# Palaeoneurophysiology and cognitive evolution in Pleistocene *Homo*: Biological and palaeoanthropological perspectives on the role of "haptic" working memory in the evolution of long-term procedural memory; <u>DRAWING NEUROSCIENCE AND PALAEOANTHROPOLOGY TOGETHER</u>.

**Michael Walker,** **DPhil, BM, BCh, Dipl.Prehist.Archaeol.(Oxon), F.S.A., F.R.A.I.**
**Honorary Emeritus Professor of Physical Anthropology,**
**Departamento de Zoología y Antropología Física, Universidad de Murcia**
**mjwalke@gmail.com**

## *Keywords*

Enhanced long-term memory, haptic memory, implicit nondeclarative long-term procedural memory, inferior parietal lobule, supramarginal gyrus, hippocampus, insula, cingulate gyrus, striatum, cuneus, cognitive evolution, co-evolution, palaeoneurophysiology, Early Pleistocene, Palaeolithic, tool-making, Acheulian, chains of behavioural activities..

## *Abstract*

Evolution in Early Pleistocene *Homo* of enhanced implicit nondeclarative procedural long-term memory is inferred from the Palaeolithic record of tool-making and manual dexterity, which implies a complex relationship between haptic memory and prospective memory in early humans that has left scant trace in the palaeoneurological record of early fossil skulls of our genus. Neurophysiological considerations drawn from research into the brain are compatible with co-evolution between development in *Homo* of early Palaeolithic behaviour, tool-making in particular, and cerebral neuronal architecture and circuitry underpinning the enhancement of memory, attention, technological aptitude, and cognitive versatility. Whereas working memory, prospective memory, and long-term memory are distributed widely in our cerebral hemispheres and cerebellum, it is noteworthy that regulatory neuronal activity facilitating their integration involves, above all, medially-situated cerebral components on which neuroscientific research is shedding light. During the Early and Middle Pleistocene there was a gradual process of evolution that brought about their integration not only with a developing neuronal substrate for tool-use in the left-sided supramarginal gyrus of our inferior parietal lobule, but also a developing neuronal substrate in our anterior prefrontal cortex for control of attention to the task in hand, literally as well as figuratively speaking, one outcome of which is a human facility for multitasking. It is inferred that gene-culture co-evolution took place involving enhancement at the neuronal level of procedural long-term memory and at the behavioural level of enhanced cognitive flexibility.

Nevertheless, natural selection favoured innate protective conservatism in the mirror-neurone system, which assuredly was a strong brake on innovative imitative learning. Moreover, If *H. erectus/ergaster* did not have adolescence as we know it, then integration of its hippocampal-prefrontal cortical activity was less complete than is ours, and therefore was less able to retain prospective memory or engage in multitasking .

## *Fred Flintstone was just an overgrown barely articulate Bart Simpson*

Although *Homo* between 1.7 and 0.7 Ma (million years ago) had our adult bodily size, this was probably reached at 8-10 years old (Dean and Smith 2009) and, as in other mammals, growth was probably determined by growth hormone (i.e. the human adolescent growth spurt probably had not yet evolved). The size of the adult brain was between one-half and three-quarters that of ours. However, myelination of ("white-matter") neurones very likely was complete before 15-16 years of age (in modern people it continues until about 25 years old). Communicative skills may have been more like those of modern four-year-olds. Adult behaviour may be envisaged as not unlike that of a barely articulate "*Lord of the Flies*" community with girls and sex. We would not feel at home with it. We would find it alarming and unnerving. It exerted a strong brake on Pleistocene cultural evolution. Moreover, life-span was short with almost no older people around to transmit knowledge and skill.

At 1.6 Ma the 8-11 year-old Nariokotome *Homo erectus* was already 1.6 m tall and his 880 $cm^3$ brain volume was nearly at adult size of 900 $cm^3$. His small brain probably would have been mature were he to have lived to be a 15-16 years old adult. Very likely the stage of his mental development, in terms of the classical Piagetian scheme, went no further than that of *concrete operative capability*, and that even the adults around him had scant mental capacity to conceptualize *formal operations* by referring to abstract considerations about the possibilities of alternative logical procedures or arguments, even were such to have been held in ***memory*** or "*kept in mind*" (cf. Piaget 1959).

Such considerations likely were limited to cause-and-effect sequences involving tangible or visible matters (and perhaps even audible or vocal cues or signals), though with some capability of understanding the outcome of making mistakes and how these might be avoided by evaluating the sequences and making adjustments to them by thinking in reverse order so as to make possible the taking of steps in order to minimize mistakes or mishaps. ***Memory matters*** if we are not to make the same mistake twice. It is likely that also there was some appreciation that several behavioural sequences were mutually exclusive, and that back-tracking in order change from one sequence to another was precluded sometimes by irreversible characteristics in the one embarked upon which were remembered (this is called “second-order cognition”). ***Memory*** is important here.

Why might that be of interest? Well, “alloparenting” (“grandmother hypothesis”) suggests the likelihood of a need for evolving cognitive complexity associated with multifarious social interaction (cf. Sterelny 2012). That, in turn, should have required noteworthy development of abilities to remember different social circumstances. The evolution of memory in the brain of early *Homo* might have undergone qualitative and quantitative change quite rapidly in terms of geological time, conceivably between 1.7 and 0.7 Ma. The part played by ***memory*** must have been important for co-evolution of cerebral and cognitive developments with communal intercourse and behavioural activities tending towards human niche adaptations of both the physical (natural) and social surroundings. It surely underpinned the origin of modernity, if we understand by that those life-ways of early *Homo* that are significantly different form those of other Hominoidea, past and present. Nevertheless, we would find them as strange as we might if we were to enter a society of adult-sized ten-year-olds with communicative skills of four-year-olds.

All the same, they weren’t like a troop of chimpanzees. *Homo* had diffused throughout the Old World, surviving and reproducing in environments unlike those of equatorial Africa or SE Asia. Consumption of animal-derived foodstuffs was widespread, as well as plant-derived ones, and roasting on fires aided rapid digestion (Wrangham 2009) which -especially fatty acids- undoubtedly enabled the metabolic support of a brain two to three times bigger than that of a chimpanzee. Recursive mental facility, shared attention, an incipient theory of mind, and the transition from self-centred gesticulations and vocalizations to an interactive communicative system involving grammatical and lexical symbolic phonations (“protolanguage”) were developing (Corballis 2011; Tomasello 2010). By 0.4 Ma even Neanderthal precursors in southwestern Europe almost undoubtedly had the anatomical capacity for speech (Martínez et al 2004, 2012).

## *Gene-culture co-evolution and memory*

There is something unsatisfying about trying to fill up the Early Pleistocene palaeoanthropological record with plausible arguments, whether drawn from the behaviour, ethology and neurobiology of great apes, or from human psychology and psycholinguistics, or even with inferences drawn from skeletal fragments and molecular genetics. What can be gleaned from the archaeological record? After 1.7 Ma in East Africa there are bifacially-flaked hand-axes and cleavers, and after 1.3 Ma flakes removed by repetitive centripetal flaking of discoidal cores, and by 1 Ma such artifacts occur in SW Asia, S Asia, and in Europe very soon afterwards, along with evidence of fire at Palaeolithic sites, I have uncovered all of these together with evidence of fire causing temperatures of 450-750ºC at the southeastern Spanish site in Murcia of Cueva Negra del Estrecho del Río Quípar which dates from ca. 0.8 Ma (Walker et al. 2013).

Sometimes called the "dual inheritance theory", the ***co-evolution of genetic lineages and early human ("cultural") behaviour*** is a plausible theory to help us interpret several aspects of cultural evolution (Boyd and Richerson 1985, 2005; Durham 1991; Richerson and Mortensen 2013). Observational learning leading to cumulative cultural transmission stands in sharp contrast to local social enhancement of independent learning without observation of others and therefore without transmission. "*The maintenance of cultural transmission requires both the accurate transmission of mental representation from experienced to inexperienced individuals and the persistence of those representations through the lives of individuals until such time that they act as models for others*" (Boyd and Richerson 2005, legend to Fig 3.1, see p. 53-7). Consideration of that statement reminds us that ***memory*** **must** be involved, as well as communicative skills. Artifacts made by hand involve their makers' memories of touching and feeling things: "***haptic memory***".

The archaeological record affords hard evidence with several pointers to the fidelity of behavioural transmission underpinned by haptic memory. Transmission was involved in ("cultural") adjustments made by our distant ancestors that had the effect of altering their physical surroundings and social circumstances ("niche-building"). Sometimes in early *Homo* these modifications may have affected the reproductive fitness of some groups, and occasionally gene frequencies. Undoubtedly natural selection had established a prerequisite genetic basis by the mid-Early Pleistocene when the first African hand-axes appeared ca. 1.7 Ma, plausibly accompanied by protolanguage (cf. Arbib 2011). Nevertheless, transmission was broken more than once. In recent Australian prehistory bifacial hand-axes and Levallois flaking were "re-invented" by anatomically modern *H. sapiens*. The fundamental point here is that biological evolution of brain circuitry underpinned a cognitive versatility that enabled the "re-invention".

My concern is with how and where in the human brain the workings of memory take place. I give pride of place to haptic memory and its interplay with the relationship between active working short-term memory and long-term procedural memory, as well as the relationships between all of these and the handling and use of tools. I am interested in how these relationships developed during the evolution of the early human brain in the Early and Middle Pleistocene. Although I was trained as an experimental neurophysiologist at Oxford and Göttingen where I participated in research on the central nervous system, it was my transition to palaeoanthropology after qualifyng as a medical doctor that eventually led to my interest in the ***evolution of human memory***.

