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Working Memory: A Cognitive Limit to Non-Human Primate Recursive Thinking Prior to Hominid Evolution

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Abstract: In this paper I explore the possibility that recursion is not part of the cognitive repertoire of non-human primates such as chimpanzees due to limited working memory capacity. Multiple lines of data, from nut cracking to the velocity and duration of cognitive development, imply that chimpanzees have a short-term memory size that limits working memory to dealing with two, or at most three, concepts at a time. If so, as a species they lack the cognitive capacity for recursive thinking to be integrated into systems of social organization and communication. If this limited working memory capacity is projected back to a common ancestor for *Pan* and *Homo*, it follows that early hominid ancestors would have had limited working memory capacity. Hence we should find evidence for expansion of working memory capacity during hominid evolution reflected in changes in the products of conceptually framed activities such as stone tool production. Data on the artifacts made by our hominid ancestors support this expansion hypothesis for hominid working memory, thereby leading to qualitative differences between *Pan* and *Homo*.

Keywords: working memory, recursion, primate behavior, hominid evolution, nut cracking

The substantial differences in cognitive abilities between *Homo sapiens* and non-human primates (see Parker and McKinney, 1999 for a recent review) simply reflect, according to some researchers (e.g., Finlay, Darlington, and Nicastro 2001; Marino, 2006, among others), quantitative extension of cognitive capacities already present in a common ancestor for *Pan* and *Homo* via allometrically scaled expansion of brain structures. Support for this viewpoint is seen in the fact that behavioral traits supposedly making *Homo sapiens* cognitively unique among the primates are also present in non-human primates. Even culture – often been viewed as providing the firmest evidence for a qualitative divide (Derksen, 2005; Holloway, 1969; Wimsatt and Griesemer, 2007) – may have precursors, it is argued, in non-human primates in the form of group specific behavior transmitted non-genetically through imitation or learning within a social context (de Waal and Tyack, 2003; Lycett, Collard, and McGrew, 2007, among others). Defining culture through behavior and its mode of transmission, though, ignores the distinction made by cultural anthropologists between custom or tradition and culture, with

the latter based not on behavior but shared systems of meaning that guide and affect behavior collectively (Geertz, 1973; Kroeber and Parsons, 1958; Keesing, 1974; Schneider, 1976) and are expressed through idea systems (Leaf, in press). The transmission definition of culture has been criticized as leading to “thin descriptions” that fail to express the richness of culture and “fall crucially short of an adequate account of the nature and transmission of culture” (Wimsatt and Griesemer, 2007, p. 237). Nonetheless, observations of this kind have greatly enhanced our understanding of the cognitive capacities of non-human primates regardless of their adequacy as counterexamples to a claimed qualitative difference between ourselves and other primates.

These counterexamples are circumscribed, though, by their tendency to focus on the consequences of, and not the neurological basis for, cognitive abilities. They do not adequately take into account relevant differences in brain organization between humans and non-human primates (Premack, 2007). Recent research has shown significant brain structure dissimilarities in comparison of humans to chimpanzees (Buxhoeveden and Casanova, 2002; Preuss, 2004; Semendeferi et al., 2001), especially in brain regions associated with social cognition (Premack, 2007) (though, it should be noted, other aspects of brain organization either do not show differences [Nimchinsky et al., 1999; Raghanti et al., 2007] or show differences just due to allometric scaling [Sherwood et al., 2006]). Neurological differences between *Homo sapiens* and the non-human primates also include differences in gene expression related to brain functioning (Cáceres et al., 2007; Preuss et al., 2004).

These neurological differences may have enabled qualitatively different abilities to arise subsequent to the speciation event that genetically separated the pongids from the hominids. To sustain this argument, though, we need to identify what might be a qualitative difference between human and non-human primates as well as its neurological basis. One plausible candidate for a qualitative difference – identified through comparison of language performance deconstructed into its underlying cognitive and biological underpinnings – is recursion. (By *recursion* is meant a procedure, production rule, function, or algorithm whose implementation includes a step in which the procedure itself is applied to the outcome of a previous step in the procedure’s implementation [Black and Rodgers, 2007; Odifreddi 2007]).¹ In a recent review of language components divided into faculty of language (broad sense) and faculty of language (narrow sense), with the former based on homologues with animal cognitive abilities, recursive constructions were identified as a cognitive capacity specific to *Homo sapiens* (Fitch, Hauser, and Chomsky, 2005; Hauser, Chomsky, and Fitch, 2002). This conclusion is supported by an experiment with cotton-top tamarins showing that they are able to infer patterns based on a finite state, but not a phrase-structure, grammar (Fitch and Hauser, 2004; Hauser, Weiss, and Marcus, 2002), thus suggesting they lack the cognitive ability to infer a recursion rule. Recursive syntactic rules underlie much of the richness of human languages, yet “little progress has been made in identifying the specific capabilities [underlying recursion] that are lacking in other animals” (Hauser, Chomsky, and Fitch, 2002, p. 1576).

One recent suggestion of a neurological basis for the absence of recursion as a cognitive process even in language-like productions of non-human primates is the size of short-term memory as it relates to working memory capacity. Aboitiz and his co-workers have suggested that language evolution involves “the acquisition of recursion ... [made] possible through the *increasing complexity of the short-term memory networks*” (Aboitiz et al., 2006, p. 51,

emphasis added; see also, Coolidge and Wynn, 2007). The proposed elaboration of neural networks involved in active memory that enabled linguistic recursion “demands significant working memory resources” (Aboitiz et al., 2006, p. 41). If so, then a restricted working memory capacity in an ancestor common to modern-day *Pan* and *Homo* may account for the absence of recursion in the cognitive repertoire of non-human primates, in general, and in *Pan*, more specifically.

In this article I argue that the chimpanzees (*Pan troglodytes* and *Pan paniscus*) have insufficient working memory capacity to enable recursion to be part of their cognitive repertoire. Given the phylogenetic position of *Pan* in comparison to other primates and their greater degree of encephalization, this would also account, retroactively, for the absence of recursion in the cognitive repertoire of other non-human primates. In the forward direction, if we postulate that a last common ancestor between *Homo* and *Pan* had the limited working memory capacity of modern *Pan*, expansion in working memory capacity in our ancestral line would have enabled recursion to uniquely become part of our cognitive repertoire and thereby led to recursion-based, qualitative changes in cognitive capacity and abilities in our species, *Homo sapiens*.

Although we cannot automatically equate behavioral and cognitive capacities of extant *Pan* with the behavioral and cognitive capacities of a last common ancestor with *Homo*, assigning the working memory capacities of modern *Pan* to a last common ancestor is evolutionarily conservative. This assignment assumes stasis in working memory capacity in the lineages leading to modern *Pan* over the 8 – 9 million years (Avers 1989; Read 1975) from a last common ancestor with *Homo*. Conversely, if there has been evolutionary increase in working memory capacity in the lineages leading to modern *Pan*, then we would be overestimating the working memory capacity of a last common ancestor and thereby assigning even more evolutionary change along the lineage leading to modern *Homo sapiens*. A contradiction only arises for the argument being made here if there has been devolution in the working memory capacity of *Pan*. This possibility is contradicted by the lack of any evidence for devolution in brain encephalization in the evolving *Pan* lineages. In addition, for specific behaviors such as the nut cracking behavior to be discussed below, standard cladistic arguments lead to assigning the mental capacity for nut cracking to a last common ancestor since the sister clades, *Pan* and *Homo*, each have the characteristic, nut cracking, whereas *Pongo*, an outlying clade, does not include nut cracking in its tool use repertoire (Fox and Bin’Muhammad, 2002, Table 1). Hence we will assume that a last common ancestor has the working memory capacity of modern *Pan* and was capable of nut cracking.

Working Memory: A Brief Overview

What constitutes working memory is not yet worked out completely and is still undergoing extensive research. (A Google Scholar search on *working memory* yields more than 20,000 articles since 2005.) The initial, domain-general view of a unitary short-term memory structure has been replaced with a more complex, multi-component working memory model (Miyake and Shah, 1999). The canonical model for working memory is derived from Baddeley and Hitch’s (1974) tripartite division of working memory into a central executive system coupled to visuospatial “sketchpad” and phonological loop subsystems (Baddeley, 1986, 2003, pp. 830, 833). Other memory components are also

associated with working memory (Case, 1995; Cowan, 1995; Fuster, 1995a; O'Reilly, Braver, and Cohen, 1999), including short-term memories for auditory and tactile sensory inputs (Pasternak and Greenlee, 2005 and references therein). Baddeley (2000) has also suggested that working memory may include an episodic buffer.

Of these components, some such as the phonological subsystem are likely to have undergone expansion during hominid evolution and the development of a verbal buffer in the phonological subsystem may be unique to *Homo sapiens* (Smith, Jonides, and Koeppe, 1996). Because of possible evolutionary differences in aspects of non-human primate working memory in comparison to human working memory (such as the phonological loop), we will consider working memory here in a general way as having “short-term-memory (STM) representational components plus a general, executive-attention component” organized in the form of “a hierarchical system” (Kane and Engle, 2002, p. 38). Short-term memory will be viewed here (whether it subsumes the buffer portion of the phonological loop, the visuospatial, or some other subsystem of working memory) as holding activated information, some subset of which will be subjected to attentional control and processing by the executive function of working memory (Cowan 1999; Engle, Tuholski, Laughlin, and Conway, 1999). Short-term memory is, in this sense, analogous to data registers in computer architecture: “The data registers of the CPU [Central Processing Unit] function as a scratch pad...” (Editors of the American Heritage Dictionaries, 2001, p. 63). The size of short-term memory is correlated strongly with the capacity of working memory (Colom et al., 2005; Conway et al., 2002).

The inclusion of attention as part of the function of working memory parallels Fuster's use of the term *attentive memory* to refer to “a broad network of associative memory” that serves “as a perceptual memory fragment in order to execute a motor act in the near future” (Fuster, 1995b, p. 64; see also Cowan, 2005). The notion of attention, or attentive memory, usefully links activation of neurological structures involved with short-term memory to outcomes in the form of motor action through the executive functioning of working memory: “attention and working memory address the fundamental limits in our ability to encode and maintain behaviorally relevant information, processes that are critical for goal-driven processing” (Awh, Vogel and Oh, 2006, p. 201). Working memory can thus be viewed as being involved in “a range of cognitive activities, such as reasoning, learning and comprehension” (Baddeley, 2003, p. 829) that enables “the temporary maintenance of limited information, where that information is kept on-line or available for immediate access by other cognitive processes” (Awh and Jonides, 2001, p. 119), “plays a critical role in integrating information during problem solving...[by holding] recently processed information ... [and maintaining] information for the construction of an overall solution to problems” (Swanson, Jerman, and Zheng, 2008, p. 368) and reflects “the ability to apply activation to memory representations, to either bring them into focus or maintain them in focus, particularly in the face of interference or distraction” (Engle, Kane, and Tuholski, 1999, p. 104). We will use this composite characterization of working memory for relating behavior patterns of chimpanzees to working memory.

The executive component of working memory is generally associated with Brodmann Areas 9 and 46 in the dorsolateral section of the prefrontal cortex (Gazzaniga, Ivry, and Mangun, 2002; Goldman-Rakic, 1987; Henson, 2001; McCarthy et al., 1994, Petrides and Pandya, 1999; Smith and Jonides, 1999). The role of the executive component of working memory in task performance coordination has been postulated to occur through top-

down control and coordination of activity of the subcortical areas to which the cortical areas are connected (Miller and Cohen, 2001). This may be seen in Greenfield's (1991) argument that "organization of hierarchically complex programs of object combination would involve input from the anterior superior prefrontal cortex (perhaps Brodmann's area 9) (Roland, 1985) to the superior part of the left posterior inferior frontal area" (Greenfield, 1991, p. 544).

Direct evidence demonstrating prefrontal signal projections from cortical to subcortical areas has been developed by Johnston and Everling (2006) for rhesus monkeys (*Macaca mulatta*). They have demonstrated that neurons firing in the dorsolateral prefrontal cortex during an antisaccade performance task "send signals selective for stimulus location, saccade direction, and task directly to the SC [superior colliculus]" (Johnston and Everling, 2006, p. 12475). The authors conclude that their experimental result "provides evidence that the DLPFC [dorsolateral prefrontal cortex] may indeed influence behavior by orchestrating the activity of target structures" (2006, p. 12477).

The role of the dorsolateral prefrontal cortex in coordinated task performance has been demonstrated in Japanese macaques (*Macaca fuscata*) by Obayashi et al. (2002). They have shown that Brodmann Areas 9 and 46 – located in the dorsolateral prefrontal cortex associated with the executive component of working memory – is increasingly activated when the macaques were required to do a two-step sequence of coordinated actions before being rewarded in comparison to a one-step action. For the two-step action, the macaques were required to use one rake located inside a clear plastic tube to retrieve a food-object in the tube through an opening in the side of the tube and then to use a second rake outside the tube to retrieve the food object. Positron emission tomography scans were used to measure brain area activation and the coordinated task was compared to the activation level occurring when the macaques only needed to use a single rake to retrieve a reward. Their results showed that "When activation in the single condition was subtracted from the double condition, [there was] a greater increase in activation of the bilateral PFC (area 9/46)" (Obayashi et al., 2002, p. 2353). Thus dorsolateral prefrontal cortex is increasingly activated with more elaborated task performance as would be expected if performance involves an increase in the number of components that must be coordinated through the executive component of working memory.

That there has been significant evolutionary change in the size of short-term memory, hence in working memory capacity for humans from a last common ancestor with the chimpanzees, is given credence by evolutionary expansion of the prefrontal cortex. The prefrontal cortex as a whole has undergone non-allometric expansion during hominid evolution (Rilling, 2006 and references therein), though it is not known if this expansion applies equally to all the areas associated with working memory. Some researchers have suggested that Area 10 (the anterior prefrontal cortex) may also be involved in the activity of working memory, especially in "processes that distinguish target and non-target stimuli during recognition in working memory" (Leung, Gore, and Goldman-Rakic, 2005 p. 1746) due to the fact that the "FP-PFC [frontopolar prefrontal cortex, Area 10] subserves cognitive functions related to the coordination, monitoring, and integration of subgoal processes within WM" (Braver and Bongiolatti, 2001, p. 535). Area 10 has undergone non-allometric expansion (Semendeferi et al., 2001), which suggests that its relationship to working memory may have become more elaborated during hominid evolution. Though data on the allometric growth pattern for Areas 9 and 46 have not yet been worked out, overall there has been extensive prefrontal cortex expansion (Finlay et al., 2001) in which "higher-order association cortices have expanded dramatically" (Rilling, 2006, p. 75).

