour (though we do believe the case has never been made convincingly). However, they cannot stand as evidence for modern *cognition* unless one can specify the cognitive abilities they require. Association with modern humans is not alone a strong enough argument for modern cognition. The record of pigment use and bead production may well document an independent evolution of symbol use. Barham (this volume) has suggested that discussion of the evolution of symbol use be dissociated from assumptions about modernity and cognition. We heartily agree.

Conclusion

At the current state of cognitive science and cognitive archaeology it is probably premature to attempt global explanations for the evolution of mind (Stout 2002). A wiser approach is to tackle more circumscribed abilities whose cognitive and neural bases are better understood. Such a piecemeal approach has disadvantages — it does not yield nice, complete narratives of human evolution — but it has the important advantage of greater reliability. We do not claim that the evolution of working memory is *the* answer. But it was certainly an important component. The problem-solving abilities that are so important to the success of modern humans are not specifically entailed by symbol use or language. They are very much entailed by working memory capacity, and any discussion of the emergence of modern cognition must take this into account.

References

- Aiello, L., 1998. The foundation of human language, in *The Origin and Diversification of Language*, eds. N.G. Jablonski & L. Aiello. San Francisco (CA): California Academy of Sciences, 21–34.
- Ando, J., Y. Ono & M. Wright., 2002. Genetic structure of spatial and verbal working memory. *Behavior Genetics* 31, 615–24.
- Ast, G., 2004. How did alternative splicing evolve? *Nature Reviews Genetics* 5, 773–82.
- Baddeley, A.D., 1993. Working memory or working attention, in *Attention: Selection, Awareness, and Control: a Tribute to Donald Broadbent*, eds. A.D. Baddeley & L. Weiskrantz. Oxford: Oxford University Press, 152–70.
- Baddeley, A.D., 2000. The episodic buffer: a new component of working memory? *Trends in Cognitive Sciences* 4, 417–23.
- Baddeley, A.D., 2001. Is working memory still working? *American Psychologist* 11, 851–64.
- Baddeley, A.D. & G. Hitch, 1974. Working memory, in *Recent Advances in Learning and Motivation*, ed. G.A. Bower. New York (NY): Academic Press, 47–90.
- Baddeley, A.D. & R. Logie, 1999. Working memory: the multiple-component model, in *Models of Working Memory: Mechanisms of Active Maintenance and Executive Control*, eds. A. Miyake & P. Shah. New York (NY): Cambridge University Press, 28–61.
- Baddeley, A., S. Gathercole & C. Papagno, 1998. The phonological loop as a languagelearning device. *Psychological Review* 105, 158–73.
- Beck, S., & A. Olek (eds.), 2003. *The Epigenome: Molecular Hide and Seek*. New York (NY): John Wiley & Sons.
- Becker, J.T., D.K. MacAndrew & J.A. Fiez, 1999. A comment on the functional localization of the phonological storage subsystem of working memory. *Brain and Cognition* 41, 27–38.
- Bickerton, D., 1998. Catastrophic evolution: the case for a single step from protolanguage to full human language, in *Approaches to the Evolution of Language: Social and Cognitive Bases*, eds. J. Hurford, M. Studdert-Kennedy & C. Knight. Cambridge: Cambridge University Press, 341–58.
- Bishop, D.T. North & C. Donlan, 1995. Genetic basis for specific language impairment: evidence from a twin study. *Developmental Medicine Child Neurology* 37, 56–71.
- Bleed, P., 1986. The optimal design of hunting weapons: maintainability or reliability? *American Antiquity* 51(4), 737–47.