In particular, the discovery at Cueva Negra (Walker et al 2013) of Palaeolithic evidence for two contemporaneous alternative behavioural sequences of stone-knapping (possibly even three) led me to consider the implications for the evolution of human cognition (Walker 2009). That discovery has led me to reflect on the evolution of brain mechanisms involving retrieval from memory which are implicit when ***choosing*** between different manual activities involving **touch** (and sight**)**, and which underpin **cognitive** mechanisms requiring extraordinarily rapid **mental rotation** of imagined objects so as to **anticipate** the **next** action or allow **correction** when unexpected accidents occur.

The very early coexistence of alternative knapping sequences, which could and did reduce stone blanks in **different** ways in order to make **different** kinds of stone tools, reflects a capacity to ***choose*** between ***different chains of behavioural activities***, and to develop ***innovative behavioural choices****.*

What is the relation between how we remember what to do and what not to do? How might such remembered awareness have been transmitted as knowledge to others in whom it became embedded with a degree of fidelity sufficient to enable intergenerational or inter-communal diffusion a million years ago?

The evolution of enhanced capacity for **long-term memory** (LTM) in *Homo*, vis-à-vis australopithecines and great apes, was a **prerequisite** for our ability to **choose** between complex chains of behaviour and **execute** them **appropriately** or **skillfully**. Shall I ride my bicycle or my motorcycle to work? Shall we bake a cake or a leg of lamb this morning? Shall I type a letter on my PC or write it with a pen? Shall I knap a stone scraper or a hand-axe? Shall we play football or basketball? Of course, such **abilities** are not inherited! ***They are learned.*** Nevertheless, our **considerable** capacity for **LTM** implies evolution in the brain of neuronal potential for ***enhancement of LTM*** ***because certainly we can keep those abilities in our mind***. Moreover, we can interrupt one chain of behavior in order to attend to something else before resuming it where we had left off, e.g. While I am lecturing to students my cell phone rings, so I switch it off and then carry on talking where I had left off – I had not forgotten what I had intended to say because I had kept in mind a ***prospective*** memory. This ability allows us to carry out activities far beyond the capability of chimps. It is important for learning them, because the apprentice learns not merely to envisage the outcome and rush to achieve it any old way (emulating the master) but instead to imitate each of the master's constituent actions faithfully albeit painstakingly.

The likelihood that the archaeological record, from the mid-Early Pleistocene onwards, affords empirical evidence that hominins participated in **self-determining** or **self-constraining chains of sequential behavioural activities**, which permitted alternatives open to freedom of choice, and thus enabled "***second-order cognitions***", is a ***palaeoanthropological* approach to cognitive evolution, the enhancement of long-term memory, and prospective memory, and transmitting skills.**

**Brakes on gene-culture evolution in Early and Middle Pleistocene *Homo*:**

Short life-span and early sexual maturity.
Adult bodily size attained early.
Small brain; small frontal, parietal, temporal lobes.
Scant communicative range of protolanguage.
Extinction of human lineages.
Extinction of transmitted skills.
Shortage of skillfull, knowledgeable adults.
Lack of human adolescent growth spurt and early anatomical maturity:
Early myelination of frontal, parietal, temporal neurones;
Relatively smaller areas with mirror-neurones;
Relatively smaller left inferior parietal lobule;
Conservative mirror-neurone system hindered innovative imitation;
Hippocampal-prefrontal coactivity was low because mature individuals faced relatively few demanding tasks and so failed to develop a prospective memory flexible enough for efficient multitasking;
Relatively fewer interoceptive giant spindle cells in anterior insula and anterior cingulate gyrus;
Underdeveloped prefrontal cortical areas for monitoring behaviour and integrating short-term woking memory with implicit procedural long-term memory.

## Neuroscientific methods

Much important experimental or medical research in neurosciences explores differences in cognitive aptitudes between humans and monkeys, often involving sight (responses to visual clues) or in the case of humans to visual or audible symbols (e.g. words). Stone-knapping (like knitting, bicycle-riding, cooking food, playing tennis, typing, house-painting, swimming, or piano-playing) is a **procedural skill** relying on **implicit nondeclarative long-term memory, LTM**. Initially, though, these skills have to be **learnt**, and learning involves **short-term working memory, WM,** or **working attention** to the task in hand. We know a great deal about how **WM** is built up in the brain, thanks to a vast amount of research undertaken over the past three decades into:

***1 Neurophysiology and neuroanatomy***: intracellular neuronal recording and microstimulation during psychophysical experiments with monkeys; functional connectivity analysis of neurones; optical-fibre and optogenetical recording;

***2 Clinical neuroimaging studies***: functional magnetic resonance imaging, **fMRI**; positron emission tomography, **PET**; repetitive transcranial magnetic stimulation, **rTMS**; high-density magnetoencephalography, **MEG**; electroencephalography, **EEG**, of event-related potentials **ERPs**;

***3 Experimental and clinical neurobiochemistry and neuropharmacology***: neuronal differentiation by means of discrete protein markers in selectively-bred transgenic animals which enhances identification of, and discrimination between, the varying biophysical properties of the growing number of neurotransmitters now recognized in different kinds of neurones; clinical correlations between brain dysfunctions, probable neurobiochemical disorders, and responses to pharmacological treatment.

## Haptic memory

***Haptic*** memory, *HM*, involves enhanced intracellular biophysical responses evoked by *touch* in some cerebral sensory neurones with ensuing network effects in functional systems of ***active working short-term memory***, *AWSTM*, by preparing motor neurones to respond instantaneously (as well as attuning other kinds of sensory neurones), and even to anticipate appropriate responses, implying recourse to acquired memory (Fuster 1999). To distinguish it from *AWSTM* induced by sight, sound, smell, taste, proprioception, etc., let us refer to *haptic* (touch) *AWSTM* as *HAWSTM*. Dorsolateral prefrontal cortex, dlPFC, is involved, though similar effects occur in parietal cortex, PC (Romo and Salinas 2001). Neurophysiological findings show that, compared with visual stimuli, a monkey's attention to *tactile* stimuli has more effect in consolidating sensory neuronal responses, an effect that increases with evermore difficult tasks, and intracellular stimulation of sensory neurones can evoke *HAWSTM* discriminatory perceptions, such as *place order* within an ordered series, implying *other* cells are involved in processing the information (ibidem; Gold and Shadlen 2007).

Psychophysical experiments show that PC sensory neurones stay active for several seconds when a monkey recognizes that an object it ***touches*** is the same as one in a photo of two different things it previously had fondled inside a black box. The importance of parietotemporal cortex, PTC, is acknowledged in intention and definition of manual behaviour, related to both prefrontal, PFC, and hippocampal, HPC, activity, as well as spatiotemporal ordering (Archambault et al 2011; Binkofski et al 1999; Bisley and Goldberg 2010; Bonini et al 2011; Jenkins anad Ranganath 2010; Lee and Rudebeck 2010; Lindner et al 2010).

Frontal, FC, and parietotemporal, PTC, cortices have expanded greatly since *Homo* first appeare (Bruner 2010a,b; Bruner and Holloway 2010; Holloway et al 2004; Weaver 2005). Touch and haptic memory, *HM*, of handling things doubtless played a part, and since 2.6 Ma have left their handiwork as stone tools in a much longer and far more abundant record (cf. Stout 2011) than exists for visual memory (≤0.1 Ma: ornamentation, decoration) or acoustic memory (≤0.01 Ma: language, music) though it is these that tend to dominate discourses in human evolutionary psychology, cognitive evolution, and even neuroscientific research and experimentation, swayed no doubt by considerations of neuroanatomical observations about visual and linguistic-acoustic neocortical cytoarchitecture.

Neuroimaging in humans shows increasingly widespread involvement of different brain regions when knapping ("Oldowan") chopping tools is replaced by bifacial ("Acheulian") stone-knapping (Stout et al 2006). Psychophysical experiments with monkeys implicate a canonical or "mirror" neurone system, *MNS*, that tracks manual activity in both prefrontal cortex, PFC, and parietotemporal cortex, PTC (Gallese et al 1996; Iacoboni et al 2005; Keysers and Fadiga 2008; Nelissen et al 2011; Rizzolatti and Craighero 2004; Rizzolatti et al 2004). In monkeys ***mime*** fails to evoke the *MNS* responses aroused in humans from which young children's capability to learn very likely evolve (Oberman and Ramachandran 2007); unlike apes, they appreciate a mimic's ***intended*** action.

A model for how the MNS is involved in imitative behaviour is as follows (Iacoboni 2005):

*1* Visual information is encoded in the superior temporal cortex;

*2* The signal is then sent to the posterior parietal cortex which provides somatosensory information about an observed action by means of parietal canonical neurones;

*3* The signal is then sent to frontal mirror neurones to code the goal of the action to be imitated;

*4* However, before a signal is sent to the primary motor cortex, an efferent copy of the motor command is sent back to the superior temporal sulcus in order to match the predicted sensory consequences of a planned imitation to the visual description of the action originally observed: if the match is good, the primary motor cortex initiates the action.

*Perhaps, therefore, the capacity of our mirror and canonical* neurones to match action-observation to action-execution has led in Homo to the memory-neurone system becoming used for imitative behaviour.*

*Comparable in several respects to mirror neurones are the "canonical" neurones which occur around the intraparietal sulcus and the superior temporal sulcus. Canonical and mirror neurones differ, because *canonical neurones do not necessarily fire in the brain of an animal when it is carrying out an action* (though some may do so). There is widespread use of the phrase "mirror-neurone system" to refer loosely to canonical as well as mirror neurones. Some neuroscientists, however, prefer to regard both canonical and mirror neurones as having such special neurophysiological properties with regard to memory that it is more appropriate to assign both of them to a category of "memory neurones" and call it a "memory-neurone system"; the hyphen here is most necessary in order to emphasize that the term refers solely to those two kinds of neurones, and that most definitely it does *not* refer to some kind of overarching "memory system of neurones" or general neuronal system for memories that otherwise might embrace also WM and LTM.