The expansion of the more frontal areas of the brain can be tracked with hominid fossil crania as frontal expansion parallels the evolutionary development of a high forehead and non-prognathic face in modern *Homo sapiens* (Lieberman, McBratney, and Krowitz, 2002). Changes in working memory due to expansion of brain size had consequences for hominid cognitive capacity (Russell, 1996) that have been linked to innovation in material culture during the Upper Paleolithic (Coolidge and Wynn, 2004, 2005). Though Coolidge and Wynn only refer to the Upper Paleolithic, changes in working memory are likely to predate that time period. The tripling of brain size in human evolution from the size for a last common ancestor with *Pan*, coupled with non-allometric expansion of prefrontal cortex during hominid evolution, provides the backdrop for the changes in short-term memory aspect of working memory discussed next.

Chimpanzee Short-Term Memory Size

Published data on *Pan troglodytes* behavior both in the wild and in captivity suggest a limit of 2-3 concepts being held simultaneously in a short term memory buffer for working memory, whether the chimpanzee is interacting with the physical or the social world. The lines of evidence are multiple: the cognitive challenges of nut cracking, spontaneous classification of objects, manipulation of entities (objects, gestures, tokens in language learning experiments, and individual interactions), recall by memory of an ordinal sequence of numbers, and the rate and time span for cognitive ontogenetic development. Of these lines of evidence, the data on recall of ordinal sequences relates most directly to the way the size of short-term memory has been measured in humans. Each of these lines of evidence will be considered in turn.

Nut Cracking Behavior

Nut cracking behavior has been studied extensively among wild-living chimpanzees at two locations: Taï National Park in Côte D'Ivoire and Bossou in Guinea (McGrew et al., 1997). The chimpanzees in these two localities differ in the way they crack nuts. At Bossou, three objects are manipulated: a rock anvil on which the nut is cracked, the nut to be cracked, and a hammer stone to crack the nut. At Taï National Park only two objects are manipulated – the nut and the hammer stone – as the chimpanzees use naturally occurring anvils in the form of surface-level roots or flat rock outcroppings (Boesch and Boesch, 1983). The Taï chimpanzees have never been observed to use loose stones as anvils (Boesch and Boesch, 1983). (These differences in nut cracking at the two localities will be discussed below in relationship to the operation of working memory.) Of all the tool-based tasks engaged in by chimpanzees, nut cracking is cognitively the most demanding (Hayashi, Mizuno, and Matsuzawa, 2005; Matsuzawa, 1996). The behavior is not biological but learned and learning seems to be difficult as shown by the fact that some chimpanzee populations “have not learned to utilize a resource that is plentifully available and technically accessible” (McGrew et al., 1997, p. 368). That nut cracking is cognitively challenging is also seen in the failure – over a two-week period – by naïve, captive chimpanzees to figure out how to crack nuts after being provisioned with nuts and hammer stones despite their attempts to open the nuts (Funk, 1985).

Nut cracking requires putting together a sequence of coordinated actions: “To accomplish the nut cracking, the infant chimpanzee must put together the five basic actions: Take (Pick), Put, Hold, Hit, and Eat” (Inoue-Nakamura and Matuzawa, 1997, p. 170). At Bossou, an anvil is selected, a nut is placed on the anvil and a hammer stone is then held and used to hit the nut, then

the nutmeat freed from the shell is eaten. As simple as the sequence may appear to us, apparently it is not for the chimpanzees and requires extensive cognitive development on the part of a growing infant before it finally learns how to crack nuts at around 3.5 years of age. Learning to crack nuts develops in parallel with the cognitive development of infant chimpanzees for object manipulation: (1) single-object manipulation at around one year of age, (2) object association manipulation involving two objects that begins around two years of age, and (3) performance of multiple actions with objects starting around three years of age (Matsuzawa, 2007; see also Figure 5 in Spinozzi et al., 1998).

Chimpanzees that learn to crack nuts do so initially through observation of one's biological mother and later by observation of other nut-cracking adults, along with trial and error attempts at nut cracking (Inoue-Nakamura and Matsuzawa, 1997; Matsuzawa, 2007). Around 1.5 years of age, infants can do in isolation any one of the actions needed for nut cracking. Around 2.5 years of age they begin putting together two of the necessary actions, such as *putting* a nut on an anvil and *hitting* it with the knuckles (Inoue-Nakamura and Matsuzawa, 1997). It is only around age 3.5 that the developing infant is able to put together the sequence of selecting a stone as an anvil, placing a nut on it and hitting it with a stone hammer so as to crack it open (Matsuzawa, 1994, 2007).

The cognitive difficulty in learning to crack nuts can be seen as well in the fact that not all chimpanzees at Bossou learn to crack nuts. Data collected over a period of 16 years (see Table 1) show that no chimpanzee learns to crack nuts before 3 years of age and about 1/4 of the juvenile-to-adult chimpanzees have never cracked nuts: "If not learnt by the end of this period [3 – 5 years of age], the skill will not be acquired..." (Biro et al., 2003, p. 216). The failure to learn to crack nuts is particularly significant since the non-nut cracking chimpanzees watch the nut-cracking chimpanzees, hence do not lack nut cracking exemplars. The chimpanzees that do not learn to crack nuts fail to recognize that three objects are necessary for cracking a nut. Instead of manipulating the three objects, they attempt to crack nuts by manipulating only two of the three objects. For example, a 7-year old female who does not crack nuts would place the nut on the anvil and then hit it with her hand or foot, a sequence comparable to the behavior of infants at around 2.5 years of age (Inoue-Nakamura and Matsuzawa, 1997, p. 170).

Table 1. Nut cracking at Bossou, Guinea¹

Crack Nuts	Age < 3.0	Age ≥ 3.0
Yes	0	22
No	22	7

¹Data from Biro et al., 2003

Failure to learn to crack nuts is not so much a problem of physical coordination in manipulating three objects (though skill is involved in efficient nut cracking), but of not understanding the relationship between anvil, nut and hammer for successful nut cracking. Or, to put it another way, it stems from inability to keep three objects in ST-WMC on which attention must be focused while engaging in goal-directed problem solving, namely opening a nut to get at the nut meat.

Nut cracking requires precisely the characteristics associated with working memory. One characterization of the executive component of working memory is that it “reflects a general capability to control attention to maintain a limited amount of information in an active state, particularly in the presence of interference” (Kane and Engle, 2002, pp. 657-658). In a similar vein, Linden (2007) comments: “Working memory (WM) is a central cognitive function at the interface of *perception and action*. It is assumed to operate whenever information has to be retained and manipulated over brief periods of time to guide an immediate response” (p. 257, emphasis added). Nut cracking requires the chimpanzee to focus on the anvil, the nut to be cracked, and the action taken with the hammer stone. It occurs in a social context and so attention must be kept on the task at hand while in the presence of other chimpanzees that may be closely watching or otherwise distracting. Attention must constantly be focused on three items – the anvil, the nut and the hammer stone – and their spatial relationship to each other, along with rapid calculations regarding how the blow should be made. The anvil is not perfectly flat, can be at an angle, and may not be steady.

The implication of nut cracking for the size of ST-WMC depends on how the action of nut cracking is characterized. Some characterizations suggest that only ST-WMC = 2 is required. For example, Greenfield (1991) considers nut cracking to just involve a “pot” strategy wherein two objects are each associated with a third object (the third object is like a pot in which the first two objects are collected) since the nut is brought to the anvil and the stone hammer is then brought to the anvil by cracking the nut. Her characterization implies only ST-WMC = 2 would be required since the two actions are done sequentially. Similarly, Parker and McKinney (1999, p. 55) consider nut cracking to consist of two sequential, interrelated bifocal coordination actions: first, the nut is coordinated with the anvil by placing the nut on the anvil and second the hammer stone is coordinated with the nut through striking it, thus making nut cracking a sequence of two bifocal actions.

Both of these characterizations would fit better the method of nut cracking at Taï than at Bossou since the anvil at Taï is a fixed object in the environment and placing the nut on the anvil can be considered to be an action separate from striking the nut once it is placed on the anvil. For nut cracking at Bossou, though, neither characterization fully takes into account the need to keep the anvil, the nut and the hammer stone active in working memory as all three objects are jointly manipulated in order to successfully crack open a nut.

For both sets of authors, only the added complexity of using a stone as a wedge to stabilize an anvil (Matsuzawa, 1996) would bring the action to the level of complexity wherein ST-WMC = 3 would be required. The wedge action is characterized by Greenfield (1991) as a subassembly strategy (two objects – the wedge and the anvil – are associated and then jointly associated with a third object – the nut to be cracked) and by Parker and McKinney (1999, p. 55) as elaborated coordination. However, the use of the wedge only requires the wedge and the anvil to be activated in working memory while achieving the goal of a stable anvil. Once the anvil is stabilized, the wedge need not be kept in activated in working memory when cracking a nut.

Due to the more complex nature of nut cracking at Bossou, ST-WMC = 2 - 3 is assumed here to characterize the short-term memory component of working memory required to successfully crack nuts. The use of a wedge – though it makes the overall sequence more complex as argued by Matsuzawa (1996) – is not assumed to require additional short-term memory due to the fact that placing a wedge under an anvil is a separate action done prior to cracking a nut. Variation in the size of short-term memory across individuals, with some only having a ST-WMC of size 2, would account for why as many as 25% of the individuals apparently never learn to crack nuts even though they observe nut cracking chimpanzees.

Alternative explanations for the failure of some chimpanzees to learn to crack nuts, other than the size of short-term memory, include the following: (1) disrupted vertical transmission – lack of a nut cracking biological mother; (2) division of labor – some individuals obtain nuts and other individuals do the nut cracking; (3) “cheater” strategy – non-nut cracking chimpanzees scrounge rather than cracking nuts; and (4) physical skills –an individual lacks the required hand and eye coordination to crack nuts. The first can be eliminated immediately since two of the females at Bossou who do not crack nuts each had an offspring that learned to crack nuts by watching other adults crack nuts (Inoue-Nakamura and Matsuzawa, 1997; Matsuzawa, 1994). The second suggestion is not supported by the reports on nut cracking at Tai or Bossou. In both regions, individuals crack the nuts they obtain. There is no report of any individual, including the chimpanzees that do not crack nuts, obtaining nuts that are then given to another individual to crack (or even just left on the ground for another individual to pick up and crack). The third suggestion is intriguing in view of the extensive literature on the way “cheating” and “scrounging” strategies may increase one’s relative fitness. This hypothesis can be tested with the data from Bossou as the conditions for discovering whether scrounging is a less-costly strategy are in place. Some infants who have just learned to crack nuts will continue to scrounge from their mothers or other adults (Inoue-Nakamura and Matsuzawa, 1997, p. 164), hence there is an opportunity for a developing infant to assess whether scrounging is a less-costly strategy than nut cracking. However, there is no reported instance of a chimpanzee known to have learned to crack nuts who then stopped cracking nuts (see Table 2, Biro et al., 2003). The fourth suggestion only applies to the age at which infants begin to use a hammer stone. Coordination and muscle development are involved at this stage since no infant under two years of age was observed to use a hammer stone (Inoue-Nakamura and Matsuzawa, 1997). Lack of coordination does not apply difficulty in cracking nuts by older chimpanzees for whom, as discussed above, failure is due to not putting together the proper sequence of actions. The evidence, then, does not support these alternative explanations.

Further evidence for the role of working memory in nut cracking can be found in the differences between nut cracking at Bossou and at Tai National Park. At Tai, anvils are part of the landscape and all of the chimpanzees crack nuts. Matsuzawa (2003) has suggested that the anvil difference in the two locations makes nut cracking at Tai a cognitively less demanding task, hence the difference in the proportion of individuals who crack nuts at the two localities.

We can flesh out his suggestion by noting that the anvils are part of the spatial background for the chimpanzees at Tai, hence they do not need to be kept in ST-WMC as an object of attention to be conceptually manipulated. This agrees with experimental work on the relationship between visual searching and working memory by Woodman, Luck and Schall, (2007). They “asked subjects to perform a visual search task during the delay interval of a visual working memory task. The 2 tasks were found to interfere with each other when the search targets changed from trial to trial, *but not when target identity remained constant*” (2007, p.

i118, emphasis added). They concluded: “a memory representation *other than one actively maintained by prefrontal cortex neurons* is used to control the search process when *the target remains constant across trials*. In contrast, more complex visual working memory mechanisms—which rely on prefrontal cortex— are necessary when the target changes frequently. Thus, it is unlikely that visual or amodal working memory representations stored in prefrontal cortex are used to control attention when the target remains constant from trial to trial.” (2007, p. i121, emphasis added). Similar results were obtained by Rossi et al. (2001) who found that primates with lesions in the prefrontal cortex performed just as well with constant visual targets, but much more poorly with visual targets that varied.

For the Tai chimpanzees, the anvils are fixed targets both within an episode of nut cracking and between episodes and are not tools to be manipulated (Sugiyama, 1997). Hence, according to the experimental results discussed above, ST-WMC = 3 would not be necessary for controlling attention on a fixed anvil while nut cracking and so even with STM = 2, nut cracking would not be hindered. In contrast, for the nut cracking at Bossou the anvils need neither be the same from one nut cracking episode to another nor is the anvil constant during an episode of nut cracking as the anvil may require stabilization. Hence STM = 3 is required since attention must be focused on the manipulation of three objects.

The lower cognitive demand for nut cracking at Tai makes it possible to focus attention on the association between hammer stones and the kind of nut to be cracked (some kinds of nuts have softer shells than others and so some hammers work better than others, depending on the kind of nut). Tai chimpanzees assess where to search for a hammer stone based on the tree from which the nuts will be obtained and often use an optimal search strategy, taking into account distance and weight, for choice of hammer stone (Boesch and Boesch, 1983). Comparable behavior has not been reported at Bossou. It appears that when a task only requires attention to be placed on two objects (in this case, hammer stone and kind of nut), behavior can be organized through working memory by assessing the characteristics of the two objects that are being coordinated and how they will be used for the task at hand.