- Coolidge, F.L. & T. Wynn, 2001. Executive functions of the frontal lobes and the evolutionary ascendancy of *Homo sapiens*. *Cambridge Archaeological Journal* 11(2), 255–60.
- Coolidge, F.L. & T. Wynn, 2005. Working memory, its executive functions, and the emergence of modern thinking. *Cambridge Archaeological Journal* 15(1), 5–26.
- Coolidge, F.L., L. Thede & S. Young, 2000. Heritability and the comorbidity of ADHD with behavioral disorders and executive function deficits: A preliminary investigation. *Developmental Neuropsychology* 17, 273–87.
- Coolidge, F.L., L. Thede & K.E. Jang, 2004. Are personality disorders psychological manifestations of executive function deficits? *Behavior Genetics* 34, 75–84.
- Dale, P., E. Simonoff, D. Bishop, *et al.*, 1998. Genetic influence on language delay in two-year-old children. *Nature Neuroscience* 1, 324–8.
- Davidson, I., 2002. The finished artefact fallacy: Acheulean hand-axes and language origins, in *The Transition to Language*, ed. A. Wray. Oxford: Oxford University Press, 180–203.
- Davidson, I. & W. Noble, 1989. The archaeology of perception: traces of depiction and language. *Current Anthropology* 30, 125–55.
- Davidson, I. & W. Noble, 1993. Tools and language in human evolution, in *Tools, Language, and Cognition in Human Evolution*, eds. K. Gibson & T. Ingold. Cambridge: Cambridge University Press, 263–88.
- Deacon, H., 1993. Planting an idea: an archaeology of stone age gatherers in South Africa. *South African Archeological Journal* 48, 86–93.
- d’Errico, F., 2001. Memories out of mind: the archaeology of the oldest memory systems, in *In the Mind’s Eye: Multidisciplinary Approaches to the Evolution of Human Cognition*, ed. A. Nowell. Ann Arbor (MI): International Monographs in Prehistory, 39–43.
- d’Errico, F., C. Henshilwood, M. Vanhaeren & V. Niekerk, 2005. *Nassarius kraussianus* shell beads from Blombos Cave: evidence for symbolic behavior in the Middle Stone Age. *Journal of Human Evolution* 48(1), 3–24.
- Dobyns, W.B., 2002. Primary microcephaly: new approaches for an old disorder. *American Journal of Medical Genetics* 112, 315–17.
- Evans, P.D., J.R. Anderson, E.J. Vallender, *et al.*, 2004. Adaptive evolution of ASPM, a major determinant of cerebral cortical size in humans. *Human Molecular Genetics* 13, 489–94.
- Evans, P.D., S. Gilbert, N. Mekel-Bobrov, *et al.*, 2005. *Microcephalin*, a gene regulating brain size, continues to evolve adaptively in humans. *Science* 309, 1717–20.
- Felsenfeld, G. & M.M. Groudine, 2003. Controlling the double helix. *Nature* 421, 448–53.
- Ferland, R.J., W. Eyaid, R.V. Collura, *et al.*, 2004. Abnormal cerebellar development and axonal decussation due to mutations in AHI1 in Joubert syndrome. *Nature Genetics* 36, 1008–13.
- Gathercole, S.E., S.J. Pickering, B. Ambridge & H. Wearing, 2004. The structure of working memory from 4 to 15 years of age. *Developmental Psychology* 40, 177–90.
- Gazzaniga, M.S., R.B. Ivry & G.R. Mangun, 2002. *Cognitive Neuroscience*. 2nd edition. New York (NY): W.W. Norton & Company.
- Georges, M., C. Charlier & N. Cockett, 2003. The callipyge locus: evidence for the *trans* interaction of reciprocally imprinted genes. *Trends in Genetics* 19, 248–52.
- Goldberg, E., 2002. *The Executive Brain: Frontal Lobes and the Civilized Mind*. London: Oxford University Press.
- Graveley, B.R., 2001. Alternative splicing: increasing diversity in the proteomic world. *Trends in Genetics* 17, 100–107.
- Gupta, P., 2003. Examining the relationship between word learning, nonword repetition, and immediate serial