The *MNS* itself is not a memory store, though it plays a part in the development elsewhere in the brain of ***prospective** memory*. New research is throwing light on *prospective memory* and planning (Gilbert 2011; see below) and involves the hippocampus, HPC (in the medial temporal cortex, MTC) which is concerned with pattern recognition (Yass and Stark 2011). and consolidation of "*permanent associative links between the pieces of information that define a long-term memory…*" (Miller and Cohen 2001), be it explicit long-term memory, *ELTM*, or implicit long-term memory, *ILTM* (Pennartz et al 2011). *ELTM* is declarative, episodic or semantic, whereas *ILTM* is nondeclarative or procedural – implicit nondeclarative procedural *ILTM* may be referred to as *INPLTM*. It has been known for over sixty years that hippocampal injuries or lesions interfere with *ELTM* in patients. Other areas of the brain are involved with memory also. Development and formation of associative memory involve the polymodal area 36 of inferotemporal cortex, ITC (probably by cross-modal integration there of haptic, visual, and acoustic inputs) according to psychophysical, neurophysiological and neuroimaging studies (Osada et al 2008). The inferior temporal cortex, ITC, alone handles effortless recall and automatic retrieval of *LTM*, though it probably receives top-down input from prefrontal cortex, PFC, for active retrieval when an effort is needed to recall something from *LTM*.

## *Implicit procedural long-term memory and haptic memory*

Chimpanzee brains differ from ours. Unlike chimps, we have a well-developed inferior parietal lobule, IPL, which is significant here (the *MNS* is involved also in our left-sided prefrontal Broca's "cap" area that chimpanzees lack). The anterior supramarginal gyrus of our left IPL in humans is involved when we humans use tools (Peeters et al 2009). *"It is, therefore, conceivable that it houses neurons with mirror-neuron–like properties (Rizzolatti & Craighero 2004) that allow for both tool use and tool-use understanding. This may support tool imitation and learning by imitation. A word of caution is of course needed, as the presence of mirror neurons has yet to be demonstrated in aSMG, and their presence is a necessary but not sufficient condition for imitation to develop*" (Orban and Rizzolatti 2012).

Intentionality apart, what is the relationship between haptic memory, *HM,* and the *MNS*-registering of manual activity, and what might we learn about how *AWSTM* relates to *ILTM*? Cerebral recursion, error-detection, and error-correction were prerequisities for both early stone-knapping and protolanguage (cf. Arbib 2011; Rizzolatti and Arbib 1998; Stout et al 2008), notwithstanding innate mirror-neurone system conservatism (demonstrated by neuroimaging) that doubtless was a protective outcome of natural selection and maintained a brake on cognitive evolution in *Homo* (cf. Calvo-Merio 2005). *ILTM* involves childhood development of preferential neuronal coding and circuitry linking frontal cortex, FC, and parietotemporal cortex, PTC, to dorsolateral striatal cortex (caudate nucleus, putamen) and hippocampal, HPC, cortex (Ashby et al 2010; Doyon and Benali 2005; Pennartz et al 2011), and throughout the limbic system, basal ganglia, and cerebellum (Balsters and Ramnani 2011; Balsters et al 2013).

Storage of *INPLTM* seems to involve synaptic modifications (mediated by neurotransmitters) in neocortical–basal ganglia feedback-loops (both negative and positive) between neocortical areas and striatal subregions, with downstream projection to habenula, pallidum, globus pallidus, ventral tegmental area and substantia nigra, linked to thalamic nuclei projecting back to the neocortical areas of origin (Hazy et al 2007; Kreitzer and Malenka 2008). **This complexity is why *ILTM* is much harder to investigate by functional connectivity analysis than are *STAWM* or even declarative episodic and semantic *ELTM*.** Whereas frontal, FC, parietotemporal, PTC, and cerebellar cortices may leave palaeoneurological endocranial signatures in hominin skulls, **medial cortical structures leave none.**

The exceptionally abundant interoceptive ("Von Economo") giant spindle cells of our extrahippocampal anterior cingulate cortex, ACC, and insula may be a Pleistocene outcome of increasing self-generated inputs to *LTM* (cf. Allman et al 2005; Petersen and Posner 2012) facilitating "*the unique capacity for the intergenerational transfer of the food and information characteristic of human extended families*" (Allman et al 2002), with the particularly large human insula affording "*a potential neural basis for enhancement of social cognition in association with increased brain size*" (Bauernfeind et al 2014).

The medial frontal, MFC, and anterior cingulate, ACC, cortical relationship is undoubtedly important in monitoring and evaluating the behaviour of oneself and others, and in detecting errors, especially when a task in hand is changing (Rushworth et al 2007; Neubert et al 2012). Human posterior cingulate relationships also are important: **our inferior parietal lobule, IPL, embraces the supramarginal gyrus, angular gyrus and parietotemporal, PT, junction,** and functional imaging shows this region to be involved with keeping close attention to matters not only visuospatial (as in the macaque's homologous area 7a) but also to **unexpected salient** aspects **regardless of whether sight, *touch*, or hearing** are involved (Husain et al 2006).

This cross-modal or polymodal ability of the large human IPL may well have been facilitated by its occupying a relatively more dorsal position in the parietal cortex, PC, than that of the extrastriatal motion-sensitive (V5/MT) area of monkeys (relatively closer to their superior parietal lobule and anterodorsal cortex beyond) which may lead to their visuospatial inputs often predominating over those of other sensory modalities. In any event, there is little doubt that IPL expansion had important consequences for the evolving human brain (so also, of course, did relative expansion of white matter, and myelination continuing into and beyond our adolescent growth-spurt). The precise genetic mechanisms underlying human cerebral evolution are unknown but may involve ASPM and MCPH1 genes (Gilbert et al 2005; Konopka and Gerschwind 2010).

Getting back to touch, when blindfolded right-handed people undertake variably-delayed match-to-sample tasks, with their right hand rotating an object such that it is either a mirror image of, or parallel to, one rotated by the left hand, functional imaging detects early activity in anterior prefrontal cortex, PFC, followed by left parieto-occipital cortical activity (Kaas et al 2007). An early sensory stage of haptic *HAWSTM* involves the primary somatosensory cortex in PC, and early in the delay period initial haptic sensory traces maintained in the contralateral (left) sensorimotor cortex are transformed into haptic spatial representations, maintenance of which engages anterior prefrontal and parieto-occipital cortices. The right-handed response involves activation of other left cerebral regions (superior and inferior temporal cortex, superior parietal lobule, superior occipital cortex, precuneus), right cerebral regions (insula, superior temporal gyrus, postcentral gyrus, inferior parietal lobule), and also bilateral activity (in the cuneus and parieto-occipital sulcus).

On increasing the delay period from 0.5 to 5 seconds, activity is seen in left anterior prefrontal, aPFC, and parieto-occipital, POC, regions and right primary motor, in FC, and occipital, OC, cortices. On increasing the delay period to 10 seconds, left-sided cerebral activity occurs in the rostral part of the occipital cortex, OC, parieto-occipital, POC, and anterior prefrontal, aPFC, cortices and the putamen, bilateral activity in the occipital cortex, OC, and right-sided activity in the right anterior cingulate, ACC, cortex. "*The involvement of occipital and parieto-occipital regions in exploration and matching is consistent with subjective reports of visual imagery from the majority of our participants and the important roles of (higher order) visual areas for spatial processing*" (ibidem); this is in line with electrophysiological findings in monkeys of the cross-modal involvement of the occipital visual cortex during haptic experiments (Zhou et al 2007). In short, *HAWSTM* for touch involves dynamic spatiotemporal neuronal networks of increasing complexity: "*associative aspects of a haptic WM task are distributed in a wide network of neurons in motor and parietal areas*" (ibidem). Other neuroimaging studies (e.g. Meyer et al 2011) draw attention to cross-modal sensory processing, reaffirming early proposals by Joaquín Fuster (1999).

The matter has relevance for functional imaging findings during stone-knapping. Plausibly, accurately repeated preparation of effective stone tools went hand-in-hand, so to speak, with preferential natural selection for those cerebral networks for appropriate *AWSTM*. Neuroimaging during stone-knapping implicates on-going monitoring in the superior parietal region of work-in-hand, involving "*dynamic coupling between multiple modes of sensory perception and motor action. Its heightened activation during Oldowan-style stone knapping clearly reflects on the complexity and elaboration of the polymodal mappings involved in the perception-through-action of knapping-related affordances*" (Stout 2005; cf. Stout 2006)

The approach was extended to include "Acheulian" bifacial stone-knapping. Of particular interest were the findings that strong inferior parietal lobule, IPL, activation occurred bilaterally during "Oldowan" tool-making, and that during "Acheulian" hand-axe preparation there was noteworthy activation of the right frontal lobe, both in the ventral premotor area and prefrontal cortex, PFC, which underlines the importance of the right hemisphere in controlling the left hand to change the position of a stone, held in it, being knapped by the right hand controlled by the left hemisphere. Ventrolateral prefrontal cortical, vlPFC, activation during "Acheulian" tool-making reflected "*cognitive demands for the coordination of ongoing, hierarchically organized action* *sequences*" and implied "*monitoring and manipulation within working memory*" (Stout et al 2008). Did absence of activation in dorsolateral prefrontal, dlPFC, and anterior cingulate cortex, ACC, mean little advance planning was involved?