A similar pattern has been reported in the Goualougo Triangle (Congo Basin) with termite foraging by chimpanzees. As with the anvils at Tai, the termite nests are part of the visual environment and so need not be activated through short-term memory. The activity requires two coordinated implements – one to get access to the termites and the other to retrieve the termites from their nest, depending on the characteristics of the termite nest; e.g., a puncturing stick to get access to a subterranean nest plus a fishing stick to retrieve the termites or perforating twigs plus probes for other kinds of termite nests (Sanz, Morgan, and Gulick, 2004).ⁱⁱ Thus termite foraging can also be characterized by the coordination, through working memory, of the two objects to be used in the task at hand.

Conceptualizing the relationship between two objects as part of problem solving also characterizes the stone flaking experiments with the Bonobo chimpanzees, Kanzi and Panbanizha (Schick et al., 1999; Toth et al., 1993) in which Kanzi formed flakes to be used in a cutting task by learning to either throw a cobble against the floor to break off flakes, or to strike one cobble with another (Savage-Rumbaugh, Fields, and Spircu, 2004). Kanzi did not learn to control the percussion angle for flaking (de Beaune, 2004) and apparently limited conceptualization to that of a hitting relationship between two objects, either between a cobble and the floor or between one cobble and another, as a way to produce a flake.

More broadly, Parker and McKinney (1999) have reviewed evidence for the ability of non-human primates to use composite tools defined as “consisting of two or more tools having

different functions that are used in sequence and in association to achieve a single goal” (Sugiyama, 1997, p. 23, as quoted in Parker and McKinney, 1999, p. 51). Nut-cracking with a hammer-stone and an anvil would be an example of a compound tool. They comment that the “Use of compound tools is rare, but indicative of the *peak* intellectual abilities of chimpanzees” (1999, p. 51, emphasis added). They also note that “coordination of two or more relationships to form a single interrelational structure” (1999, p. 55), such as inserting one stick inside of another to make a longer tool, occurs at later ages in chimpanzees than humans. Parker and McKinney comment that unifocal coordination (use of a single tool) occurs in chimpanzees at 40 months, compared to around 20 months for humans; bifocal coordination (use of two objects in a coordinated manner) occurs at 60 months, compared to around 30 months for humans; and elaborated coordination (use of three or more objects in a coordinated manner) occurs at 114 months, compared to around 50 months for humans (data from Matsuzawa [1994]). The fact that instances of elaborated coordination (such as using a stone as a wedge to stabilize an anvil when nut-cracking [Matsuzawa 1994]) have only been observed in a few adults and juveniles leads Parker and McKinney to conclude that simple elaborated coordination “lies near the limit of the cognitive abilities of chimpanzees” (1999, p. 55). Similarly, Greenfield (1991) considers that rudimentary subassembly strategies (strategies using bifocal coordination for acting on a third object) are at the cognitive limit of chimpanzees.

Finally, we note that the failure of one fourth of the chimpanzees at Bossou to ever learn to crack nuts is matched by experimental evidence on teaching chimpanzees to crack nuts. Three naïve, adult chimpanzees who had previously not been exposed to nut cracking were exposed to human models of nut cracking after being provided with anvils and stone hammers from Bossou (Hayashi et al., 2005). The experimenters kept detailed records of all instances of the chimpanzees’ interaction with either stones and/or nuts as objects (see Table 2) versus instances of nut cracking. Only two of the three chimpanzees involved in the experiment learned the necessary sequence for cracking nuts. Though the sample size of $n = 3$ does not allow for robust statistical comparison, the proportion of experimental subjects that did not learn to crack nuts is consistent with the proportion of non-nut cracking chimpanzees at Bossou.

Table 2. Experimental nut cracking, three naïve subjects

Number of Objects ¹	Ai	Chloe	Pan
1 stone or 1 nut	110	205	394
2 objects, stones and/or nuts	33	45	98
3 objects, stones and/or nuts	4	0	1
3 objects, nut cracking	0	21	23

¹Data from Hayashi, Mizuno, and Matsuzawa, 2005

Other experiments that dealt with chimpanzees learning to crack nuts have had similar proportions. Of 16 semi-captive chimpanzees released on a natural island in Liberia, 13 learned to crack nuts after one of the chimpanzees was observed to crack nuts and 3 did not (Hannah and McGrew, 1987). In another experiment in which captive chimpanzees were taught to crack nuts via human exemplars, three of five chimpanzees learned to do so and two did not (Sumita, Kitahara-Frjisch, and Norikoshi, 1985).

In sum, the data on nut-cracking and other instances of tools usage by chimpanzees is consistent with the hypothesis that ST-WMC is in the 2 – 3 range. Though some chimpanzees can manipulate three objects, instances of so doing, excepting the presence of nut cracking among some (but not all) chimpanzee populations, are rare. This contrasts with the numerous observations on coordinated use of two tools or objects in a variety of different contexts and for different modes of resource procurement (see Table 1, Sugiyama 1996). Working with two tools simultaneously appears to be well within the range of chimpanzee cognitive abilities, whereas coordinated usage of three objects appears to be beyond the capacity of a significant proportion (25%) of chimpanzees.

Spontaneous Classification of Objects

Results from experimental work on spontaneous classification of objects by chimpanzees, using an experimental design developed by Jonas Langer (1980, 1986) for the study of logicomathematical concept development in human infants, is consistent with the above conclusions about the size of the chimpanzee short-term working memory component (ST-WMC). Langer’s experimental method is based on detailed analysis of video recordings made while human infants spontaneously form groups of objects. The objects are differentiated by attributes such as color or shape. The infants are allowed to spontaneously manipulate the objects without constraint, prior training or goal-rewarded behavior. The object groupings formed by an infant are classified according to a protocol developed by Langer. Briefly, the action of an

infant is scored (in part) according to the number of groups of objects that are formed, the internal structure of a group (e.g., mixed if objects with different attributes are grouped together and similar if the objects in the group share an attribute in common), operations the infant does on the objects in a single group (such as removal or replacement of objects in a group), and operations done on objects involving more than one group at a time. When more than one group is formed, the groups are scored as to whether they are contemporaneous (formed at the same time) or not.

The protocol allows for a series of levels of increasing complexity to be defined, going from first order classifications where just a single group of similar objects is formed, to classifications in which more than one group is formed contemporaneously but the groups need not share commonality across group members (e.g., the group membership may be based on different attributes). Second (and higher) order classifications are those in which it is the relation among the relations upon which groups are formed that is activated; e.g., two (or more groups) are formed contemporaneously and share the same relation for group membership, such as each group is based on objects with the same color though the color may be different between the groups. Though the researchers do not refer to working memory, the conditions for working memory to be actively involved, as discussed above, seem likely, especially for the cognitively more demanding second and higher order classifications where attention must be focused not only on the group being formed but also on how one group relates to another group.

The research on human infants has been extended to two species of monkeys (*Cebus apella* and *Macaca fascicularis*) and chimpanzees (*Pan troglodytes* and *Pan paniscus*). Two results obtained from this line of research are directly relevant to the argument being made here. First, for each of monkeys, apes or humans, the sequence for the first appearance of a given level of performance is age-related across the three groups of primates in a comparable, relative manner, though differing absolutely in the order human, ape and then monkey infants. Contrariwise, the age at which performance ceases to increase in complexity is the reverse of the age order for the first appearance of a performance level (Langer, 2006). Second, the maximum level of classification complexity expressed by the non-human primates is as follows. The two monkey species never go beyond first order classifications (Spinozzi, 1993 and references therein). Chimpanzees begin forming first order classifications around two years of age, though constructing two contemporaneous groupings remains infrequent until four years of age when 19% of the group formations consist of two groups (Spinozzi, 1993, Table 2). The formation of 2nd order classifications by chimpanzees only begins around five years of age (Potí et al., 1999, Spinozzi et al., 1999). Three contemporaneous groups were formed rarely and only then with some of the language trained and human enculturated bonobo chimpanzees. No 3rd order classifications were formed and contemporaneous groupings never involved four or more groups (Potí et al., 1999; Spinozzi et al., 1999).

In sharp contrast, human infants begin to make 1st order classifications with a few objects around 12 months of age and continue to develop 1st order classifications during the second year using large numbers of objects (which does not occur with the chimpanzees [Spinozzi et al., 1999]). Human infants begin forming two contemporaneous groupings around 18 months and around three years of age start forming three or more contemporaneous groupings (Potí et al., 1999), a performance level which must occur before forming 3rd order classifications (Langer, 1986). Forming multiple groups “enables [human infants] to develop the multi-category classifying required to generate more complex class relations between sets” (Spinozzi et al. 1999, p. 158). Spinozzi et al. conclude: “The present study only found classifying by bonobo and common chimpanzees,

ages 6–21 years, comparable to that of 24- to 30-month-old human children ... [and is] limited to constructing small contemporaneous sets, that is, no more than two sets of three objects each at a time. As a consequence, their classifying did not progress beyond second-order categorizing” (1999, p. 169).

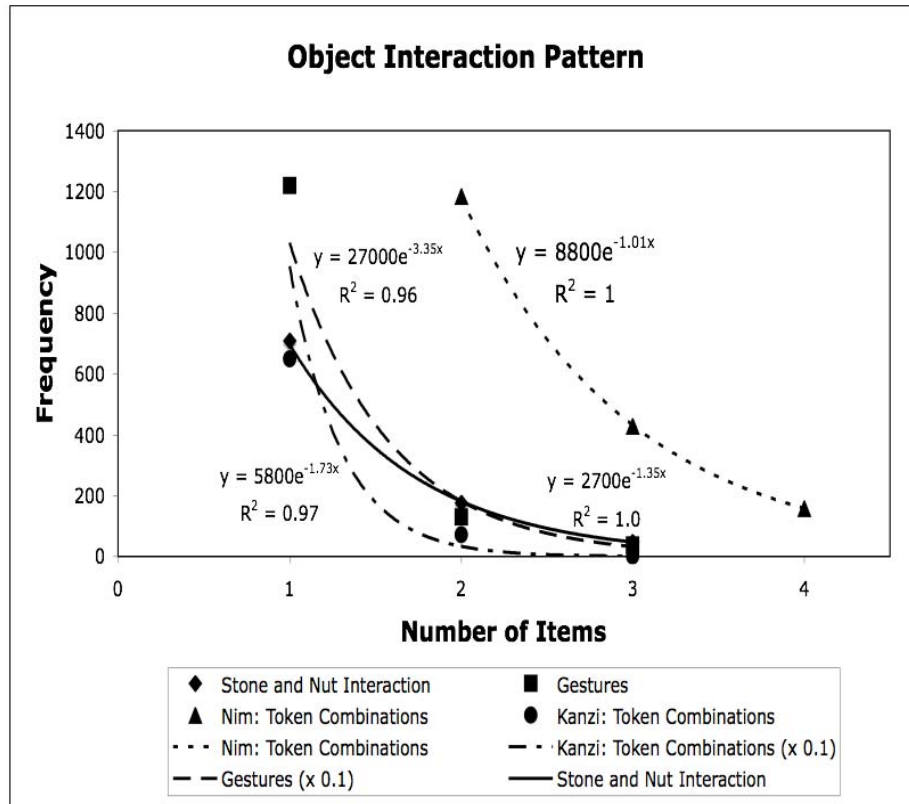
These differences between humans and chimpanzees – number of groups and level of classification – are consistent with chimpanzee working memory constrained by a short-term memory component of size 2 - 3. Chimpanzees rarely form more than two contemporaneously formed groups and in the few instances they do so it does not rise to the level of 3rd order classifications (Potí et al., 1999). Forming a 3rd order categorization would require that attention be focused on the similarity relation for the objects within three groups simultaneously, as well as the relation between these relations, which would be difficult to achieve with a short-term memory component for working memory of two (or even three).

Spontaneous manipulation of objects, it should be noted, does not establish the upper bound on possible cognitive capabilities (Potí et al., 1999), but indicates the level of conceptualization that seems to be involved in ordinary activities. Experimental work by McGonigle and Chalmers (2006) with *Cebus apella* demonstrates that even though under spontaneous conditions *Cebus* monkeys construct, at most, 1st order classifications and so do not exhibit the necessary conditions for a hierarchically-based classification (Langer, 1986), nonetheless under an appropriately structured, long-term (four years) and rewarded training program, *Cebus* monkeys can learn to form classifications that are structurally hierarchical.

Data on Unit Interaction Patterns

If the size of ST-WMC limits the number of units upon which attention is directed through working memory, then we should find a substantial drop-off in the frequency with which attention is paid to units involved in an activity as the number of units involved increases. Data presented here showing a drop-off is consistent with a small value for the size of short-term memory, though they are not definitive since the conditions under which the behaviors occur for the data sets being considered do not have a firm relationship between the number of units involved in an activity and the size of ST-WMC. The data to be considered are the frequency with which individual chimpanzees manipulate 1, 2 or 3 units during an activity. The units are: (1) objects, (2) gestures, (3) word tokens and (4) individuals.

Figure 1. Exponential decrease in frequency of interaction.



Object Manipulation

Regardless of subject, the frequency of interaction events with stones and/or nuts as objects (see Table 2, excluding nut cracking events) drops off exponentially (see Figure 1), suggesting a fixed transition probability, p , between manipulating n and $n+1$ objects. Interaction with 3 objects seldom occurs spontaneously, thus suggesting that nut cracking enables a degree of interaction with three objects that otherwise would not occur except by channeling focus on a pattern of object manipulation that leads to a reward consisting of the nutmeat from the cracked nut.

Gesture Sequences

The pattern of an exponentially decreasing frequency of interaction with stone objects is repeated with data on gesture sequences. Chimpanzees use various gestures to gain attention or to solicit play by juveniles. The specific gestures depend on the attention state of the intended recipient, can be individually learned, and are combined into sequences (Liebal, Call, and Tomasello, 2004).

Table 3. Gesture sequences

Length of Sequence	1	2	3	> 3
Frequency	1,220	130	38	39

¹Data from Liebal, Call, and Tomasello, 2004

The length and frequency of gesture sequences for a group of 19 captive chimpanzees (*Pan troglodytes*) are summarized in Table 3. The gestures with sequence length ≥ 3 occur more frequently than expected from an exponential decline in frequencies (see Figure 1), hence would appear to be disconfirming evidence. However, the longer sequences are primarily due to repetition of gestures when they do not succeed in attracting the attention of the intended recipient: “chimpanzee gesture sequences may not be premeditated constructions, but rather are post hoc responses to an unresponsive recipient” (Liebal, Call, and Tomasello, 2004, p. 394) and so the longer sequences are blocks of shorter sequences, hence do not require anything more than a small ST-WMC.