- recall in adults. *The Quarterly Journal of Experimental Psychology* 56A, 1213–36.
- Hambrick, D.Z., M. Kane & R. Engle, 2005. The role of working memory in higher-level cognition: domain-specific versus domain-general perspectives, in *Cognition & Intelligence: Identifying the Mechanisms of the Mind*, eds. R. Sternberg & J. Pretz. Cambridge: Cambridge University Press, 104–21.
- Hansell, N.K., M.J. Wright, G.A. Smith, G.M. Geffen, L.B. Geffen & N.G. Martin, 2001. Genetic influence on ERP slow wave measures of working memory. *Behavior Genetics* 31, 603–14.
- Hauser, M., N. Chomsky & W. Fitch, 2002. The faculty of language: What is it, who has it, and how did it evolve? *Science* 298, 1569–79.
- Hodgson, D., 2000. Art, perception and information processing: an evolutionary perspective. *Rock Art Research* 17, 3–34.
- Hodgson, D., 2003. Primitives in palaeoart and the visual brain: the building-blocks of representation in art and perception. *Rock Art Research* 20, 116–17.
- International Rice Genome Sequencing Project, 2005. The map-based sequence of the rice genome. *Nature* 436, 793–800.
- Jackson, A.P., H. Eastwood, S.M. Bell, *et al.*, 2002. Identification of microcephalin, a protein implicated in determining the size of the human brain. *American Journal of Human Genetics* 71, 36–142.
- Kane, M.J. & R.W. Engle, 2000. Working memory capacity, proactive interference, and divided attention: limits on long-term memory retrieval. *Journal of Experimental Psychology: Learning, Memory, & Cognition* 26, 333–58.
- Kane, M.J., & R.W. Engle, 2002. The role of the prefrontal cortex in working memory capacity, executive attention, and general fluid intelligence: an individual-differences perspective. *Psychonomic Bulletin & Review* 9, 637–71.
- Klein, R.G. & B. Edgar, 2002. *The Dawn of Human Culture*. New York (NY): John Wiley & Sons.
- Kyllonen, P., 1996. Is working memory capacity Spearman's g ?, in *Human Abilities: Their Nature and Measurement*, eds. I. Dennis & P. Tapsfield. Mahwah (NJ): Lawrence Erlbaum, 49–75.
- Kyllonen, P. & R. Christal, 1990. Reasoning ability is (little more than) working-memory capacity? *Intelligence* 14, 389–433.
- Lai, C.S.L., S. Fisher, J. Hurst, *et al.*, 2000. The SPCH1 region on human 7q31: genomic characterization of the critical interval and localization of translocations associated with speech and language disorder. *American Journal of Human Genetics* 67, 357–68.
- Lai, C.S.L., S.W. Fisher, J.A. Hurst, F. Vargha-Khadem & A. P. Monaco, 2001. A novel forkhead-domain gene is mutated in a severe speech and language disorder. *Nature* 413, 519–23.
- Lezak, M.D., 1982. The problem of assessing executive functions. *International Journal of Psychology* 17, 281–97.
- Lezak, M.D., 1995. *Neuropsychological Assessment*. 3rd edition. New York (NY): Oxford University Press.
- Luria, A.R., 1966. *Higher Cortical Function in Man*. New York (NY): Basic Books.
- Marshack, A., 1991. The Tai plaque and calendrical notation in the Upper Palaeolithic. *Cambridge Archaeological Journal* 1(1), 25–61.
- Matsuzawa, T. (ed.), 2001. *Primate Origins of Human Cognition and Behavior*. Tokyo: Springer-Verlag.
- Mithen, S., 1996. *The Prehistory of the Mind*. London: Thames & Hudson.
- Miyake, A. & P. Shah (eds.), 1999. *Models of Working Memory: Mechanisms of Active Maintenance and Executive Control*. New York (NY): Cambridge University Press.
- Nissim-Rafina, M. & B. Kerem, 2002. Splicing regulation as a potential genetic modifier. *Trends in Genetics* 18, 123–7.
- Noble, W. & I. Davidson, 1996. *Human Evolution, Language, and Mind: a Psychological and Archaeological Inquiry*. Cambridge: Cambridge University Press.
- Oswalt, W., 1976. *An Anthropological Analysis of Food-Getting Technology*. New York (NY): John Wiley.
- Pennington, B.F., 2002. *The Development of Psychopathology*. New York (NY): Guilford Press.
- Pinker, S., 2002. *The Blank Slate*. London: Penguin Books.
- Rijsdijk, F.V., P.A. Vernon & D.I. Boomsma, 2002. Application of hierarchical genetic models to raven and WAIS subtests: a Dutch twin study. *Behavior Genetics* 32, 199–210.
- Russell, J., 1996. Development and evolution of the symbolic function: the role of working memory, in *Modelling the Early Human Mind*, eds. P. Mellars & K. Gibson. (McDonald Institute Monographs.) Cambridge: McDonald Institute for Archaeological Research, 159–77.
- Shepard, R., 1997. The genetic basis of human scientific knowledge, in *Characterizing Human Psychological Adaptation*, eds. G. Bock & G. Cardew. London: Wiley & Sons, 4–13.
- Soffer, O., 1989. Storage, sedentism and the Eurasian Palaeolithic record. *Antiquity* 63, 719–32.
- Stout, D., 2002. Skill and cognition in stone tool production. *Current Anthropology* 43, 693–722.
- Straus, L.G., 1996. The archaeology of the Pleistocene–Holocene transition in southwest Europe, in *Humans at the End of the Ice Age: the Archaeology of the Pleistocene–Holocene Transition*, eds. L.G. Straus, B.V. Eriksen, J. Erlandson & D. Yesner. New York (NY): Plenum Press, 83–99.
- Tomblin, J.B. & P.R. Buckwalter, 1998. Heritability of poor language achievement among twins. *Journal of Speech, Language, and Hearing Research* 41, 188–99.
- Turkheimer, E., 2000. Three laws of behavior genetics and what they mean. *Current Directions in Psychological Science* 9, 160–64.
- Woods, G.C., J. Bond & W. Enard, 2005. Autosomal recessive primary microcephaly (MCPH): a review of clinical, molecular, and evolutionary findings. *American Journal of Human Genetics* 76, 717–28.
- Wynn, T. & F. Coolidge, 2003. The role of working memory in the evolution of managed foraging. *Before Farming* 2(1), 1–16.
- Wynn, T. & F. Coolidge, 2004. The expert Neandertal mind. *Journal of Human Evolution* 46, 467–87.