Not necessarily, because neuroimaging of subjects, who were performing tasks involving varying degrees of complexity of both *AWSTM* and spatial processing, revealed a significant interactive effect on right posterior hippocampal, HPC, and bilateral parahippocampal activity, with increasing spatial complexity of the task, which was not found by increasing the demand on *WM*, and it was suggested that that those cerebral areas "*may play a critical role in processing complex spatial representations, which, in turn, may form the basis of short- and long-term mnemonic processes*" (Lee and Rudebeck, 2010). Finely-tuned behavioural timing is associated also with parahippocampal activity and may play a part in *ILTM* (Jenkins and Ranganath 2010).

## ***Prospective memory***

Especially interesting from the viewpoint of behavioural modification is the demonstration (by functional connectivity analysis of magnetic resonance imaging) that distracting someone's attention away from his "*prospective memory*" concerning an intended behaviour, and towards some other matter, allows, nevertheless, the former intention to be kept in medial temporal cortex, MTC. Here there is noteworthy bilateral hippocampal (HPC) activity whenever activity in the rostrolateral prefrontal cortices (rlPFC) is correlated with postponement of the execution of the former intention, and also involved are the insulas and anterior cingulate cortices (ACC) (Gilbert 2011). The neurobiological implication for apprenticeship is clear. Moreover, it appears that "*the hippocampus and prefrontal cortex are coactive in early adolescence regardless of task demands or performance, in contrast to the pattern seen in late adolescents and adults, when these regions are coactive only under high task demands... neural circuitry underlying working memory changes during adolescent development*" (Finn et al 2010). **If *H. erectus/ergaster* did not have adolescence as we know it, then integration of its hippocampal-prefrontal activity was underdeveloped compared to ours, and was less able to retain prospective memory and engage in multitasking.**

Because prospective memory involves recall, it is a hard task to disentangle the relationship in the brain between episodic and habitual referents of prospective memory, that is to say, between its event-related and time-related contents, which over time seem to change inversely on habitual repetition of a task where close attention can be relaxed. Neuroimaging and EEG-ERP studies on humans find that occipital cortex is involved, including particularly the cuneus, and also the parietal cortex including the precuneus and IPL, as well as the superior temporal gyrus, cerebellum, ACC, dorsolateral PFC and especially right PFC where activity decreases over time when the content of prospective memory is time-related and where lesions impair prospective memory (Burgess et al 2001, 2011; Gonneaud et al 2014; Volle et al 2011; West 2011). Once again some cerebral areas are involved that lie medially and therefore leave no palaeoneurological signature.

Only recently have relationships been determined between time-based aspects of human prospective memory and cerebral areas. It is difficult to design psychophysical experiments to investigate them in apes or monkeys. Holding things in mind while diverting attention to others is a remarkable aspect of human attention and planning. Rather than the craniological record, plausibly it is the Palaeolithic record that affords us the best testimony to the evolutionary enhancement of implicit nondeclarative long-term procedural memory and of the effective prospective memory that allowed some things to be kept in mind while other things were being held in the hand and subjected to complex haptic operations. Memory matters.

When haptic (or other) procedural or habitual tasks that demand attention are interrupted we often can retain them in prospective memory and soon return to them, or even alternate between them seamlessly (multitasking). No doubt this was very hard indeed for Early Pleistocene *Homo* brains in which rigid neuronal circuits were established early in life. Our prospective memory is an evolutionary outcome from 2 million years of integrating active working short-term attention with implicit procedural long-term memory.

## *A haptic perspective on Early Pleistocene cognitive versatility*

The widespread distribution and intimate reciprocal relationship between *AWSTM* and *LTM* make attempts to seek precise neuronal cytoarchitectural entities look like a wild goose chase with regard to haptic memory, *HM*, whether in *AWSTM* or *ILTM* modes. Yet we are confronted by the Early Pleistocene record of stone tools which has regular irregularities and irregular regularities that suggest existence of a specifically human *ILTM* mode rather than uniform, genetically-determined, inherited, instinctive behaviour (though heritability of *AWSTM* facility in monozygotic twins is reported: Blokland et al 2011). Most likely, haptic *ILTM* acquisition involved interaction between childhood learning in a social context (cf. Boyd and Richerson 2005, legend to Fig 3.1, see p. 53-57; cf. Stout 2011) and natural selection for both cerebral morphology and patterns of neuronal ontogenesis continuing until late adolescence. Pathways laid down in early childhood consolidate behavioural patterns involving logicomathematical cognition and appreciation of combinativity (Langer 2006), and perhaps alternative “mental templates” characterized by second-order cognition, none of which are typical in wild apes.

Evidence for patterns of alternative self-determining or self-constraining chains of sequential behavioural activities exists in the later Early Pleistocene Palaeolithic record of East Africa where “Oldowan” chopping tools coexist with flakes with retouched edges and “Acheulian” bifaces by 1.7 Ma (Lepre et al 2011; Roche et al 2003), and by 1.3 Ma with “Levalloisian” core-reduction (de la Torre et al 2003). The coexistence demonstrates not only manual dexterity and technological aptitude but above all the cognitive versatility of Early Pleistocene *Homo* whose brain shows expansion of prefrontal and parietotemporal cortices *vis-à-vis Australopithecus*. *Homo* spread to Eurasia where similarly diverse stone tools occur ca. 1 Ma (Arzarello et al 2012; Bar-Yosef and Goren-Inbar 1993; Goren-Inbar and Saragusti 1996; Goren-Inbar et al 2000; Pappu et al 2011; Vallverdú et al 2014; Walker et al 2013). Perhaps cooked food facilitated cerebral evolution (Wrangham 2009); even if Early Pleistocene *Homo* did not control fire (*pace* Alperson-Afil and Goren-Inbar 2010; Goren-Inbar et al 2004), fire caused so little instinctive fear that ca. 1 Ma it was taken into caves from South Africa to Spain (Berna et al 2012; Walker et al 213), indicative of developing cognitive awareness.

Over the extensive spatiotemporal dimensions of the Early and Middle Pleistocene, patterns of alternative self-determining or self-constraining chains of sequential behavioural activities in modifying stone are not best interpreted primarily from a quasi-ethnographic standpoint of reduction sequences (‘*chaînes opératoires*’) of individual knappers from day to day, but instead from an evolutionary biological viewpoint of emerging human cognition which implies intergenerational appreciation involving many different participants over long periods of time (Walker 2009).

Among several aspects, one has received much attention, namely, the relationship between recognition of different volumes implied by non-secant, symmetrical secant, and asymmetrical secant form (White and Pettitt 1995), and alternative repeatable knapping strategies, learned in order to give alternative outcomes repeatedly: e.g. flaked “Acheulian” bifaces with a more-or-less symmetrical secant plane *vis-à-vis* centripetal flaking to prepare discoidal cores with an asymmetrical secant plane for desired ultimate removal of an oval, triangular or oblong “Levalloisian” flake (leaving behind a corresponding negative scar on a small core that cannot be reduced further), though it is likely that stone tools resulting from “Acheulian” and “Levalloisian” reduction sequences reflect the limited mechanical outcomes that are possible from sequential or recurrent psychomotor and neuromuscular interactions between visuotactile and manual responses to the clues left on a core undergoing rotation during knapping (cf. van Peer 1992, p. 35-54). In reality, the matter is more complicated because some hand–axes have twisted profiles (Roe 1968); 1968) and others have broken, incomplete or partial symmetry (Wynn 2002; see also Abramiuk 2012 p. 188-192).

A useful formal distinction enshrined in archaeological notions of "*façonnage*", or fashioning, and "*débitage*", or extracted flakes (Boëda et al 1990), may be an oversimplification (cf. Stout 2011), but is helpful from a cognitive viewpoint, especially if combined with concepts of symmetry and asymmetry (see, for example, Wynn and Coolidge 2010). Fashioning an almond-shape biface out of a flat almond-shape stone may allow the knapper to keep in sight an ostensive relationship between the shape of the stone and that of the flaked biface. The same goes, in part, when blades are struck from a prepared prismatic core (like staves being removed from the surface of a barrel, so to speak).

Very different indeed is the situation the "Levallois" knapper confronts. Here the desired final flake ("*éclat préférentiel*") to be extracted lies, as it were, "hidden" from view, less foreseeable than the yolk inside a hen's egg, and "unimaginable" simply from looking at the external shape of the stone before the "Levallois" reduction sequence begins. "*Early stone-knapping techniques like Levallois … and early stone tool types such as twisted profile handaxes… require a complexity of images held in… working memory… No more complex form of stone knapping* ever *appears*" (Coolidge and Wynn 2005, their emphasis); and from one particular refitted Levalloisian knapping sequence existence of an underlying "*plan-like principle*" that likely had set out a practical objective whilst letting the knapper monitor the work in hand so as to allow transformation in a fluid yet structured "*configuration of possibilities*" (Schlanger 1996).

Again, where hand-axes are symmetrical, then "*spatiotemporal substitution and symmetry operations*" were required that are more complex, cognitively-speaking, than are "*the spatial concepts necessary to manufacture blades*" (Wynn 1979), because they involve envisaging shapes and volumes from alternative perspectives, rotated in the mind, whilst paying attention to congruence a (Wynn 1989, 2000), and this is even more true of "Levalloisian" core-reduction. Tom Wynn (1993, 1995) interprets hand-axes as exemplifying evolution of "*constellations*" of behavioural plans of action that involve feature-correspondence as well as the complex cognitive skill of reversibility, which, nevertheless, could well have been learned and communicated by simply observing and copying.