Word Token Combinations

Two widely reported series of experiments using word symbol/token combinations with semantic content and based on self-generated syntactical rules provide data on the frequency with which combinations of tokens are spontaneously formed under experimental conditions. One set of experiments used an individual from *Pan troglodytes* (Nim) and the other an individual from *Pan paniscus* (Kanzi). Whether the experiments demonstrate at least a rudimentary grammar in the form of syntactical rules for symbol combination is not at issue here (see Cowley and Spurrett, [2003] for a review of the issues surrounding Kanzi’s linguistic performance). Rather, the data will be summarized, as with the gesture data, using the frequencies for the length of symbol combinations formed by Nim or by Kanzi (see Table 4).

Table 4. Token combinations, Nim and Kanzi

Number of tokens	Nim ¹	Kanzi ²	Kanzi (Analyzed Data)
1 token	–	12,260	(6,850)
2 tokens	11,845	1,294	723
> 2 tokens	–	129	(72)
3 tokens	4,292	–	~ 8
4 tokens	1,587	–	–
> 4 tokens	1,487	–	–

¹Data from Terrace et al., 1979

²Data from Greenfield and Savage-Rumbaugh, 1990

The frequency data for Nim decrease exponentially (see Figure 1). Combinations of three (or more) signs appear to be unstructured: “Nim’s three-sign combinations showed no evidence of lexical regularities, nor did they elaborate or qualify what he signed when he produced a two-sign combination” (Terrace et al., 1979, p. 900). Similarly, Kanzi’s use of tokens follows an exponential curve (see Figure 1).

The exponential curve for the Kanzi data is based on the 72 events with > 2 tokens from column 4, Table 4, not the entry for 3-token events. The three-token combinations for Kanzi are repeated combinations and (apparently) only 8 three-token combinations occurred more than once in the data set after questionable observations had been removed (see column 4, Table 4). The two-token combinations in column 4 represent 56% of the 1,294 combinations with 2 tokens [column 3, Table 4], so assuming the same rate of rejection for the one-token events; the analyzed data set had about 6,850 one-token events and 72 events with at least 2 tokens.) The repeated, 3-token events are rare.

The Kanzi data have been interpreted as showing that Kanzi uses syntactic rules with semantic content (Greenfield and Savage-Rumbaugh, 1990, 1993), though some primatologists are less sanguine (Cheney and Seyfarth, 1997). If the repeated three-token events have syntactic structure and semantic content, their production presumably would have had positive utility for Kanzi. Nonetheless, they are a small proportion of all events with > 2 tokens. This suggests that cognitively coherent three-token events were not easy for Kanzi to produce. As noted by Parker and McKinney, chimpanzee (and other great apes) word/token combinations “peak at ... the two-word stage in production” (1999, p. 192).

The exponential curve for Kanzi’s and Nim’s performance contrasts sharply with the pattern for human infants at the same age. As discussed by Bickerton (1991a), human infants at the same age as Kanzi (22 months) use single element utterances 43% of the time, two element utterances 38% of the time, and > 2 element utterances 19% of the time and “two-word utterances outnumbered single-word utterances in the next and all subsequent months”

(Bickerton 1991a, p. 553; data from Bickerton, 1991b). Whatever may be the semantic content of the word/token combinations produced by Nim and Kanzi, then, the exponential drop in frequencies shows that their rate of production is driven by a fixed transition probability from n to $n + 1$ event occurrences and not by the utility of producing word/token combinations for inter-individual communication as occurs with human infants.

Interpersonal Interactions

Quantitative data on the frequency of dyadic versus triadic interactions among chimpanzees have not been published, but qualitative observations indicate clearly that triads are unusual. Chimpanzee communication has been characterized as unidirectional and only involving dyadic interactions (Tomasello, 1998); more specifically “chimpanzee gestures are used almost exclusively to regulate dyadic social interactions such as play, sex, and grooming, not to effect *triadic* interactions involving a partner and third entity, as is characteristic of human infants’ early gestures and language” (Tomasello, 1998, p. 10, emphasis in the original). Similarly, Tomonaga et al. comment: “At present, we have not observed complex triadic exchanges among the mother-infant chimpanzees and objects which are based on ‘shared attention’ or ‘reciprocity.’ It is still unclear as to whether this is a *cognitive constraint* or if this ability will emerge as the chimpanzees age” (2004, p. 234, emphasis added; see also Parker and McKinney, 1999, p. 200). Nor does learning to crack nuts involve a triadic relationship consisting of mother, infant and object as occurs with human infant learning (Matsuzawa, 2007).

In all of these examples, there is no indication that chimpanzees act upon three (or more) units in an integrated manner as we might expect if chimpanzee ST-WMC were, say, comparable to human ST-WMC. One reason for not doing so may be lack of circumstances in these examples for the more complex behavior, though if Kanzi attaches semantic meaning to token sequences and was not constrained by ST-WMC from forming longer sequences, then we might expect Kanzi to form more of the longer token sequences than is the case. Supporting this argument is the fact that Kanzi produced at most 2nd order spontaneous classifications (Spinozzi et al., 1999).

Direct Measure of Short-term Memory: Number Span

The last data set on chimpanzee behavior to be considered here provides direct evidence for the size of ST-WMC for *Pan troglodytes*. The chimpanzee Ai (see Table 2) was taught both to use Arabic number symbols (1 – 9) to represent the numerical size of a collection of objects and to touch any subset of the number symbols in their ordinal order.ⁱⁱⁱ Her experimental task was to observe 5 numbers on a touch-sensitive computer screen and then to touch the location of the numbers sequentially from smaller to larger, with the experimental condition that when the first number was touched, each of the other numbers would be blanked out with a white (visible) square. Ai had about a 95% correct rate for recalling 4 numbers in order out of 5, about a 65% correct rate for 5 numbers out of 5 (Kawai and Matsuzawa, 2000b), and about a 30% correct rate for 6 numbers out of 6 (Kawai and Matsuzawa, 2000a).

Though the authors interpreted these data as indicating that Ai has a working memory of 5 (Kawai and Matsuzawa, 2000a), the experimental conditions do not support their conclusion. The last choice is forced and so only the 1st four numbers would need to be memorized for Ai to answer 5 numbers correctly when there a total of 5 numbers on the screen. In addition, the first number is touched while all the numbers are visible and so its location does not need to be

memorized. Hence touching the locations in the correct order for a sequence of 5 numbers only requires memorizing 3 number locations. Ai's performance of 65% correct for 5 numbers is only slightly better than the 50% correct rate that would be obtained by memorizing the 2nd and 3rd number locations, randomly guessing the 4th number location, and then touching the remaining 5th square. Similarly, the drop from 65% to 30% correct for a 6 numbers in a sequence of 6 numbers implies that the 5th number in the sequence is a random guess. Thus, these data imply that Ai has a short-term memory of 2, consistent with her failure to learn to crack nuts (see Table 2; see also Cowan, 2000).

Subsequent experiments (Inoue and Matsuzawa, 2007a) with Ai and other chimpanzees provide data (Inoue and Matsuzawa, 2007b) both corroborating a ST-WMC size of about 2 and suggesting that "eidetic imagery" (Inoue and Matsuzawa, 2007a, p. R1005) plays a confounding role in the response patterns. These additional experiments also demonstrate that chimpanzees can learn to identify the numerical order for larger sets of numbers after extensive training, much like what has been reported for human enhanced learning of digital recall in tests of short-term memory capacity (Chase and Ericsson, 1981). According to the data provided by Inoue and Matsuzawa (2007b) from the more recent experiments, Ai is now correct 80% of the time for a set of 5 numbers (but still only correct about 30% of the time with 6 numbers) in response to training. However, two other chimpanzees without training are only correct about 60 – 65% of the time with a set of 4 numbers, again implying a ST-WMC of at most 2. One chimpanzee, though, has learned, after extensive training, to correctly identify the numerical order for a set of 9 numbers from memory even when the numbers are shown on the screen for just 210 milliseconds (shorter than the time needed for eye scanning of the screen). These data have been interpreted by Inoue and Matsuzawa (2007a) to mean that he is using eidetic memory. If so, his performance is not a measure of the size of ST-WMC. That eidetic memory may be involved in memory recall, as well as the use of extensive training for recalling larger sets of numbers in numerical order from memory, argue strongly against the authors' claim that these new experiments demonstrate "extraordinary working memory capability for numerical recollection" (Inoue and Matsuzawa, 2007a, p. R1004) by chimpanzees.

These experiments on number recall are consistent with ST-WMC around 2, or at most 3, when the measure of recall performance is based on the minimal number of memorized number locations consistent with the experimental results. The number recall experiments are a promising way to measure ST-WMC directly, but future experiments need to be better designed if the goal is to measure ST-WMC. If eidetic memory is prevalent among chimpanzees, then the research design will need to focus on ways to distinguish between ST-WMC and eidetic number recall.

Working Memory Development

Another way we can estimate the size of ST-WMC is through projecting the pattern for growth of ST-WMC during the time period for brain development in humans onto the time period for brain growth in chimpanzees. Numerous studies show increase in ST-WMC and/or working memory capacity paralleling the physiological development and organization of the prefrontal cortex through childhood and adolescence (e.g., Casey, Giedd, and Thomas, 2000; Hale, Bronik, and Fry, 1997; Luciana and Nelson, 1998; Vuontela et al., 2003). For our purposes here, we will consider a subset of this general pattern; namely, growth rate in ST-WMC during physiological development.

Thirteen longitudinal data sets from eleven separate studies were culled from the

literature and combined to form a composite data set for determining the pattern and rate of growth of ST-WMC from 7 – 144 months. Ages are reported in summary manner using whole year categories. Statistical tests of significance are not utilized here due to the small number of age categories for most of the studies and the fact that the regression models are based on mean response values for each age category, hence individual variability in response values has been averaged out in the reported data.

The data sets measured short-term memory as follows. For the earliest ages (see Diamond and Doar, 1989), short-term memory was measured through Delayed Response. While the infant watches, an object is placed in one of two identical wells and after a brief delay the infant is allowed to try and retrieve the object. The maximum time delay over which the infant correctly selects the well with the object is the measure of short-term memory. For the next age-cohort, short-term memory was measured by Alp (1994) with imitation sorting in which two to eight toys are sorted into two canisters and the child must repeat the sorting. The score is largest number of sorted toys for which the child can correctly repeat the sorting. For the next data set, Carlson et al. (2002) used three short-term memory tests – repeat a list of digits in reverse order, repeat a list of words in reverse order, and say a label for each object, then count the objects, and lastly say the label and number for each object. Since there is high correlation among these three measures, the mean value for each age group was computed and used as a summary measure. A less direct measure of short-term memory was used by Corr ea (1995) and Kidd and Bavin (2002), who each tested the extent to which children made errors in subject-focused relative clauses. Luciana and Nelson (1998) tested for spatial short-term memory span through the subject being required, at each round of the experiment, to recall the spatial location of a square for which a condition had been satisfied in a previous round. Spatial short-term memory was tested by Kempf et al. (2000) with the toy figure, Mr. Peanut, and with Corsi Blocks. Numerical short-term memory was tested by Siegel and Ryan (1989) in a test in which the subject counted the dots on each of a set of cards and then had to recall the counts. Word short-term memory was measured in another test by asking the subject to supply the missing word for the end of each sentence in a set of sentences and then to recall all of the supplied words. Finally Swanson, Jerman, and Zheng (2008) used 4 tests of short-term memory, 3 of which are averaged together here due to high inter-correlations.

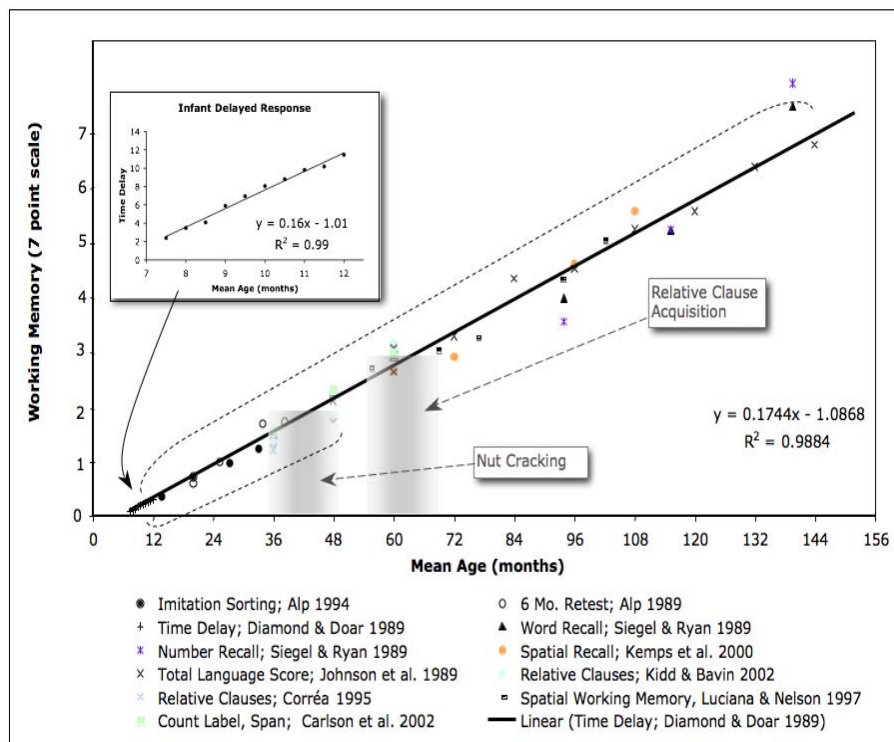
In addition, one data set that measured change in working memory capacity (Swanson, Jerman, and Zheng 1999) was included for comparison with change in ST-WMC capacity. Working memory capacity is measured by tests that require attention be paid to one kind of information while other information has to be recalled from memory. Four tests were used, but combined here into a single, summary measure due to high inter-correlations for the four measures.

The methods used to measure short-term memory differed across the researchers and no single test can be effectively applied to all age categories. For the latter reason, no attempt will be made to determine an age-based trajectory for the size of short-term memory. Instead, rates of change (i.e., velocity) will be examined in accordance with Swanson's (1999) observation that age-based development of working memory is not task specific.

The data sets were combined as follows. From the Diamond and Doar (1989) longitudinal data set, the regression line $y = 0.17x - 1.09$ was computed ($r^2 = 0.99$, $p < 0.001$), where y is the measure of time delay used in the Diamond and Doar longitudinal study and x is age in months. For all other data sets, the weighted mean age, \bar{x} , was used to compute a scaling factor $f = (0.17 \bar{x} - 1.09) / \bar{y}$, where \bar{y} is the weighted mean

response value for the measure used in that data set. Finally, rescaled response values, $y_r = f * y$, were computed and the values (x, y_r) were graphed in a scattergram plot (see Figure 2). The vertical axis (but not any of the slope values, b) was rescaled with a 7-point scale to correspond to $ST-WMC = 7$ for *Homo sapiens* at puberty, with the latter taken to be 144 months. Though Cowan (2001, 2005) has argued for a four-chunk limit “when supplementary storage mechanisms are disabled” (2005, p. 133), the four-chunk limit is “a starting point under the simplest of circumstances, on the road to the eventual goal of quantifying working memory storage limits in more complex situations” (2005, p. 149). In addition, he comments, “a limited storage capacity can be divided ... among up to about six (or seven?) items using a rehearsal process to supplement the capacity-limited facility” (2005, p. 152). The latter appears to characterize the conditions under which chimpanzees are engaging in nut cracking, hence the use of the 7-point scale for humans for comparison with the working memory capacity of chimpanzees.

Figure 2. Each data set is scaled so that the mean of the data set is on the extrapolated regression line (see inset). Dashed lines show growth period for humans and chimpanzees. Graph shows both linear growth for working memory across all data sets and a single, constant growth rate from 7 to 144 months.



Consistency among the slope values (velocity in growth of the size of short-term memory) was assessed by computing a 95% confidence interval (CI) for the slope value from a linear regression fit to each of the 13 data sets (see Table 5). All the CIs overlap, showing that the data sets, including the measurements for growth in working memory capacity, consistently

estimate a single, constant value, β , for the velocity in change of the size of short-term memory from 6 to 144 months. Linear growth in human short-term working memory implies it is not driven simply by brain growth as the latter is characterized by initially high velocity at birth with a marked decrease in the rate of change in velocity occurring around 18 – 24 months after birth (see Figure 9, Leigh, 2004).

Table 5. Estimated Regression Slopes, b

n^1	Weighted mean age (months)	n^2	b value	95% confidence interval ³	Source (type of test)
6⁴	9.8	10	0.17	(0.16, 0.19)	Diamond and Doar, 1989 (delayed response)
52	23.6	4	0.15	(0.11, 0.19)	Alp, 1994 (imitation recall)
37	28.4	4	0.23	(0.09, 0.37)	Alp, 1994 (6 month retest)
47	49.0	3	0.19	(0.12, 0.26)	Carlson et al., 2002 (list repeating in reverse order)
60	49.2	3	0.25	(0.16, 0.33)	Corréa, 1995 (relative clause comprehension)
42	51.6	3	0.26	(-0.69, 1.21)	Kidd and Bavin, 2002 (relative clause comprehension)
144	57.7	8	0.17	(0.15, 0.19)	Johnson et al., 1989
168	62.5	5	0.18	(0.10, 0.25)	Luciana and Nelson, 1998 (spatial memory)
60	84.0	4	0.22	(0.11, 0.32)	Kemps et al., 2000 (spatial memory)
74	107.4	3	0.27	(-0.15, 0.69)	Siegel and Ryan, 1989 (word memory)
74	107.4	3	0.33	(-0.05, 0.71)	Siegel and Ryan, 1989 (counting memory)
285	107.7	5	0.14	(0.05, 0.23)	Swanson, 2008 (short term memory)
404	107.5	3	0.15	(0.14, 0.16)	Swanson, 1999 (working memory capacity)

¹ Number of subjects

² Number of age categories

³ Sample size for confidence intervals is the number of age categories

⁴ Longitudinal study on 6 infants

For all but three of the data sets, the 95% CI is narrow, thereby demonstrating little residual variation in a linear regression fit to a data set. The two data sets with $n > 7$ are shown in bold. Both have very narrow and almost identical CIs ([0.15, 0.19] and [0.16, 0.19]), hence provide further evidence for a constant velocity in the growth of the size of short-term memory. The intersection of the CI intervals is [16, 19] and the weighted average estimate for the velocity, β , is 0.18 delay units per month (measured in delay units since all data sets were standardized against the regression line for the Diamond and Doar (1999) data set with slope $b = 0.17$). The velocity in memory units can be computed from assuming 0 units at age 6 months (extrapolated

from the regression line shown in the inset in Figure 2) to 7 units at 144 months. This yields a velocity of 1 short-term memory unit per 19 months or 0.053 units per month.

Whereas humans reach puberty after 144 months, puberty in chimpanzees occurs after about 80 months (Copeland et al., 1985; Marson et al., 1991). The shorter physiological developmental time for chimpanzees implies a shorter developmental span for cognitive development even without considering the later onset of cognitive capacities in chimpanzees in comparison to humans (Parker and McKinney, 1999). Most of the brain growth for chimpanzees occurs by 36 months and ceases by 60 months. For humans, most of the brain growth occurs by 72 months and continues (albeit at a much slower and decreasing velocity) until at least puberty (see Figure 6 and Figure 9, Leigh, 2004). The age-based, brain growth velocity curve for chimpanzees is substantially lower than that for humans over the first two, post-birth years, whether measured by absolute or relative velocity (relative velocity is the absolute velocity divided by the predicted adult brain size; see Figure 9, Leigh, 2004). As a consequence, although physiological development in humans is characterized by neoteny (Lanyon, 2006 and references therein), cognitive development is more extensive due to higher growth velocities and so is precocial: “the *onset* age for the origins of classifying by primates is youngest in humans, intermediate in great apes, and oldest in monkeys. The *velocity* at which classifying develops is fastest in humans, intermediate in great apes, and slowest in monkeys ... The *offset* age when primates stop developing classificatory cognition is youngest in monkeys, intermediate in great apes, and oldest in humans.” (Langer, 2006, p. 41, emphasis in the original). Cognitive development in humans leads to ontogenetic adultification, not neontenization, due to its earlier onset, velocity, and extended duration (Langer, 2005; Parker and McKinney, 1999).

A conservative velocity assumption for chimpanzee short-term memory developmental would be the velocity for *Homo sapiens*. Under this assumption, the growth trajectory for humans would predict an ST-WMC = 2 at around 42 months for chimpanzees when they are learning to crack nuts, in contrast with an ST-WMC = 3 around 62 months for *Homo sapiens* when children are generally able to comprehend recursively based relative clauses (Corrêa, 1995; Hamburger and Crain, 1982; Sheldon 1974; Tavakolian, 1981) (see shaded areas in Figure 2). Comprehension of relative clauses depends on increase in “children’s overall ability to keep the stimulus sentence in immediate memory,” and begins around 3 to 4 years of age due to the development of “children’s ability to cope with the internal processing of the RC [relative clause],” which begins between ages of 4 to 5 (Corrêa, 1995, pp. 197, 199; Kidd and Bavin, 2002).

A similar, developmental divergence pattern between humans and chimpanzees can also be seen with 2nd order classifications appearing around 3 years of age for chimpanzees but without the chimpanzees ever forming the 3rd order classifications that begins to be used by humans around 4-5 years of age. This pattern of comparable cognitive abilities occurring in humans and chimpanzees up to around 3 years of age followed by human divergence with increasing age matches Premack’s (1986) argument that concepts appearing during human cognitive development after 3 years of age are never found in chimpanzees.

The development pattern for both chimpanzees and humans of beginning with a small working memory capacity is consistent with an argument by Newport (1990) on the advantage of beginning with a small working memory when learning a language, along with subsequent experimental work by Elman (1993) on training neural nets to process complex sentences: “Training succeeds only when networks begin with limited working memory and gradually ‘mature’ to the adult state...successful learning may depend on starting small” (p. 71). This

developmental pattern is also noted in simulations of the evolution of language acquisition proficiency by Hurford (1999): “Whatever it is in the infant that ‘starts small’ and then grows, its growth facilitating language acquisition, the rate of this growth seems likely to be controlled in large part by genetic facts [and] . . . is likely to be the product of Darwinian natural selection. . . . the evolution of such a growing trait (here labeled ‘working memory’) can be modeled, with an adult value being reached around puberty” (p. 26). Evidence that a small short-term memory enhances language learning, though, is equivocal (Cowan, 2005 and references therein), but an infant’s small short-term memory does not inhibit initial language learning.) Hence the *Homo sapiens* developmental pattern shown in Figure 2 beyond about 42 months would be the evolutionary extension of a short-term memory developmental trajectory that terminates for *Pan* around 42-48 months of age with ST-WMC of 2 or 3 at most. If the velocity for ontogenetic short-term memory growth in chimpanzees is less than that for humans, as the evidence on classification indicates, the ontogenetic divergence between chimpanzees and humans would be even more pronounced.

Discussion

The data reviewed here consistently point to a chimpanzee working memory being constrained by ST-WMC = 2 or 3. If ST-WMC = 2, then short-term memory is below what is necessary for recursive reasoning. With ST-WMC = 3, short-term would be a marginal size for recursion to be part of the executive function of working memory. Thus we may conclude that the short-term memory size is not large enough for recursive mental operations to be cognitively assessable by all members of *Pan troglodytes* or *Pan paniscus*, if at all. As noted by Langer (2005): “only the cognition of human infants among young primates become fully recursive” (p. 316). This occurs around four years of age (Langer, personal communication, 2008). In his characterization of an infant’s ontogenetic development across levels of classification, only with fully 3rd order classifications – beyond the ontogenetic cognitive development of chimpanzees – does one have recursion as part of spontaneous classifications. Thus, the constraints on working memory imposed by ST-WMC = 2 or 3 would account for the lack of any clear examples of recursive reasoning or activity on the part of non-human primates.

Working memory capacity, of course, is both more complex than what is implied by a single, numerical score for ST-WMC and, as discussed above, is not a unitary phenomenon. Nonetheless, evolutionary change in ST-WMC from that of chimpanzees – whose value is taken to be indicative of the ST-WMC value for a last common ancestor for chimpanzees and humans – to that of modern *Homo sapiens* should be paralleled by an evolutionary sequence of demonstrably increasing cognitive complexity in the conceptual basis for, and production of, stone tool artifacts during hominid evolution. Next we consider whether changes in artifact production during hominid evolution changed in parallel with change in working memory in the predicted manner.

Evolutionary changes in the cognitive complexity of artifacts can be seen in changes in the dimensionality underlying stone tool form and production. Early hominid stone tools (~ 2.0 mya) such as Oldowan choppers are conceptually 1-dimensional as they are based on producing an edge on a cobble (Pigeot, 1991; Wynn and McGrew, 1989). The conceptual framework only incorporates 2-dimensions around 1/2 million years later with the introduction of shaped tools, such as handaxes, whose production requires mapping a two dimensional concept onto a stone object (Boëda, Geneste, and Meignen, 1990; Pigeot, 1991; Wynn, 2002). It is only with the

introduction of the Upper Paleolithic blade tool industry that volume is incorporated in the stone knapper's conceptual control over artifact production (Boëda, 1990; Pigeot, 1991). None of these conceptual dimensions are expressed, even in rudimentary form, in non-human primate tool making and use.

Within the broad outline of tools increasing in conceptual complexity from non-dimensional to three dimensional, evolutionary changes in stone tool production can be divided more finely into seven stages, of which the 3rd through the 7th relate to stone tool production during hominid evolution over the past 2.5 million years (Read and van der Leeuw, 2008 and references therein). Briefly, the stages, concepts involved, date of first known occurrence (in parentheses), and exemplars are as follows.

Stage i. Dimensionality: none (pre-hominid divergence) (a) Concept: object with already existing attribute necessary for the task at hand; production action: repetition. An example would be a small branch used to extract termites. The branch already has the required attribute (long, thin rod) and the production action is one of repeatedly removing a side branch or leaf from the branch so the main part of the branch can be inserted into a termite mound. (b) Concept: relationship among object attributes. Exemplar: nut cracking with rock hammer and anvil. No modification is made of the objects.

Stage ii. Dimensionality: zero-dimensional (unknown dating, above 2.6 Myr BP). Concept: imposed attribute; production action: repetition. Exemplars would include crushing of leaves by chimpanzees to form a sponge to sop up water, or the occasional flake removals from a cobble by hominids to obtain a flake used in scavenging meat from a predator kill.

Stage iii. Dimensionality: zero-dimensional (~2.6 Myr BP). Concept: flaking; production action: repetition. Flaking is controlled through the striking angle required for conchoidal fracturing. More than one flake may be removed from a nodule (repetition of flaking), but without any apparent pattern among the flake removals. The goal appears to be one of removing individual flakes to be used in some task.

Stage iv. Dimensionality: one-dimensional (2.0 Myr BP). Concept: edge; production action: iteration;. Exemplar: Oldowan choppers. The intent appears to be to remove flakes from a cobble so as to form a cutting edge. Flaking is done iteratively, with the location of the next flake removal guided by the scar from the last flake removal. The flakes are now waste products.

Stage v. Dimensionality: two-dimensional (1.5 Myr BP). (a) Concept: closed curve, edge as a generative element; production action: iteration. Exemplar: simple handaxes formed by a closed curve (edge) around a nodule with some flake removals from the surface area bounded by the closed curve. The edge generates a two dimensional surface (the space enclosed by the closed curve). (b) Concept: surface; production action: iteration (500 kyr BP). Exemplar: "classic" handaxes for which surface flake removals are the means used to shape the hand axe and to produce its edge. The boundary and the surface within the boundary are conceptualized jointly to guide the process of flake removals.