As Wynn (1995) put it: "*it would be difficult to overemphasize just how strange the handaxe is … it does not fit easily into our understanding of what tools are, and its makers do not fit easily into our understanding of what humans are.*" It is worth bearing this matter in mind also when considering "Levallois" cores. Although the "*standard interpretation is that a core was prepared in such a way that a flake of predetermined shape could be removed … it does not seem likely that such cores represented a novelty in planning beginning at the time the Levalloisian technique is said to appear. Rather, such cores had been used for producing flakes almost from the very beginning, and continued to be so used even after knappers began to strike large flakes from them*" (Noble and Davidson 1996, p. 200).

## *Tool-making, communicating skills, and a common core for WM-LTM evolution*

"*Stone tool-making is… characterized by multiple levels of intentional organization. …it displays surprising similarities to the multi-level organization of human language. Recent functional brain imaging studies of stone tool-making… demonstrate overlap with neural circuits involved in language processing… consistent with the hypothesis that language and toolmaking share key requirements for the construction of hierarchically structured action sequences and evolved together in a mutually reinforcing way"* (Stout and Chaminade 2009).

Whilst this may have evolved in piece-meal fashion over a very long span of Pleistocene time (cf. Arbib 2011), it is a plausible conjecture that language was present at times when choices were made between alternative chains of behavioural activities leading to very different Paleolithic outcomes, as at Cueva Negra del Estrecho del Río Quípar at 0.8 Ma..

The facilitative part language could have played raises a question of whether fluency might have increased as human populations increased. Selection pressure for fluency could have been an outcome of exponentially-increasing interactions between growing numbers of people. Gene-culture co-evolution is a plausible conjecture. Related to it is a conjecture that inclusive fitness of some communities may have been enhanced by fluency (at the expense of others such as Neanderthals?). Nevertheless, speech is ***not*** necessary for observational learning though it could have come to play an increasing part in cumulative cultural transmission.

Maybe in those later Middle Pleistocene communities which underwent greatest demographical growth, acceleration in both rate and frequency of interpersonal discourse gave rise to positive feedback, in non-linear fashion, with cascade effects, thereby further channelling those lines of future self-organization that would be followed, with abandonment of others. Perhaps one that would be followed was a growing tendency towards assemblages of small retouched flake-tools, and production of these especially by asymmetrical secant-plane techniques of core-reduction, perception of which could have gone hand in hand with neuroanatomical adjustments in brain-circuitry favouring non-linear evolution, in self-organizing manner, in large-brained, later Middle and early Upper Pleistocene *Homo*. If natural selection came into play at both biological and behavioural levels, advantages accruing from assemblages of small stone tools may have permitted growing demographic abundance, density, and proximity of communities in Africa, southwestern Asia and Europe, furthering an increase in interpersonal contact and discourse.

Nevertheless, such speculation fails to address the matter of how and when language appeared, and what relation, if any, its appearance may have had to the making of stone tools more complex than the simple (“Oldowan”) pebble and chopping tools that had existed before 1.7 Ma (and did ***not*** disappear from the archaeological record thereafter). This is not the place to rehearse inferential arguments about the part played (or not) by hominin troop or group size, evolutionary arguments that appeal to psycholinguistics or the behaviour of great apes, or even considerations about anatomical or palaeontological observations (see, for instance, Aiello and Dunbar 1993; Martin 1998; Wray 2002; Carruthers anad Chamberlain 2000; Bickerton 1996; Larson et al 2010; Lieberman 2006).

Instead, two somewhat different aspects draw my attention. First, there is Terrence Deacon’s plausible inference that the learning of language in children is constrained by their cerebral limitations to active working short-term memory (*AWSTM*) and capacity for associative learning, because their young brains are still developing (such that these limitations have an effect of producing biased replication of language structure: Deacon 1997). Secondly, nevertheless, well before they begin to talk, our 18-month-old infants have logicomathematical (or mathematicoloigcal) capabilities for combinativity, demonstrated by research in developmental psychology, that are not reached by chimpanzees until 5 or 6 years of age by which time our garrulous infants are driving everyone around them round the bend (see various chapters in Parker et al 2000, especially Langer, 2000). These two considerations lead to a reflexion that maybe the wiring of an infant’s brain is more significant than language as a pointer to how physical objects are appreciated and how different permutations and combinations are handled (figuratively and manually) of both reversible and irreversible operations that involve envisaging shapes and volumes from alternative perspectives, rotated in the mind, whilst paying attention to congruence and learning how to eliminate impossible or incongruent ones by reference to recursive processes involving AWSTM and INPLTN. Plausible arguments, based on the MNS and other neuroscientific evidence, as well as drawn from hominoid ethology, hold that gestural and manual complexity underlay incipient language and its recursive facility (Corballis 2002, 2011; Tomasello 2010).

Appreciation of alternative perspectives implies choice between future activities or behaviour. The idea of "future memory" was proposed 30 years ago (Ingvar 1985). No great leap of the imagination is needed to join that up to neuroscientist Antonio Damasio's proposal that the human brain is uniquely capable of envisaging a subjective "*second order narrative*".

Damasio wrote

"*…when the brain is producing not just images of an object, not just images of an organism responding to the object, but a third kind of image, that of an organism in the act of perceiving and responding to an object…*

"*The minimal neural device capable of producing subjectivity thus requires early sensory cortices (including the somatosensory), sensory and motor cortical association regions, and subcortical nuclei (especially thalamus and basal ganglia) with convergence properties capable of acting as third-party ensembles.*

"*This basic neural device does not need language. The metaself construction I envision is purely nonverbal, a schematic view of the main protagonists from a perspective external to both. In effect, the third-party view constitutes, moment-by-moment, a non-verbal narrative document of what is happening to those protagonists. The narrative can be accomplished without language, using the elementary representational tools of the sensory and motor systems in space and time. I see no reason why animals without language would not make such narratives.*

"*Humans have available second order narrative capacities, provided by language, which can engender verbal narratives out of nonverbal ones. The refined form of subjectivity that is ours would emerge from the latter process. Language may not be the source of the self, but it is certainly the source of the "I""* (Damasio 1994).

That conclusion is close to what some psychologists call autonoesis: our ability to envisage ourselves in past or future situations. Damasio's proposal is based on his elegant "***somatic marker hypothesis***". It is not hard to see a relation between it and the "***theory of mind***" of psycholinguists and the philosophers of mind. In particular, the importance of *shared attention* for the theory of mind involves the MNS (Tomasello 2010).

An important distinction that is much overlooked in discussions about language and tool-making is that language is, par excellence, the outcome of *declarative explicit* LTM (ELTM), whereas stone-knapping is an instance of *implicit non-declarative* **procedural** LTM (INPLTM). Some have regarded technological evolution of stone-knapping during the Palaeolithic as being a consequence of increasing "enhancement "of AWSTM, an "enhancement" favoured by gene-culture co-evolution. In particular, it has been alleged that this developed necessarily, because of Levallois flaking techniques imply a "*complexity of images held in the visuospatial sketchpad of working memory*" (Coolidge and Wynn 2005) though they took note that "…*early stone-knapping techniques like Levallois suggest complex motor skills and procedural memory…*" A more economical proposal is to say simply that the considerable capacity for LTM in *Homo*, and especially INPLTM, implies evolution in the brain of neuronal potential for ***enhancement of LTM*.**

A semantic difficulty stems from scientists trained in different disciplines talking past one another (it is sometimes viewed as an epistemological problem). Experimental neurophysiologists can identify WM as a ***neuronal*** phenomenon, separable from that of ***attention***. In contrast, psychologists are more interested in the *attentional aspect*, and, despite their addiction to WM, from their perspective working *attention* is perhaps a preferable expression (Baddeley 2001). In this respect, it is worth remarking that much psychological research involves psychometrical analysis, little of which investigates how subjects make decisions about forthcoming actions or the part played by implicit procedural long-term memory in determining them.

By contrast, even when studying prospective memory, psychological research tends to concentrate its efforts on delay-response-type testing in relation to explicit declarative long-term memory as well as to responses from active working short-time memory (see, for instance, McDaniel and Einstein 2007; Smith 2011). For some psychologists LTM is still a "black box", lacking the so-called "domains" that they claim exist "within" WM. Typical of their unease is the following, "*Everything an expert knows is stored n the neural network of long-term memory (LTM). Psychology is a bit vague about what qualifies as long, but in general it is any period of time longer than a few seconds*" (Wynn and Coolidge 2012, p. 61-62). With regard to Neanderthal stone-knapping expertise, archaeologist Tom Wynn and psychologist Fred Coolidge feel more at home with working memory, which "*in general … is associated with the highest levels of cognition*" (ibidem, p. 44), notwithstanding "*abundant evidence for Neandertal procedural memory*" (ibidem, p. 42). For reasons I have summarized briefly in the section on ***Prospective memory***, to assert that INPLTM had not evolved in *Homo* by 1 Ma defies not only the early Palaeolithic record but also the gradual genetic evolution of the nuclear genome that underpins the theory of natural selection.

The celebrated neuroscientist Joaquín Fuster wrote "*Neuroimaging in the human has failed to demonstrate a clear specialization of separate prefrontal areas in spatial and nonspatial working memory…*" and he insists that, "*Working memory is as widely distributed as the long-term memory that supports it… working memory is emerging as a mechanism of temporal integration essentially based on the concurrent and recurrent activation of cell-assemblies in long-term memory networks of frontal and posterior cortex*" (Fuster 2001). It is hard to envisage how human cerebral evolution might have led to spectacular enhancement of HAWSTM whilst having scant impact on that of INPLTM.