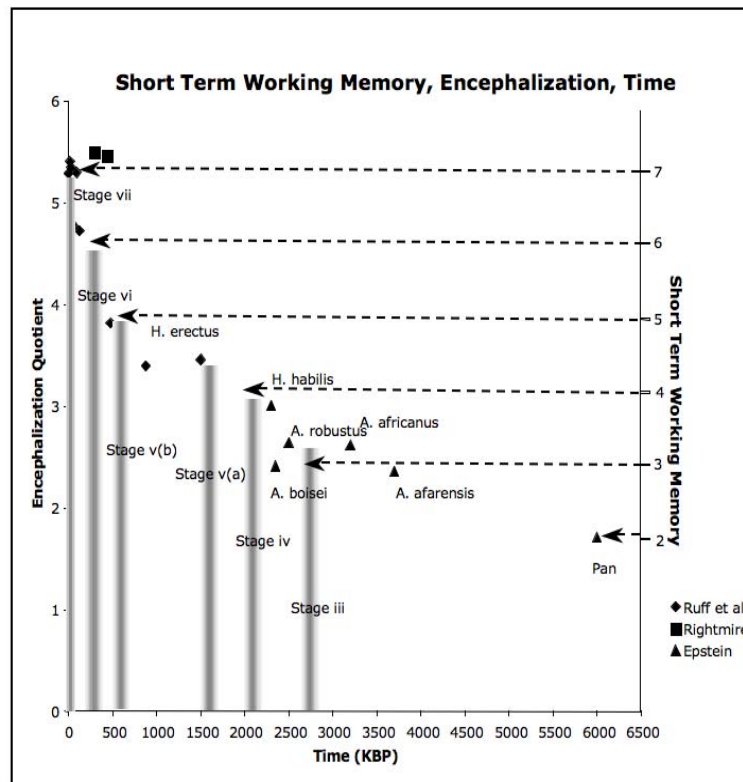
Stage vi. Dimensionality: two-dimensional (300 kyr BP). Concept: surface; production action: algorithm;. Exemplar: technique known as Levallois flake removals (named for the Levallois region in France where tools made with this technique were first discovered). Up to this time, a flake removal is essentially a one-step process controlled by the force of the striking blow used to remove a flake and the characteristics of the striking instrument. The flake was often a waste product. The Levallois technique contrasts with flake removal by being a multi-step process in which the goal is to produce flakes that will then be modified in different ways to

make a variety of tools.

Stage vii. Dimensionality: three-dimensional (less than 50 kyr BP). Concept: intersection of planes; production action: recursion. Exemplar: prismatic blade production using a soft hammer or indirect percussion. Blades were then modified to form a wide variety of tools. The core has to be conceptualized in three dimensions as a series of intersecting planes in order to conceptualize how to control the blade removal process so that long, narrow blades are removed consistently (Boëda, 1990). The technique is recursive as the output of the algorithm for blade production (the stone core from which the blade is removed) is a core already prepared for applying the algorithm again. Hundreds of blades can be produced through recursive application of the algorithm.

The time sequence for these changes in stone tool production correlate well with both encephalization as a proxy measure for linear change in ST-WMC and major hominid morphological changes during hominid evolution (see Figure 3).

Figure 3. Correlation of change in encephalization among hominid phylogenetic groups with change in the conceptual basis for stone tool production divided into 7 stages (only stages iii to vii relate to stone tool production) and with increase in the short term memory component of working memory. Vertical “fuzzy” bars identify the time period for changes in stone tool production.



(Using encephalization as a proxy measure for working memory capacity is supported by a meta-analysis of 86 studies demonstrating that working memory is significantly correlated with Evolutionary Psychology – ISSN 1474-7049 – Volume 6(4). 2008. -701-

measures of intellectual ability [Ackerman, Beier, and Boyle 2005] and the fact that encephalization is also correlated with intellectual ability [Williams 2002].) Thus the postulated sequence of changes in the conceptual complexity of stone tools paralleling increase in working memory capacity is justified by these data.

The last two stages, Stages *vi* – *vii*, provide the first archaeological evidence for a recursive process, rather than simple iteration, as an elaborated part of stone tool production. Iteration in the earlier stages involves a sequence of flake removals from the stone tool that is being manufactured, each with its location determined by the general goal of the tool making. The previous blow does not prepare the stone nodule for the next removal. Iteration (but not repetition) is absent from non-human primate tool production (Read and van der Leeuw, 2008 and references therein).

Around 300,000 BP a major innovation in stone tool technology – the Levallois technique for flake removals – changed stone tool knapping from iterative flake removal to the repeated execution of an algorithm: “The characterization of the Levallois method given by Boëda (1995) clearly shows the sense in which this method becomes an algorithm for the production of flakes, rather than simply a particular method for the removal of a flake” (Read and van der Leeuw, 2008, p. 1963). The algorithm is used to prepare the surface of a flint nodule from which a flake will be removed. The removed flake is then shaped into the desired stone tool. Next, the surface of the nodule with the scar due to the flake removal is reworked so that the Levallois algorithm can be used again to remove another flake. This might be repeated for two or three flake removals.

The Levallois algorithm for flake production is not fully recursive since the stone surface that is the output of the algorithm (the stone surface with a scar due to the flake removal) must be modified before another flake can be removed using the Levallois algorithm. Around 50,000 BP, during the Upper Paleolithic, yet another technology – prismatic blade tool production – becomes widespread and is based on true recursion. For prismatic blade production, a stone nodule with a flat, striking platform is formed and then blades are recursively removed by striking the edge of the striking platform. The removal of one blade prepares the core for the removal of the next blade without any intermediate, preparatory steps (Read and van der Leeuw, 2008 and references therein); that is, the algorithm for blade removal has as its output a form on which the algorithm can be directly applied, and so on, until perhaps 100s of blades (as would be expected with true recursion) have been removed.^{iv}

Blade technology flourished during the Upper Paleolithic and gave rise to a plethora of tools based on recursion (Hoffecker, 2007). Coolidge and Wynn (2004, 2005) have suggested that this florescence may relate to a genetic mutation expanding the capacity of the central executive component of working memory around 80,000 BP, between Stages *vi* and *vii*. Associated with this florescence is the appearance of new and more complex forms of social organization dependent upon culturally constructed kinship systems based on the recursive logic of genealogical tracing (Read 2001, Read in press a). By cultural, as opposed to biological, kin is meant kin determined through a culturally constructed system of kin relations expressed as a society specific kinship terminology (Parkin, 1997; Read, 2001, in press a). (A kinship terminology is a generative, conceptual system of kin terms through which the relation conditions that determine those who are one’s relatives [Read, 1984, 2001, in press] can be computed. Briefly, person B is kin to person A [and reciprocally, person A is kin to person B] when person A has a kin term that may be used [properly] to refer to person B, where the kin terms have been conceptually generated in a manner similar to an algebraic

structure.) A kinship terminology is transmitted through enculturation with the consequence that a kinship terminology is composed of shared knowledge (Read, Lane, and van der Leeuw, in press). Cultural kinship is grounded in (though not determined by) reproduction as it is culturally understood (Scheffler and Lounsbury, 1971; Keesing, 1975), not by the facts of biological reproduction. The neurological changes that enabled recursion to become part of the cognitive repertoire of *Homo* thus had profound consequences reaching far beyond the implications it had for language production.

Conclusion

The data reviewed here suggest a short-term memory size of two or three for *Pan*. An evolutionary sequence beginning from ST-WMC = 2 or 3 for a common ancestor to *Pan* and *Homo sapiens* to 7 in modern *Homo sapiens* is consistent with the archaeological pattern of changes in the conceptual and technological basis for stone tools from early hominids (around 2.6 mya) through the Upper Paleolithic. It is not until there is substantial increase in ST-WMC (hence in working memory capacity) that we find evidence for the precursor of recursion based technologies appearing about 300,000 BP followed, after another 200,000 years and with further increase in ST-WMC, by the florescence of stone tool blade technology, the introduction of symbolic forms of expression initially in the form of beads (d'Errico et al., 2005), and more complex forms of social organization, all during the Upper Paleolithic (Bar-Yosef, 2002). An initial, small short term component of working memory in a common ancestor to *Pan* and *Homo* would also account for the lack of evidence for recursion-based behaviors in non-human primates. In contrast, ST-WMC > 3 in the common ancestor and carried forward to modern *Pan* would require a *greater* velocity for the growth of short-term memory size during ontogenetic cognitive development from birth to puberty in *Pan* than is true for *Homo sapiens*. A greater velocity would run contrary to the evidence showing the reverse pattern for the ontogenetic development of classification by chimpanzees in comparison to humans (Langer, 2005, 2006). Finally, a large ST-WMC for the common ancestor would also pose the problem of why, in the evolutionary pathway leading to modern *Pan*, did an ancestor to *Pan* have working memory comparable to that of *Homo sapiens* yet this lineage failed to evolve linguistic/symbolic/kinship based forms of social organization and communication despite having the same evolutionary time span for their evolution as did *Homo sapiens*. All of these arguments point to a small ST-WMC in a common ancestor to *Pan* and *Homo*, hence absence of recursive cognitive processes. Without the cognitive ability to exploit recursive, conceptual systems, the *Pan* evolutionary pathway had only relatively little elaboration in comparison to the *Homo* evolutionary pathway. This raises the question of what triggered the increase in the size of short-term memory in the pathway leading to modern *Homo sapiens*, but that is another topic. The evidence provided here favors a qualitative difference in cognitive abilities arising between *Homo* and *Pan* due to the difference in the short-term memory component of working memory that precludes the generative richness of recursive conceptual systems from being part of the cognitive repertoire of *Pan*.

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References

- Aboitiz, F., García, R.R., Bosman, C., and Brunetti, E. (2006). Cortical memory mechanisms and language origins. *Brain and Language*, 98, 40-56.
- Ackerman, P.L., Beier, M.E., and Boyle, M.O. (2005). Working memory and intelligence: The same or different constructs? *Psychological Bulletin*, 131, 30-60.
- Alp, I.E. (1994). Measuring the size of working memory in very young children: The imitation sorting task. *International Journal of Behavioral Development*, 17, 125-141.
- Avers, C. J. (1989). *Process and pattern in evolution*. Oxford: Oxford University Press.
- Awh, E., and Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*, 5, 119-126.
- Awh, E., Vogel, E.K. and Oh, S.H. (2006). Interactions between attention and working memory. *Neuroscience*, 139, 201-208.
- Baddeley, A. (1986). *Working memory*. Oxford: Oxford University Press.
- Baddeley, A. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences*, 4, 417-423.
- Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews: Neuroscience*, 4, 830-839.
- Baddeley, A.D., and Hitch, G.J. (1974). The psychology of learning and motivation. In G.A. Bower (Ed.). *Recent advances in learning and motivation* (pp. 47-89). New York: Academic Press.
- Bar-Yosef, O. (2002). The Upper Paleolithic revolution. *Annual Review of Anthropology*, 31, 363-393.
- Bickerton, D. (1991a). Syntax is not as simple as it seems. *Behavioral and Brain Sciences*, 14, 552-553.
- Bickerton, D. (1991b). The pace of syntactic acquisition. *Proceedings of the Annual Meetings of the Berkeley Linguistics Society*, 17, 41-52.
- Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., and Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. *Animal Cognition*, 6, 213-223.
- Black, P. E., and Rodgers, P. (2007). Recursion. In P. E. Black (Ed.), *Dictionary of algorithms and data structures*. U.S. National Institute of Standards and Technology. (Accessed June 26, 2008). URL = <http://www.nist.gov/dads/HTML/recursion.html>
- Boëda, E. (1990). De la surface au volume: analyse des conceptions des débitages Levallois et laminaires. In C. Farizy (Ed.), *Paléolithique moyen récent et Paléolithique supérieur ancien en Europe. Ruptures et transitions: Examen critique des documents archéologiques* (pp. 63-68). Nemours: Mémoires du Musée de Préhistoire d'Ile de France, 3.
- Boëda, E. (1995). Levallois: A volumetric construction, methods, a technique. In H.L. Dibble and O. Bar-Yosef (Eds.), *The definition and interpretation of Levallois technology* (pp. 41-67). Madison: Prehistory Press.
- Boëda, E., Geneste, J.-M., and Meignen, L. (1990). Identification de chaînes opératoires lithiques du Paléolithique ancien et moyen. *Paléo*, 2, 43-80.
- Boesch, C., and Boesch, H. (1983). Optimisation of nut-cracking with natural hammers by

- wild chimpanzees. *Behaviour*, 83, 265-286.
- Braver, T. S., and Bongiolatti, S.R. (2002). The role of frontopolar cortex in subgoal processing during working memory. *NeuroImage*, 15, 523-536.
- Buxhoeveden, D., and Casanova, M.F. (2002). The minicolumn and evolution of the brain. *Brain, Behavior and Evolution*, 60, 125-151.
- Cáceres, M., Suwyn, C., Maddox, M., Thomas, J.W., and Preuss, T.M. (2007). Increased cortical expression of two synaptogenic thrombospondins in human brain evolution. *Cerebral Cortex*, 17, 2312-2321.
- Carlson, S.M., Moses, L.J., and Breton, C. (2002). How specific is the relation between executive function and theory of mind? Contributions of inhibitory control and working memory. *Infant and Child Development*, 11, 73-92.
- Case, R. (1995). Capacity-based explanations of working memory growth: A brief history and reevaluation. In F.E. Weinert and W. Schneider (Eds.), *Memory performance and competencies: Issues in growth and development* (pp. 23-44). Mahwah: Lawrence Erlbaum Associates.
- Casey, B.J., Giedd, J.N., and Thomas, K.M. (2000). Structural and functional brain development and its relation to cognitive development. *Biological Psychology* 54, 241-257.
- Chase, W.G., and Ericsson, K.A. (1981). Skilled memory. In J.R., Anderson (Ed.), *Cognitive skills and their acquisition* (pp. 141-189). Hillsdale: Erlbaum.
- Cheney, D.L., and Seyfarth, R.M. (1997). Why animals don't have language. *The Tanner Lectures on Human Values*, 19, 173-210.
- Colom, R., C. Flores-Mendoza, M. A. Quiroga, and Privado, J. (2005). Working memory and general intelligence: The role of short-term storage. *Personality and Individual Differences*, 39, 1005-1014.
- Conway, A. R. A., Cowan, N., Bunting, M.F., Theriault, D.J., and Minkoff, S.R.B. (2002). A latent variable analysis of working memory capacity, short-term memory capacity, processing speed, and general fluid intelligence. *Intelligence*, 30, 163-183.
- Coolidge, F. L., and Wynn, T. (2004). A cognitive and neuropsychological perspective on the Châtelperronian. *Journal of Anthropological Research*, 60, 55-73.
- Coolidge, F.L., and Wynn, T. (2005). Working memory, its executive functions, and the emergence of modern thinking. *Cambridge Archaeological Journal*, 15, 5-26.
- Coolidge, F.L., and Wynn, T. (2007). The working memory account of Neandertal cognition – How phonological storage capacity may be related to recursion and the pragmatics of modern speech. *Journal of Human Evolution*, 52, 707-710.
- Copeland, K. C., Eichberg, J.W., Parker, C.R., and Bartke, A. (1985). Puberty in the chimpanzee: Somatomedin-C and its relationship to somatic growth and steroid hormone concentrations. *Journal of Clinical Endocrinology and Metabolism*, 60, 1154-1160.
- Corrêa, L.M.S. (1995). An alternative assessment of children's comprehension of relative clauses. *Journal of Psycholinguistic Research*, 24, 183-203.
- Cowan, N. (1995). *Attention and memory: An integrated framework*. Oxford Psychology Series, No. 26. Oxford: Oxford University Press.
- Cowan, N. (1999). *Attention and memory: An integrated framework*. Oxford: Oxford University Press.
- Cowan, N. (2000). The magical number 4 in short-term memory: A reconsideration of