An intriguing possibility is the part that may have been played in human evolution by increasingly rapid transmission between our much-expanded anterior insular and anterior cingulate cortices by our interoceptive giant spindle (von Economo) cells (Craig 2009). These medially-situated parts of the cerebral hemispheres seem to be involved in mental time-keeping, maintenance of attention and also to the "feeling of knowing" or "meta-memory" (Kikyo et al 2002) – which echoes Antonio Damasio (2000). The bilateral AIC-ACC system, together with the inferior frontal gyrus (IFG), forms a highly connected "core" system for task-dependent control of goal-directed behaviour and sensory processing (Dosenbach et al 2007). Recent findings concerning rule-specific neurones in the human anterior prefrontal cortex, along the lines initiated by Joaquín Fuster 30 years ago, suggest that the greatly expanded synaptic connections of our APF and IFG interact not only with neighbouring language areas but particularly with the AIC-ACC "core" to set up cognitive operations and manage multiple task sets, and an interesting possibility is that these evolutionary changes are associated with humans' capacity to manage a wide repertoire of task sets and represent highly abstract concepts (Sakai 2008).

## *Concluding remarks*

To conjecture that implicit nondeclarative procedural long-term memory, including complex prospective memory, had not evolved in *Homo* by 1 Ma defies not only an early Palaeolithic record that testifies to the contribution of early human haptic memory, but also the gradual genetic evolution of the nuclear genome that underpins the theory of natural selection. From a standpoint of evolutionary biology, it is implausible to conjecture an exceptional episode of evolutionary acceleration in the second half of the Middle Pleistocene in order to account for neuronal changes which on the one hand associate tool-use with the left supramarginal gyrus of our inferior parietal lobule, and which on the other have enhanced the capacity in *Homo* (vis-à-vis australopithecines and great aopes) for implicit nondeclarative procedural long-term memory and prospective memory, as well as haptic active working short-term memory. Plausibly, already those changes had begun by 1.7 Ma. That non-linear co-evolution existed in our genus between biological and behavioural change owes in all likelihood to brakes put on the co-evolutionary process by the early maturation of Early Pleistocene *Homo* and the correspondingly early myelination of those areas in the frontal, parietal and temporal lobes which today are involved in the aforementioned capacity as well as in linguistic aptitude. In short, neurophysiological considerations drawn from research into the brain are compatible with co-evolution between development in *Homo* of early Palaeolithic behaviour, tool-making in particular, and cerebral neuronal architecture and circuitry underpinning the enhancement of memory, attention, technological aptitude, and cognitive versatility.

## *References*

Abramiuk MA. *The Foundations Of Cognitive Archaeology*. Cambridge, Massachussetts and London: The MIT Press; 2012.

Aiello L, Dunbar R. Neocortex size, group size and the evolution of language. *Current Anthropology* 34: 184-193; 1993.

Allman J, Hakeem A, Watson K. Two phylogenetic specializations in the human brain. *Neuroscientist* 8, 335-346; 2002.

Allman JM, Watson KK, Tetreault NA, Hakeem AY. Intuition and autism: a possible role for Von Economo neurons. *Trends in Cognitive Sciences* 9, 367–73; 2005.

Alperson-Afil N, Goren-Inbar N. editors. *The Acheulian Site Of Gesher Benot Ya'aqov, Volume II. Ancient Flames And Controlled Use of Fire.* Berlin and London; Springer; 2010.

Arbib MA. From mirror neurons to complex imitation in the evolution of language and tool use. *Annual Review of Anthropology* 40,257–73; 2011.

Archambault PS, Ferrari-Toniolo S, Battaglia-Mayer A. Online control of hand trajectory and evolution of motor intention in the parietofrontal system. *The Journal of Neuroscience* 31, 742–752; 2011.

Arzarello M, Pavia G, Peretto C, Petronio C, Sardella R. Evidence of an Early Pleistocene hominin presence at Pirro Nord (Apricena, Foggia, southern Italy): P13 site. *Quaternary International* 267, 56-62; 2012

Ashby FG, Turner BP, Horvitz JC. Cortical and basal ganglia contributions to habit learning and automaticity. *Trends in Cognitive Sciences* 14, 208-2.15; 2010.

Baddeley AD. Is working memory still working? *American Psychologist* 11: 851-864; 2001.

Balsters JH, Ramnani N. Cerebellar plasticity during the automation of rule-based information. *Journal of Neuroscience* 31, 2305-2312; 2011.

Balsters JH, Whelan CD, Robertson IH, Ramnani N. Cerebellum and cognition; evidence for the encoding of higher order rules. *Cerebral Cortex* 23, 1433-1443; 2013.

Bar-Yosef O, Goren-Inbar N. *The Lithic Assemblages of `Ubeidiya. A Lower Palaeolithic Site in the Jordan Valley*. Jerusalem: Hebrew University of Jerusalem, Monographs of the Institute of Archaeology and Israel Exploration Society, "Qedem Monograph 34"; 1993.

Bauernfeind AL, de Sousa AA, Avasthi T, Dobson SD, Raghanti MA, Lewandowski AH, Zilles K, Semendeferi K, Allman JM, Craig AD, Hof PR, Sherwood CC. A volumetric comparison of the insular cortex and its subregions in primates. *Journal of Human Evolution* 64, 263-279; 2014.

Berna F, Goldberg P, Horwitz LK, Brink J, Holt S, Bamford M, Chazan M. Microstratigraphic evidence of in situ fire in the Acheulean strata of Wonderwerk Cave, Northern Cape province, South Africa. *Proceedings of the National Academy of Sciences USA* 109: 1215-1220; 2012.

Bickerton D. *Language And Human Behavior*, Seattle: Washington University Press; 1996.

Binkofski F, Buccino G, Stephan KM, Rizzolatti G, Seitz RJ, Freund H-J. A parieto-premotor network for object manipulation: evidence from neuroimaging. *Experimental Brain Research* 128, 210–213;1999.

Bisley JW, Goldberg ME. Attention, intention, and priority in the parietal lobe. *Annual Review of Neuroscience* 33, 1–21; 2010.

Blokland GAM, McMahon KL, Thompson PM, Martin NG, de Zubicaray GI, Wright MJ. Heritability of working memory brain activation. *The Journal of Neuroscience* 31, 10882–10890; 2011.

Boëda E, Geneste J-M, Meignen L.1990. Identification de chaînes opératoires lithiques du Paléolithique ancien et moyen. *Paléo* 2, 43-80; 1990.

Bonini L, Serventi FU, Simone L, Rozzi S, Ferrari PF, Fogassi L. Grasping neurons of monkey parietal and premotor cortices encode action goals at distinct levels of abstraction during complex action sequences. *The Journal of Neuroscience* 31, 5876–5887; 2011.

Boyd R, Richerson PJ. *Culture And The Evolutionary Process*. Chicago and London: Chicago University Press; 1985.

Boyd R, Richerson PJ. *The Origin And Evolution Of Cultures*. Oxford and New York: Oxford University Press; 2005.

Bruner E. Morphological differences in the parietal lobes within the human genus. A neurofunctional perspectice. *Current Anthropology* 51, Supplement 1 2010a, p. 557-588.

Bruner E The evolution of the parietal cortical areas in the human genus: between structure and cognition. In Broadfield D, Yuan M, Schick K, Toth N, editors. *The Human Brain Evolving: Paleoneurological Studies In Honor Of Ralph L. Holloway*. Gosport, Indiana: The Stone Age Institute, Stone Age Institute Press, and Bloomington, Indiana, Indiana University: "Stone Age Institute Publication Series Number 4"; 2010b. p. 83-96.

Bruner E, Holloway RL. A bivariate approach to the widening of the frontal lobes in the genus *Homo*. *Journal of Human Evolution* 58, 138–146, 2010.

Burgess, P. W., Quayle, A., Frith, C. D., Brain regions involved in prospective memory as determined by positron emission tomography Neuropsychologia 39 545–555, 2001;

Burgess, P. W., Gonen-Yaacovi, G., Volle, E., Functional neuroimaging studies of prospective memory: What have we learnt so far? Neuropsychologia 49: 2246-2257; 2011.

Calvo-Merino B, Glaser DE, Grezes J, Passingham RE, Haggard P. Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex* 15, 1243-1249; 2005.

Carruthers P, Chamberlain A, editors. *Evolution And The Human Mind. Modularity, Language And Meta-cognition*. Cambridge: Cambridge University Press; 2000.

Coolidge FL, Wynn T. Working memory, its executive functions, and the emergence of modern thinking. *Cambridge Archaeological Journal* 15, 5-26; 2005.

Corballis MC. Did language evolve from manual gestures? In Wray A, editor. *The Transition To Language*. Oxford and New York: Oxford University Press; 2002. p. 161-179.

Corballis MC. *The Recursive Mind. The Origins Of Human Language, Thought And Civilization*. Princeton and Oxford: Princeton University Press; 2011.

Craig AD. How do you feel – now? The anterior insula and human awareness. *Nature Reviews Neuroscience* 10: 59-70; 2009.

Damasio A. *Descartes' Error. Emotion, Reason And The Human Brain*, New York: Avon; 1994.

Damasio A. *The Feeling Of What Happens. Body, Emotion And The Making Of Consciousness*. London: William Heinemann: 2000.

de la Torre I, Mora R, Domínguez-Rodrigo M, de Luque L, Alcalá, L. The Oldowan industry of Peninj and its bearing on the reconstruction of the technological skills of Lower Pleistocene hominids. *Journal of Human Evolution* 44, 203-224¸ 2003.