- mental storage capacity. *Behavioral and Brain Sciences*, 24, 87-185.
- Cowan, N. (2005). *Working memory capacity*. New York: Psychology Press.
- Cowley, S., and Spurrett, D. (2003). Putting apes (body and language) together again: A review article of Savage-Rumbaugh, S., Taylor, T.J., and Shanker, S.G. *Apes, Language, and the Human Mind* (Oxford: 1999) and Clark, A. *Being There: Putting Brain, Body, and World Together Again* (MIT: 1997). *Language Sciences*, 25, 289-318.
- D'Errico, F., Henshilwood, C., Vanhaeren, M., and van Niekerk, K. (2005). *Nassarius kraussianus* shell beads from Blombos Cave: Evidence for symbolic behaviour in the Middle Stone Age. *Journal of Human Evolution*, 48, 3-24.
- de Beaune, S. A. (2004). The invention of technology. *Current Anthropology*, 45, 139-162.
- de Waal, F.B.M., and Tyack, P.L. (Eds.). (2003). *Animal social complexity: Intelligence, culture, and individualized societies*. Cambridge: Harvard University Press.
- Derksen, M. (2005). Against integration: Why evolution cannot unify the social sciences. *Theory & Psychology*, 15, 139-162.
- Diamond, A., and Doar, B. (1989). The performance of human infants on a measure of frontal cortex function, the delayed-response task. *Developmental Psychobiology*, 22, 271-294.
- Editors of the American Heritage Dictionaries.(2001). *Dictionary of computer and internet words: An A to Z guide to hardware, software, and cyberspace*. Boston: Houghton Mifflin Reference Books.
- Elman, J. (1993). Learning and development in neural networks: The importance of starting small. *Cognition*, 48, 71-99.
- Engle, R.W., Kane, M.J., and Tuholski, S.W. (1999). Individual differences in working memory capacity and what they tell us about controlled attention, general fluid intelligence, and functions of the prefrontal cortex. In A. Miyake and P. Shah (Eds.), *Models of working memory: Mechanisms of active maintenance and executive control* (pp. 102-134). Cambridge: Cambridge University Press.
- Engle, R.W., Tuholski, S.W., Laughlin, J.E., and Conway, C.M. (1999). Working memory, short-term memory, and general fluid intelligence: A latent-variable approach. *Journal of Experimental Psychology: General*, 128, 309-331.
- Epstein, H. T. (2002). Evolution of the reasoning brain. *Behavior and Brain Science*, 25, 408-409.
- Finlay, B. L., Darlington, R.B., and Nicastro, N. (2001). Developmental structure in brain evolution. *Behavioral and Brain Sciences*, 24, 263-308.
- Fitch, W.T., and Hauser, M.D. (2004). Computational constraints on syntactic processing in a nonhuman primate. *Science*, 303, 377-380.
- Fitch, W.T., Hauser, M.D., and Chomsky, N. (2005). The evolution of the language faculty: Clarifications and implications. *Cognition*, 97, 179-210.
- Fox, E., and bin'Muhammad, I. (2002). Brief communication: New tool use by wild Sumatran orangutans (*Pongo pygmaeus abelii*). *American Journal of Physical Anthropology*, 119, 186-188.
- Funk, M. (1985). Werkzeugegebrauch beim öffnen von Nüssen: Unterschiedliche Bewältigungen des problems bei Schimpansen und Oragn-Utans. MA Thesis, University of Zürich.
- Fuster, J.M. (1995a). *Memory in the cerebral cortex*. Cambridge: MIT Press.

- Fuster, J.M. (1995b). Memory in the cortex of the primates. *Biological Research* 28, 59-72.
- Gazzaniga, M. S., Ivry, R.B., and Mangun, G.R. (2002). *Cognitive neuroscience: The biology of the mind* (2nd ed.). New York: W. W. Norton.
- Geertz, C. (1973). *The interpretation of cultures*. New York: Basic Books.
- Goldman-Rakic, P. S. (1987). Circuitry of primate prefrontal cortex and regulation of behavior by representational memory. In F. Plum (Ed.), *Handbook of physiology: The nervous system* (pp. 373-414). Bethesda, MD: American Physiological Society.
- Greenfield, P. (1991). Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. *Behavioral and Brain Sciences*, 14, 531-595.
- Greenfield, P., and Savage-Rumbaugh, E.S. (1990). Grammatical combination in Pan paniscus: Processes of learning and invention in the evolution and development of language. In S.T. Parker and K.R. Gibson (Eds.), *"Language" and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 540-578). Cambridge: Cambridge University Press.
- Greenfield, P., and Savage-Rumbaugh, E.S. (1993). Comparing communicative competence in child and chimps: Pragmatics of repetition. *Journal of Child Language*, 20, 1-26.
- Hale, S., Bronik, M.D., and Fry, A.F. (1997). Verbal and spatial working memory in school-age children: Developmental differences in susceptibility to interference. *Developmental Psychology*, 33, 364-371.
- Hamburger, H., and Crain, S. (1982). Relative acquisition. In S.A. Kuczaj (Ed.), *Language development: Volume I, syntax and semantics* (pp. 245-274). Hillsdale: Lawrence Erlbaum Associates, Inc.
- Hannah, A., and McGrew, W.C. (1987). Chimpanzees using stones to crack open oil palm nuts in Liberia. *Primates*, 28, 31-46.
- Hauser, M.D., Chomsky, N., and Fitch, W.T. (2002). The faculty of language: What is it, who has it and how did it evolve? *Science*, 298, 1569-1579.
- Hauser, M.D., Weiss, D., and Marcus, G. (2002). Rule learning by cotton-top tamarins. *Cognition*, 86, B15-B22.
- Hayashi, M., Mizuno, Y., and Matsuzawa, T. (2005). How does stone-tool use emerge? Introduction of stones and nuts to naïve chimpanzees in captivity. *Primates*, 46, 91-102.
- Henson, R. (2001). Neural working memory. In J. Andrade (Ed.), *Working memory in perspective* (pp. 151-173). Philadelphia: Psychology Press.
- Hoffecker, J. F. (2007). Representation and recursion in the archaeological record. *Journal of Archaeological Method and Theory*, 14, 359-387.
- Holloway, R.L. (1969). Culture: A human domain. *Current Anthropology*, 10, 395-412.
- Hurford, J. (1999). Functional innateness: Explaining the critical period for language acquisition. In M. Darnell, E. Moravcsik, F. Newmeyer, M. Noonan, and K. Wheatley (Eds.), *Functionalism and formalism in linguistics, Volume II: Case studies* (pp. 341-363). Amsterdam: John Benjamins.
- Inoue, S., and Matsuzawa, T. (2007a). Working memory of numerals in chimpanzees. *Current Biology*, 17, R1004-R1005.
- Inoue, S., and Matsuzawa, T. (2007b). Supplemental data: Working memory of numerals in chimpanzees. *Current Biology*, 17, R1004-R1005. (Accessed December 3, 2007).

URL = <http://www.current-biology.com/cgi/content/full/17/23/R1004/DC1>

- Inoue-Nakamura, N., and Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *111*, 159-173.
- Johnston, K., and Everling, S. (2006). Monkey dorsolateral prefrontal cortex sends task-selective signals directly to the superior colliculus. *The Journal of Neuroscience*, *26*, 12471-12478.
- Johnson, J., Fabian, V., and Pascual-Leone, J. (1989). Quantitative hardware stages that constrain language development. *Human Development*, *32*, 245-271.
- Kane, M.J., and Engle, R.W. (2002). The role of prefrontal cortex in working-memory capacity, executive attention, and general fluid intelligence: An individual-differences perspective. *Psychonomic Bulletin & Review*, *9*, 637-71.
- Kawai, N., and Matsuzawa, T. (2000a). "Magical number 5" in a chimpanzee. *Behavioral and Brain Sciences*, *24*, 127-128.
- Kawai, N., and Matsuzawa, T. (2000b). Numerical memory span in a chimpanzee. *Nature*, *403*, 39-40.
- Keesing, R.M. (1974). Theories of culture. *Annual Review of Anthropology*, *3*, 73-97.
- Keesing, R.M. (1975). *Kin groups and social structure*. New York: Holt, Rinehart and Winston.
- Kemps, E., De Rammelaere, S., and Desmet, T. (2000). The development of working memory: Exploring the complementarity of two models. *Journal of Experimental Psychology*, *77*, 89-109.
- Kidd, E., and Bavin, E.L. (2002). English-speaking children's comprehension of relative clauses: Evidence for general-cognitive and language-specific constraints on development. *Journal of Psycholinguistic Research*, *31*, 599-617.
- Kroeber, A.L., and Parsons, T. (1958). The concepts of culture and of social system. *American Sociological Review*, *23*, 582-583.
- Langer, J. (1980). *The origins of logic: Six to twelve months*. New York: Academic Press.
- Langer, J. (1986). *The origins of logic: One to two years*. New York: Academic Press.
- Langer, J. (2005). The primate phylogeny of cognitive ontogeny. In J. Valsiner (Ed.), *Heinz Werner and developmental science* (pp. 307-319). Berlin: Springer.
- Langer, J. (2006). The heterochronic evolution of primate cognitive development. *Biological Theory*, *1*, 41-43.
- Lanyon, S. J. (2006). A saltationist approach for the evolution of human cognition and language. In A. Cangelosi, A. D. M. Smith, and S. Kenny (Eds.), *Proceedings of the 6th International Conference on the Evolution of Language* (pp. 176-183). Singapore: World Scientific.
- Leaf, M. (in press). *Human organizations and social theory*. Urbana: University of Illinois Press.
- Leigh, S. R. (2004). Brain growth, life history, and cognition in primate and human evolution. *American Journal of Primatology*, *62*, 139-164.
- Leung, H.C., Gore, J.C., and Goldman-Rakic, P.S. (2005). Differential anterior prefrontal activation during the recognition stage of a spatial working memory task. *Cerebral Cortex*, *15*, 1741-1749.
- Liebal, K., Call, J., and Tomasello, M. (2004). Use of gesture sequences in chimpanzees. *American Journal of Primatology*, *64*, 377-396.
- Lieberman, D.E., McBratney, B.M., and Krowitz, G. (2002). The evolution and

- development of cranial form in *Homo sapiens*. *Proceedings of the National Academy of Sciences, USA*, 99, 1134-1139.
- Linden, D.E. (2007). The working memory networks of the human brain. *The Neuroscientist*, 13, 257-267.
- Luciana, M., and Nelson, C.A. (1998). The functional emergence of prefrontally-guided working memory systems in four- to eight-year old children. *Neuropsychologia*, 36, 273-293.
- Lycett, S.J., Collard, M., and McGrew, W.C. (2007). Phylogenetic analyses of behavior support existence of culture among wild chimpanzees. *Proceedings of the National Academy of Sciences, USA*, 104, 17588-17592.
- Marino, L. (2006). Absolute brain size: Did we throw out the baby with the bathwater? *Proceedings of the National Academy of Sciences, USA*, 103, 13563-13564.
- Marson, J., Meuris, S., Cooper, R.W., and Jouannet, P. (1991). Puberty in the male chimpanzee: Time-related variations in luteinizing hormone, follicle-stimulating hormone, and testosterone. *Biology of Reproduction*, 44, 456-460.
- Martin, R. D. (1981). Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature*, 293, 57-60.
- Matsuzawa, T. (1994). Field experiments on use of stone tools by chimpanzees in the wild. In R.W. Wrangham, W.C. McGrew, F.B.M. de Waal, and P.G. Heltne (Eds.), *Chimpanzee cultures* (pp. 351-370). Cambridge: Harvard University Press.
- Matsuzawa, T. (1996). Chimpanzee intelligence in nature and in captivity: Isomorphism of symbol use and tool use. In W.C. McGrew, L.F. Marchant, and T. Nishida (Eds.), *Great ape societies* (pp. 196-209). Cambridge: Cambridge University Press.
- Matsuzawa, T. (2003). Koshima monkeys and Bossou chimpanzees: Long-term research on culture in nonhuman primates. In F.B.M. de Waal and P.L. Tyack (Eds.), *Animal social complexity* (pp. 374-387). Cambridge: Harvard University Press.
- Matsuzawa, T. (2007). Comparative cognitive development. *Developmental Science*, 10, 97-103.
- McCarthy, G., Blamire, A.M., Puce, A., Nobre, A.C., Bloch, G., Hyder, F., Goldman-Rakic, P.S., and Shulman, R.G. (1994). Functional magnetic resonance imaging of human prefrontal cortex activation during a spatial working memory task. *Proceedings of the National Academy of Sciences, USA*, 91, 8690-8694.
- McGonigle, B., and Chalmers, M. (2006). Ordering and executive functioning as a window on the evolution and development of cognitive systems. *International Journal of Comparative Psychology*, 19, 241-267.
- McGrew, W.C., Ham, R.M., White, L.J.T., Tutin, C.E.G., and Fernandez, M. (1997). Why don't chimpanzees in Gabon crack nuts? *International Journal of Primatology*, 18, 353-374.
- Miller, E. K., and J. D. Cohen. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience* 24, 167-202.
- Miyake, A., and Shah, P. (1999). Emerging general consensus, unresolved theoretical issues, and future research directions. In A. Miyake and P. Shah (Eds.), *Models of working memory: Mechanisms of active maintenance and executive control* (pp. 442-481). Cambridge: Cambridge University Press.
- Newport, E.L. (1990). Maturational constraints on language learning. *Cognitive Science*, 14, 11-29.

- Nimchinsky, E., Gilissen, A., E., Allman, J.M., Perl, D.P., Erwin, J.M., and Hof, P.R. (1999). A neuronal morphologic type unique to humans and great apes. *Proceedings of the National Academy of Sciences, USA*, 96, 5258-5273.
- Obayashi, S., Suhara, T., Nagai, Y., Maeda, J., Hihara, S., and Irigi, A. (2002). Macaque prefrontal activity associated with extensive tool use. *NeuroReport*, 13, 2349-2354.
- Odifreddi, P. (2007). Recursive Functions. In E. N. Zalta (Ed.), *The Stanford encyclopedia of philosophy*. (Accessed June 26, 2008). URL = <http://plato.stanford.edu/archives/sum2007/entries/recursive-functions>
- O'Reilly, R., Braver, T.S., and Cohen, J.D. (1999). A biologically based computational model of working memory. In A. Miyake and P. Shah (Eds.), *Models of working memory: Mechanisms of active maintenance and executive control* (pp. 373-411). Cambridge: Cambridge University Press.
- Parker, S. T., and McKinney, M.L. (1999). *The evolution of cognitive development in monkeys, apes, and humans*. Baltimore: The Johns Hopkins University Press.
- Parkin, R. (1997). *Kinship: An introduction to basic concepts*. London: Blackwell.
- Pasternak, T., and Greenlee, M.W. (2005). Working memory in primate sensory systems. *Nature Reviews: Neuroscience*, 6, 97-107.
- Petrides, M., and Pandya, D.M. (1999). Dorsolateral prefrontal cortex: Comparative cytoarchitectonic analysis in the human and the macaque brain and corticocortical connection patterns. *European Journal of Neuroscience*, 11, 1011-1036.
- Pigeot, N. (1991). Réflexions sur l'histoire technique de l'homme: De l'évolution cognitive à l'évolution culturelle. *Paléo*, 3, 167-200.
- Potì, P., Langer, J., Savage-Rumbaugh, S., and Brakke, K.E. (1999). Spontaneous logicomathematical constructions by chimpanzees (*Pan troglodytes*, *P. paniscus*). *Animal Cognition*, 2, 147-156.
- Premack, D. (1986). *Gavagai! Or the future history of the animal language controversy*. Cambridge: MIT Press.
- Premack, D. (2007). Human and animal cognition: Continuity and discontinuity. *Proceedings of the National Academy of Sciences, USA*, 104, 13861-13867.
- Preuss, T.M. (2004). What is it like to be a human? In M.S. Gazzaniga (Ed.), *The cognitive neurosciences III* (3rd ed.) (pp. 5-22). Cambridge: MIT Press.
- Preuss, T.M., Cáceres, M., Oldham, M.C., and Geschwind, D.H. (2004). Human brain evolution: Insights from microarrays. *Nature Reviews Genetics*, 5, 850-860.
- Raghanti, M.A., Stimpson, C.D., Marcinkiewicz, J.L., Erwin, J.M., Hof, P.R., and Sherwood, C.C. (2007). Differences in cortical serotonergic innervation among humans, chimpanzees, and Macaque monkeys: A comparative study. *Cerebral Cortex Advance Access (June 22, 2007)*.
- Read, D. (1975). Hominid phylogeny, neutral mutations and "molecular clocks." *Systematic Zoology*, 24, 209-21
- Read, D. (1984). An algebraic account of the American Kinship terminology. *Current Anthropology*, 25, 417-440.
- Read, D. (2001). What is kinship? In R. Feinberg and M. Ottenheimer (Eds.), *The cultural analysis of kinship: The legacy of David Schneider and its implications for anthropological relativism* (pp. 78-117). Urbana: University of Illinois Press.
- Read, D. (in press a). Kinship theory: The need for a paradigm shift. *Ethnology*, 46.
- Read, D. (in press b). Learning natural numbers is conceptually different than learning

- counting numbers. *Brain and Behavioral Science*.
- Read, D., Lane, D., and van der Leeuw, S. (in press). The innovation innovation. In D. Lane, D. Pumain, S. van der Leeuw and G. West (Eds.), *Complexity perspectives on innovation and social change*. Berlin: Springer Verlag.
- Read, D., and van der Leeuw, S. (2008). Biology is only part of the story ... *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 363, 1959-1968.
- Rightmire, G. P. (2004). Brain size and encephalization in Early to Mid-Pleistocene *Homo Americanus*. *Journal of Physical Anthropology*, 124, 109–123.
- Rilling, J. K. (2006). Human and nonhuman primate brains: Are they allometrically scaled versions of the same design? *Evolutionary Anthropology*, 15, 65-77.
- Roland, P.E. (1985). Cortical organization of voluntary behavior in man. *Human Neurobiology*, 4, 155-167.
- Rossi, A. F., Harris B.J., Bichot, N.P., Desimone, R., and Ungerleider, L.G. (2001). Deficits in target selection in monkeys with prefrontal lesions. *Society for Neuroscience Abstracts*, 27, 574-579.
- Ruff, C. B., Trinkhaus, E., and Holliday, T.W. (1997). Body mass and encephalization in Pleistocene *Homo*. *Nature* 387, 173–176.
- Russell, J. (1996). Development and evolution of the symbolic function: The role of working memory. In P. Mellars and K.R. Gibson (Eds.), *Modeling the early human mind* (pp. 159 – 170). Oxford: McDonald Institute Monographs.
- Sanz, C., Morgan, D., and Gulick, S. (2004). New insights into chimpanzees, tools, and termites from the Congo Basin. *The American Naturalist*, 164, 567-581.
- Savage-Rumbaugh, E.S., McDonald, K., Seveik, R.A., Hopkins, W.D., and Rubert, E. (1986). Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). *Journal of Experimental Psychology: General*, 115, 211-235.
- Scheffler, H.W., and Lounsbury, F.G. (1971). *A study in structural semantics: The Sirionó kinship system*. Englewood Cliffs: Prentice-Hall.
- Schick, K. D., Toth, N., Garufi, G., and Savage-Rumbaugh, E.S. (1999). Continuing investigations into the stone tool-making and tool-using capabilities of a Bonogo (*Pan paniscus*). *Journal Of Archaeological Science*, 26, 821-832.
- Schneider, D. (1976). Notes toward a theory of culture. In K. Basso and H. Selby (Eds.), *Meaning in anthropology* (pp. 197-220). Albuquerque: University of New Mexico Press.
- Semendeferi, K., Armstrong, E., Schleicher, A., Zilles, K., and Van Hoesen, G.W. (2001). Prefrontal cortex in humans and apes: A comparative study of area 10. *American Journal of Physical Anthropology*, 114, 224-241.
- Sheldon, A. (1974). The role of parallel function in the acquisition of relative clauses in English. *Journal of Verbal Learning & Verbal Behavior*, 13, 272-281.
- Sherwood, C.C., Stimpson, C.D., Raghanti, M.A., Wildman, D.E., Uddin, M., Grossman, L.I., Goodman, M., Redmond, J.C., Bonar, C.J., Erwin, J.M., and Hof, P.R. (2006). Evolution of increased glia-neuron ratios in the human frontal cortex. *Proceedings of the National Academy of Sciences, USA*, 103, 13606-13611.
- Siegel, L.S., and Ryan, E.B. (1989). The development of working memory in normally achieving and subtypes of learning disabled children. *Child Development*, 60, 973-

980.

- Smith, E. E., and Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science*, 283, 1657-1661.
- Smith, E. E., Jonides, J., and Koeppe, R.A. (1996). Dissociating verbal and spatial working memory using PET. *Cerebral Cortex*, 6, 11-20.
- Spinozzi, G. (1993). The development of spontaneous classificatory behavior in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 107, 193-200.
- Spinozzi, G., Natale, F., Langer, J., and Schlesinger, M. (1998). Developing classification in action: II. Young chimpanzees (*Pan troglodytes*). *Human Evolution*, 13, 125-139.
- Spinozzi, G., Natale, F., Langer, J., and Brakke, K.E. (1999). Spontaneous class grouping behavior by bonobos (*Pan paniscus*) and common chimpanzees (*P. troglodytes*). *Animal Cognition*, 2, 157-170.
- Sugiyama, Y. (1997). Social tradition and the use of tool-composites by wild chimpanzees. *Evolutionary Anthropology*, 6, 23-27.
- Sumita, J., Kitahara-Frjisch, J., and Norikoshi, K. (1985). The acquisition of stone-tool use in captive chimpanzees. *Primates*, 26, 168-181.
- Swanson, H.L. (1999). What develops in working memory? A life span perspective. *Developmental Psychology*, 35, 986-1000.
- Swanson, H. L., Jerman, O., and Zheng, X. (2008). Growth in working memory and mathematical problem solving in children at risk and not at risk for serious math difficulties. *Journal of Educational Psychology*, 100, 343-379.
- Tavakolian, S. (1981). The conjoined clause analysis of relative clauses. In S. Tavakolian (Ed.), *Language acquisition and linguistic theory* (pp. 167 – 187). Cambridge: MIT Press.
- Terrace, H.S., Petitto, L.A., Sanders, R.J., and Bever, T.G. (1979). Can an ape create a sentence? *Science*, 206, 891-902.
- Tomasello, M. (1998). Uniquely primate, uniquely human. *Developmental Science*, 1, 1-30.
- Tomonaga, M., Tanaka, M., Matsuzawa, T., Myowa-Yamakoshi, M., Kosugi, D., Mizuno, Y., Okamoto, S. Yamaguchi, M.K., and Bard, K.A. (2004). Development of social cognition in infant chimpanzees (*Pan troglodytes*): Face recognition, smiling, gaze, and the lack of triadic interactions. *Japanese Psychological Research*, 46, 227-235.
- Toth, N., Schick, E. S., Savage-Rumbaugh, S. R. A., and Rumbaugh, D. (1993). The Oldowan reassessed. *Journal of Archaeological Science*, 12, 101-120.
- Vuontela, V., Steenari, M.R., Carlson, S.E., Koivisto, J., Fjällberg, M., and Aronen, E.T. (2003). Audiospatial and visuospatial working memory in 6-13 year old school children. *Learning & Memory*, 10, 74-81.
- Williams, M.F. (2002). Primate encephalization and intelligence. *Medical Hypotheses*, 58, 284-290.
- Wimsatt, W.C., and Griesemer, J.R. (2007). Reproducing entrenchments to scaffold culture: The central role of development in cultural evolution. In R. Sansom and R.N. Brandon (Eds.), *Integrating evolution and development: From theory to practice* (pp. 227-324). Cambridge: MIT Press.
- Woodman, G. F., Luck, S.J., and Schall, J.D. (2007). The role of working memory representations in the control of attention. *Cerebral Cortex*, 17 (suppl. 1), i118 - i124.
- Wynn, T. (2002). Archaeology and cognitive evolution. *Behavioral and Brain Sciences*, 25,

389-438.

Wynn, T., and McGrew, W.C. (1989). An ape's view of the Oldowan. *Man, New Series*, 24, 383-398.

ⁱ A recursive procedure applies itself to its own outcome. Recursion may lead to combinations of elements used in the recursion, but recursion is not the same as taking combinations of elements, the definition used by Hoffecker (2007) in a recent review of recursion in the production of artifacts studied by archaeologists: “*recursion* or the capacity for generating a potentially infinite array of varying combinations of their elements” (2007, p. 361, emphasis in the original).

A simple example of recursion is constructing one's family tree using the procedure “Identify, for a person that has just been identified, the mother and father of that person.” The procedure begins by identifying a person as the starting point and then identifying who is that person's mother and who is that person's father. Next the procedure is applied to each of these persons; that is, identify the mother and father of that have just been identified. Then the procedure must be applied to each of these persons, and so on.

The power of a recursive procedure lies in self-referencing. Though the procedure only has a finite number of steps, it may be reapplied unendingly to the outcomes of the procedure at each step. Recursive procedures can thus, in principle, generate an infinite set of outcomes. Practically speaking, there are ending conditions for repeated application of the procedure, such as (in the above example) not knowing who are the mother and the father of the currently identified person. Linguistically, recursion occurs with sentence embedding: “I met the person who talked to the taxi driver who drove his mother home.”

ⁱⁱ Matsuzawa (1996) has suggested the following scale for characterizing the complexity of tool use: Level 0 – no tools are used on the task focal object; Level 1 – a single tool acts on the focal object; Level 2 – two tools are used in coordination to act on the focal object; Level 3 – three tools are used in coordination to act on the focal object; and so on. Strict application of this scale would require labeling nut cracking at Bossou and at Taï, as well as termite foraging at the Goualougo Triangle, as Level 2 usage of tools. The argument presented here suggests that the scale should be based on the number of coordinated objects used in the task regardless of whether the focal object is one of the coordinated objects. Thus nut cracking at Bossou would become Level 3 and thereby differentiated from nut cracking at Taï and termite foraging at the Goualougo Triangle, where tool usage would be Level 2, as only two rock objects need to be coordinated.

ⁱⁱⁱ Whether Ai has a number concept is not established by these data. Recognizing that two sets are of the same size through, for example, 1-1 matching is not equivalent to having a concept of numbers as part of a symbolic system for doing computations with quantities (Read, in press b).

^{iv} This might sound like a blade analogy to flake removal through iteration, but it is not. Flake removal mainly requires control of the angle through which force is applied (either by striking with another object or through applying pressure with an instrument) to the surface from which a flake will be removed. Prismatic blade removal is a far more

demanding process in which a core nodule must be specially prepared with a flat surface on one end so that the artisan can strike the edge of the nodule and remove a long, narrow blade as long as the height of the nodule. The blade scar from one removal also guides the force transmitted through the nodule from the blow to the edge of the flat surface for the next removal. One blade removal literally prepares the core for the next blade removal; hence it is a recursive process.