Deacon T. *The Symbolic Species. The Co-evolution Of Language And The Brain*. New York and London: W.W.Norton; 1997.

Dean MC, Smith H. Chapter 10. Growth and development of the Nariokotome youth KNM-WT 15000, In: Grine FE, Fleagle JG, Leakey RE, editors. *The First Humans: Origin And Early Evolution Of The Genus Homo*. Berlin: Springer, "Vertebrate Palaeobiology and Paleoanthropology Series"; 2009. p. 101-117.

Dosenbach NUF, Fair DA, Miezin FM, Cohen AL, Wenger KK, Dosenbach RAT, Fox MD, Snyder AZ, Vincent JL, Raichle ME, Schlaggar BL, Petersen SE. Distinct brain networks for adaptive and stable task control in humans, *Proceedings of the National Academy of Sciences of the USA* 104: 11073-11078; 2007.

Doyon J, Benali H. Reorganization and plasticity in the adult brain during learning of motor skills. *Current Opinion in Neurobiology* 15, 161–167; 2005.

Durham WH. *Coevolution: Genes, Culture And Human Diversity*. Stanford: Stanford University Press; 1991.

Finn AS, Sheridan MA, Kam CLH, Hinshaw S, D'Esposito M. Longitudinal evidence for functional specialization of the neural circuit supporting working memory in the human brain. *The Journal of Neuroscience* 30, 11062–11067; 2010.

Fuster JM. *Memory In The Cerebral Cortex*. Cambridge, Massachussetts and London: The MIT Press, "A Bradford Book"; 1999.

Fuster JM. The prefrontal cortex – an update: time is of the essence. *Neuron* 30: 319-333; 2001.

Gallese V, Fadiga L, Fogassi L, Rizzolatti, G. Action recognition in the premotor cortex. *Brain* 119, 593-609;1996.

Gilbert SJ. Decoding the content of delayed intentions. *The Journal of Neuroscience* 31, 2888-2894; 2011.

Gilbert SL, Dobyns WB, Lahn BT. Genetic links between brain development and brain evolution. *Nature Reviews Genetics* 6, 581-590; 2005.

Gold JI, Shadlen MN. The neural basis of decision making. *Annual Review of Neuroscience* 30: 535-574; 2007.

Gonneaud J, Rauchs G, Groussard M, Landeau B, Mézenge F, de La Sayette V, Eustache F, Desgranges B. How do we process event-based and time-based intentions in the brain? an fMRI study of prospective memory in healthy individuals. Human Brain Mapping 35, 3066-3082; 2014.

Goren-Inbar N, Saragusti I. An Acheulian biface assemblage from the site of Gesher Benot Ya'aqov, Israel: Indications of African affinities. *Journal of Field Archaeology* 23, 15-30; 1996.

Goren-Inbar N, Feibel CS, Verosub KI, Melamed Y, Kislev ME, Tchernov E, Saragusti I. Pleistocene milestones on the Out-of-Africa corridor at Gesher Benot Ya'aqov, Israel. *Science* 289, 944-947; 2000.

Goren-Inbar N, Alperson N, Kislev ME, Simchoni O, Melamed I, Ben-Nun A, Werker E. Evidence of hominin control of fire at Gesher Benot Ya'akov, Israel. *Science* 304, 725-727; 2004.

Hazy TE, Frank MJ, O´Reilly RC. Towards an executive without a homunculus: computational models of the prefrontal cortex/basal ganglia system. *Philosophical Transactions of the Royal Society series B Biological Sciences* 362, 1601-1613 (Prescott J, Bryson JJ, Seth AK, editors. *Modelling Natural Action Selection*); 2007.

Holloway RL, Broadfield DC, Yuan MS. *Brain Endocasts: The Paleoneurological Evidence.* New York: Wiley-Liss, "The Human Fossil Record Volume 3"; 2004.

Husain M, Nachev P. Space and the parietal cortex. *Trends in Cognitive Sciences* 11, 30-36; 2006.

Iacoboni M. Understanding others: imitation, language, empathy. In Hurley S, Chater, N, editors. *Perspectives On Imitation: From Cognitive Neuroscience To Social Science*. Cambridge, Massachussetts and London: The MIT Press; 2005. p.77-99.

Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G. Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology* 3(3), e79, 0001-0007; 2005.

Ingvar DH. `Memory of the future´: an essay on the temporal organization of conscious awareness. *Human Neurobiology* 4: 127-136; 1985.

Jenkins LJ, Ranganath C. Prefrontal and medial temporal lobe activity at encoding predicts temporal context memory. *The Journal of Neuroscience* 30, 15558 –15565; 2010.

Kaas AL, van Mier H, Goebel R. The neural correlates of human working memory for haptically explored object orientations. *Cerebral Cortex* 17, 1637-1649; 2007.

Keysers C, Fadiga L, editors. *The Mirror Neuron System. A Special Issue Of Social Neuroscience.* London: Psychology Press; 2008.

Kikyo H, Ohki K, Miyashita Y. Neural correlates for feeling-of-knowing: an fMRI parametric analysis, *Neuron* 36: 177-186¸2002.

Konopka G, Geschwind DH. Human brain evolution: harnessing the genomics (r)evolution to link genes, cognition, and behavior. *Neuron* 68, 231-244; 2010.

Kreitzer AC, Malenka RC. Striatal plasticity and basal ganglia circuit function. *Neuron* 60, 543-554; 2008.

Langer J. The heterochronic evolution of Primate cognitive development. In Parker ST, Langer J, McKinney ML, editors. *Biology, Brains And Behavior. The Evolution Of Human Development*. Santa Fe: School of American Research, SAR Press, “School of American Research Advanced Seminar Series”, and Oxford: James Currey; 2000. p. 215-235)

Langer J. The heterochronic evolution of primate cognitive development. *Biological Theory* 1, 41-43 (Konrad Lorenz Institute for Evolution and Cognition Research); 2006.

Larson RK, Déprez V, Yamakido H, editors. *The Evolution Of Human Language. Biolinguistic Perspectives*. Cambridge: Cambridge University Press; 2010.

Lee ACH, Rudebeck SR. Investigating the interaction between spatial perception and working memory in the human medial temporal lobe. *Journal of Cognitive Neuroscience* 22, 2823–2835; 2010.

Lepre CJ, Roche H, Kent DV, Harmand S, Quinn RL, Brugal J-P, Texier P-J, Lenoble A, Feibel CS. An earlier origin for the Acheulian. *Nature* 477, 82-85; 2011.

Lieberman P. *Toward An Evolutionary Biology Of Language*, Cambridge, Massachussetts and London: The Belknap Press of Harvard University Press; 2006.

Lindner A, Iyer A, Kagan I, Andersen RA. Human posterior parietal cortex plans where to reach and what to avoid. *The Journal of Neuroscience* 30, 11715–11725; 2010.

Martin RD. Comparative aspects of brain evolution: scaling, energy costs and confounding variables. In Jablonski NG, Aiello L, editors. *The Origin And Diversification Of Language*, San Francisco: California Academy of Sciences, “Wattis Symposium Series in Anthropology” Memoirs of the California Academy of Sciences Number 24; 1998. p. 35-68.

Martínez I, Rosa. M, Quam R, Jarabo P, Lorenzo C, Bonmatí A, Gómez-Olivencia A, Gracia A, Arsuaga JL. Communicative capacities in Middle Pleistocene humans from the Sierra de Atapuerca in Spain. Quaternary International 295, 94-101; 2012.

Martínez I, Rosa M, Arsuaga J-L, Jarabo P, Quam R, Lorenzo C, Gracia A, Carretero J-M, Bermúdez de Castro J-M, Carbonell E. Auditory capacities in Middle Pleistocene humans from the Sierra de Atapuerca in Spain.Proceedings of the National Academy of Sciences 101, 9976-9981; 2004.

McDaniel MA, Einstein GO. *Prospective Memory. An Overview And Synthesis Of An Emerging Field*. Los Angeles and London: SAGE Publications “Cognitive Psychology Program”; 2007.

Meyer K, Kaplan JT, Essex R, Damasio H, Damasio A.. Seeing touch is correlated with content-specific activity in primary somatosensory cortex. *Cerebral Cortex* 21, 2113-2121; 2011.

Miller EK, Cohen JD. An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience* 24, 167-202; 2001.

Nelissen K, Borra E, Gerbella M, Rozzi S, Luppino G, Vanduffel W, Rizzolatti G, Orban GA. Action observation circuits in the macaque monkey cortex. *The Journal of Neuroscience* 31, 3743–3756; 2011.

Neubert FS, Mars RB, Thomas AG, Sallet J, Rushworth MFS. Comparison of human ventral frontal cortex areas for cognitive control and language with areas in monkey frontal cortex. *Neuron* 81, 700-713; 2012.

Noble W, Davidson I. *Human Evolution, Language And Mind. A Psychological And Archaeological Inquiry*. Cambridge: Cambridge University Press; 1996.

Oberman LM, Ramachandran VS. The simulating social mind: the role of the mirror neuron system and simulation in the social and communicative deficits of autism spectrum disorders. *Psychological Bulletin* 133, 310-327; 2007.

Orban GA, Rizzolatti G. An area specifically devoted to tool use in human left inferior parietal lobule. *Behavioral and Brain Sciences* 35: 234; 2012.

Osada T, Adachi Y, Kimura HM, Miyashita Y. Towards understanding of the cortical network underlying associative memory. *Philosophical Transactions of the Royal Society series B Biological Sciences* 363, 2187-2199 (*Japan: Its Tradition and Hot Topics in Biological Sciences*); 2008.

Pappu S, Gunnell Y, Akhilesh K, Braucher R, Taieb M, Demory F, Thouvery N. Early Pleistocene presence of Acheulian hominins in south India. *Science* 331, 1596-1599; 2011.

Parker ST, Langer J, McKinney ML, editors. *Biology, Brains And Behavior. The Evolution Of Human Development*. Santa Fe: School of American Research, SAR Press, “School of American Research Advanced Seminar Series”, and Oxford: James Currey; 2000.

Peeters R., Simone L, Neliseen K, Fabbri-Destro M, Vanduffel W, Rizzolatti G, Orban GA. The representation of tool use in humans and monkeys: common and uniquely human features. *The Journal of Neuroscience* 29: 11523-115239; 2009.

Pennartz CMA, Ito R, Verschure PFMJ, Battaglia FP, Robbins TW. The hippocampal–striatal axis in learning, prediction and goal-directed behavior. *Trends in Neurosciences* 34, 548-559; 2011.

Petersen SE, Posner MI. The attention system of the human brain: 20 years after. *Annual Review of Neuroscience* 35, 73–89; 2012.

Piaget J. *The Language And Thought Of The Child*. London: Routledge & Kegan Paul; 1959.

Richerson PJ, Mortensen C, editors. *Cultural Evolution. Society, Technology, Language, And Religion*. Cambridge, Massachussetts and London: The MIT Press; 2013.

Rizzolatti G, Arbib MA. Language within our grasp. *Trends in Neurosciences* 21, 188-194; 1998.

Rizzolatti G, Craighero L. The mirror-neuron system. *Annual Review of Neuroscience* 27, 169-192; 2004.

Rizzolatti, G, Fogassi L, Gallese V. Cortical mechanisms subserving object grasping, action understanding, and imitation. In Gazzaniga MS, editor. *The Cognitive Neurosciences III*, Cambridge, Massachussetts and London: The MIT Press, “A Bradford Book”; 2004. p. 427-440.

Roche H, Brugal J-P, Delagnes A, Feibel C, Harmand S, Kibunjia M, Prat S, Texier P-J. Les sites archéologiques plio-pléistocènes de la formation de Nachukui, Ouest-Turkana, Kenya: bilan synthétique 1997–2001. *Comptes Rendus Palévol* 2, 663-673; 2003.

Roe DA. British Lower and Middle Palaeolithic hand-axe groups, *Proceedings of the Prehistoric Society* 34: 1-82.

Romo R, Salinas E. Touch and go: decision-making mechanisms in somatosensation. *Annual Review of Neuroscience B* 24, 107-137; 2001.

Rushworth MFS, Buckley MJ, Behrens TEJ, Walton ME, Bannerman DM. Functional organization of the medial frontal cortex. *Current Opinion in Neurobiology* 17, 220-227; 2007.

Sakai K. Task Set and Prefrontal Cortex. *Annual Review of Neuroscience* 31:219-245; 2008.

Schlanger N. Understanding Levallois: lithic technology and cognitive archaeology. *Cambridge Archaeological Journal* 6, 231-254; 1996.

Smith RE, editor. *Prospective Memory*. Cambridge Massachussetts and Göttingen: Zeitschrift für Psychologie/Journal of Psychology 2019 number 2 (Hogrefe Publishing); 2011.

Sterelny K. *The Evolved Apprentice. How Evolution Made Humans Unique*. Cambridge, Massachussetts and London: The MIT Press, “A Bradford Book”; 2012.

Stout D. Neural foundations of perception and action in stone knapping. In Roux V, Bril B, editors. *Stone Knapping, The Necessary Conditions For A Uniquely Hominin Behaviour*. Cambridge: University of Cambridge, McDonald Institute for Archaeological Research, “McDonald Institute Monographs”; 2005. p. 273-286.

Stout D. Oldowan toolmaking and hominin brain evolution: theory and research using positron emission tomography (PET). In Toth N, Schick K, editors. *The Oldowan: Case Studies Into The Earliest Stone Age*. Gosport, Indiana: The Stone Age Institute, Stone Age Institute Press, “Stone Age Institute Publication Series Number 1”; 2006. p. 267-305.

Stout D. Stone-toolmaking and the evolution of human culture and cognition. *Philosophical Transactions of the Royal Society series B Biological Sciences* 366, 1050-1059; 2011.

Stout D, Chaminade T. Making tools and making sense: Complex, intentional behaviour in human evolution. *Cambridge Archaeological Journal* 19: 85-96; 2009.

Stout D, Toth N, Schick K. Comparing the neural foundations of Oldowan and Acheulean toolmaking: a pilot study using positron emission tomography (PET). In Toth N, Schick K, editors. *The Oldowan: Case Studies Into The Earliest Stone Age*. Gosport, Indiana: The Stone Age Institute, Stone Age Institute Press, and Bloomington, Indiana, Indiana University: “Stone Age Institute Publication Series Number 1”; 2006. p. 321-331.

Stout D, Toth N, Schick K, Chaminade T. Neural correlates of Early Stone Age toolmaking: technology, language and cognition in human evolution. *Philosophical Transactions of the Royal Society series B Biological Sciences* 363, 1939-1949 (Renfrew C, Frith C, Malafouris L, editors, *The Sapient Mind: Archaeology Meets Neuroscience*); 2008.

Tomasello M. *Origins Of Human Communication* Cambridge, Massachussetts, and London: The MIT Press, “A Bradford Book”; 2010.

Vallverdú J, Saladié P, Rosas A, Huguet R, Cáceres I, Mosquera M, Garcia-Tabernero A, Estalrrich A, Lozano-Fernández I, Pineda-Alcalá A, Carrancho A, Villalaín JJ, Bourlès D, Braucher R, Lebatard A, Vilalta J, Esteban-Nadal M, Bennàsar ML, Bastir M, López-Polín L, Ollé A, Vergé JM, Ros-Montoya S, Martínez-Navarro B, García A, Martinell J, Expósito M, Burjachs F, Agustí J, Carbonell E. Age and Date for Early Arrival of the Acheulian in Europe (Barranc de la Boella, la Canonja, Spain) *PLOS ONE* 9 iIssue 7 e103634; 2014.

van Peer P. *The Levallois Reduction Strategy*. Madison: Prehistory Press, “Monographs in World Archaeology 13”; 1992.

Volle, E., Gonen-Yaacovi, G., Costello, A. de L., Gilbert, S. J., Burgess, P. W., The role of rostral prefrontal cortex in prospective memory: A voxel-based lesion study Neuropsychologia 49 2185– 2198 2011;

Walker MJ. Long–term memory and Middle Pleistocene `Mysterians´. In de Beaune SA, Coolidge FL, Wynn T, editors. *Cognitive Archaeology And Human Evolution*. Cambridge and New York: Cambridge University Press; 2009. p. 75-84.

Walker MJ, López-Martínez M, Carrión-García JS, Rodríguez-Estrella T, San-Nicolás-del-Toro M, Schwenninger J-L, López-Jiménez A, Ortega-Rodrigáñez J, Haber-Uriarte M, Polo-Camacho J-L, García-Torres J, Campillo-Boj M, Avilés-Fernández A, Zack W. Cueva Negra del Estrecho del Río Quípar (Murcia, Spain): A late Early Pleistocene hominin site with an “Acheulo-Levalloiso-Mousteroid” Palaeolithic assemblage, *Quaternary International* 294, 135-159; 2013.

Weaver AH. Reciprocal evolution of the cerebellum and neocortex in fossil humans. *Proceedings of the National Academy of Sciences USA* 102: 3576-3580; 2005.

West, R. The temporal dynamics of prospective memory: A review of the ERP and prospective memory literature. Neuropsychologia 49, 2233-45; 2011.

White M, Pettitt P. Technology of early Palaeolithic western Europe: innovation, variability and a unified framework. *Lithics* 16: 27-40; 1995.

Wrangham R. *Catching Fire. How Cooking Made Us Human.* London: Profile Books; 2009.

Wray A, editor. *The Transition To Language*. Oxford and New York: Oxford University Press; 2002.

Wynn T. The intelligence of later Acheulean hominids. *Man* 14, 371-391, 1979.

Wynn T. *The Evolution Of Spatial Competence*. Urbana and Chicago: University of Illinois Press, “Illinois Studies in Anthropology No. 17”; 1989.

Wynn T. Layers of thinking in tool behavior. In Gibson KR, Ingold T, editors. *Tools, Language And Cognition In Human Evolution*. Cambridge: Cambridge University Press; 1993. p. 389-406.

Wynn T. Handaxe enigmas. *World Archaeology* 27, 10-24; 1995.

Wynn T. Symmetry and the evolution of the modular linguistic mind. In Carruthers P, Chamberlain A, editors. *Evolution And The Human Mind: Modularity, Language, And Meta-cognition*. Cambridge: Cambridge University Press, 2000. p. 113-139.

Wynn T., Archaeology and cognitive evolution, *Behavioral and Brain Sciences* 25: 389-438; 2002.

Wynn T, Coolidge FL. How Levallois reduction is similar to, and not similar to, playing chess. In Nowell A, Davidson I, editors. *Stone Tools And The Evolution of Human Cognition*. Boulder: University Press of Colorado; 2010. p. 83-103.

Wynn T, Coolidge FL. *How To Think Like A Neandertal*. Oxford and New York: Oxford University Press; 2012.

Yassa MA, Stark CEL. Pattern separation in the hippocampus. *Trends in Neuroscience* 34, 548-559; 2011.

Zhou YD, Ardestani A, Fuster JM. Distributed and associative working memory. *Cerebral Cortex* 17 Supplement, 17477-17487; 2007.