



SYSTEMATIC REVISION/STATE OF THE ART

## Finding our way: a review on the evolution of human spatial cognition

Maria Ana Correia<sup>1\*</sup>, Eugénia Cunha<sup>2</sup>, Susana Carvalho<sup>3,4</sup>

<sup>1</sup>Division of Biological Anthropology, Department of Archaeology & Anthropology, University of Cambridge, Cambridge, UK

<sup>2</sup>Department of Life Sciences, Faculty of Sciences and Technology, University of Coimbra, Coimbra, Portugal

<sup>3</sup>Center for the Advanced Study of Hominid Paleobiology, George Washington University, Washington (DC), USA

<sup>4</sup>Interdisciplinary Center for Archaeology and Evolution of Human Behavior, FCSH, University of Algarve, Campus de Gambelas, Faro, Portugal

\*Corresponding author: [mamac2@cam.ac.uk](mailto:mamac2@cam.ac.uk)

Article received on the 28<sup>th</sup> of May of 2014 and accepted on the 6<sup>th</sup> of September of 2014

### ABSTRACT

Most developmental processes, from the molecular to the cognitive level, have many similarities throughout the animal kingdom. The aim of the present study was to examine the evolution of human spatial cognition by contextualizing it in a developmental cognition framework. In order to achieve this, a thorough literature review on significant research was conducted, including data from primatology, cognitive science, archaeology and human evolution. The fascinating result of this literature review consists in the novel suggestion that ontogenic data can be useful for understanding human cognitive evolution. Further investigation in this field is required to achieve more conclusive results.

*Keywords: working memory; cognitive development; human evolution; stone tools.*

\*\*\*

## RESUMO

A maior parte dos processos de desenvolvimento, do nível molecular ao nível cognitivo, apresentam muitas semelhanças em todo o do reino animal. O objectivo do presente estudo consistiu em examinar a evolução da cognição espacial humana, contextualizando-a com informação relativa ao desenvolvimento cognitivo. Foi elaborada uma exaustiva revisão da literatura relevante em várias áreas de pesquisa, incluindo a primatologia, a cognição, a arqueologia e a evolução humana. O principal resultado deste trabalho consiste na constatação, que até certo ponto se comprova, de que os dados de ontogenia podem ser úteis na compreensão dos percursos e conformações da evolução cognitiva humana. Para obter dados mais conclusivos é necessária investigação continuada.

*Palavras-chave: memória de trabalho; desenvolvimento cognitivo; evolução humana; instrumentos líticos.*

## Introduction

*How we came to be* has always been one of the fundamental questions that plague human beings. How did we become who we are, with such (apparent) different minds from our closest relatives, the apes? In other words, what are the ultimate causes and timing of the evolution of human cognition? This is not just a matter of philosophical questioning, as praiseworthy as that can be, but may also shed light on the workings of the modern mind and help the development of neuroscience. Also, as Herbert Spencer stated in 1870: “Mind can be understood only by showing how mind is evolved” (Spencer, 1870: 291).

However, if one defines cognition as the ability of living creatures to adaptively modify their behaviour in order to decide what to do next (Huber, 2000), then the evolution of

cognition becomes very hard to study in the archaeological record because behaviour does not fossilize. Only its results do.

One possible solution for this problem came from cognitive archaeology, which is a relatively new branch of archaeology that approaches the archaeological record from the perspective of psychological theories and methods (Wynn, 2002).

But because the different aspects of modern cognition, like the different anatomic characteristics, are likely to have evolved at different times for different reasons (Wynn and Coolidge, 2011), this study will use the cognitive archaeology approach focusing on the evolution of human spatial cognition, with a special emphasis on the *Homo* lineage. This method is promising once one considers that many human activities are organized in space (Wynn, 2010). This line of enquiry

becomes even more intriguing when contemplating that recent studies link spatial cognition with language and social abilities, suggesting that these might have evolved in a complex interrelational synchrony (Gentner, 2007; Grove and Coward, 2008; Vieira, 2010).

Considering that these cognitive skills only develop fully in adulthood and, that cognitive archaeology strives precisely to use modern cognitive theories to analyse the archaeological record, then it would be interesting to look into it from the scope of cognitive development theory. More exactly, if one considers that developmental processes have reproductive consequences, then cognitive development must have been a target of natural selection, leading to the evolution of adaptive developmental trajectories. In fact, the evolution of large brains and novel brain structures presupposes evolutionary modification of ontogenetic programs (Zollikofer and de León, 2013). In other words, developmental and evolutionary accounts of cognition are complementary and can provide powerful insight into the human history (Fiddick and Barrett, 2001). Finally, the development of spatial cognition in children is a step-wise process that results in observable behaviours with results organized in space (Vasilyeva and Lourenco, 2012). Others have already attempted using developmental approaches to study the archaeological record, e.g. Wynn (1985), whom, in his article “Piaget, stone tools and the evolution of human intelligence” considers the changes in the stone tool technologies applying a Piagetian framework. Much has been discovered, however, between 1985 and nowadays; and,

so, a new and improved probe into this line of thought could prove to wield novel exciting results.

Thus, the hypothesis that we sought to test was: does child spatial cognitive development retrace the evolution of human spatial cognition? Or, at the very least, by comparing child developmental science and the evolution of human spatial cognition can similarities and/or disparities be found that will help shed light on the subject of human evolution?

Hence, the goal of this article is to bring together the fields of cognitive development and of evolution of spatial cognition, through a thorough literature review, which will framework the topic and explore possible bridges between different fields of study, such as primatology, neuroscience and, obviously, archaeology.

It is our belief that interesting patterns emerged, which are worth discussion and that this evolutive-developmental approach has the potential to give an important input into the subject of human evolution.

### **Evolution of human cognition**

As stated above, cognition can be defined as the ability of living creatures to adaptively modify their behaviour in order to decide what to do next (Huber, 2000). The evolution of cognition itself, however, is more difficult to approach as already briefly discussed, for several reasons. First of all, there's the problem that the proceedings that led to our evolution are not reproducible and, as such, very hard to test (Wynn, 1985, 2002).

Secondly, the archaeological record, is still the only 'direct' way one has to access the events and contexts in which human evolution took place. However, these are usually very fractioned; suffer from a sliding scale of resolution – in other words, as a general rule, the older the site, the worst its preservation (Foley, 1996), although this depends on the specifics of the site, such as temperature and humidity; and finally, are strongly subjected to the researcher's interpretation (d'Errico *et al.*, 2003; Wynn, 2010). Also, this same researcher is strongly influenced by his field of study and although there has been an increasing strive for multidisciplinary, there is still a lot of ground to cover in order to have an inclusive as possible approach to this sort of problem (Thornton, 2012).

All of this amounts (more or less) to a troubling methodological problem. How to approach the evolution of cognition is the main issue (Foley, 1996). Cognitive archaeology uses two approaches to overcome this. The first depends on a current cognitive theory to identify patterns in the archaeological record that reflect specific cognitive abilities. The second relies on the experiment reproduction of the prehistoric activities, resorting to modern participants who act as surrogates for the extinct hominins. These are not mutually exclusive (Wynn 2002; 2010).

Nowadays, one of the most well developed and most widely used models is the multi component working memory model, initially constructed by Baddeley and Hitch (1974). Working memory refers to the mind's ability to hold and process

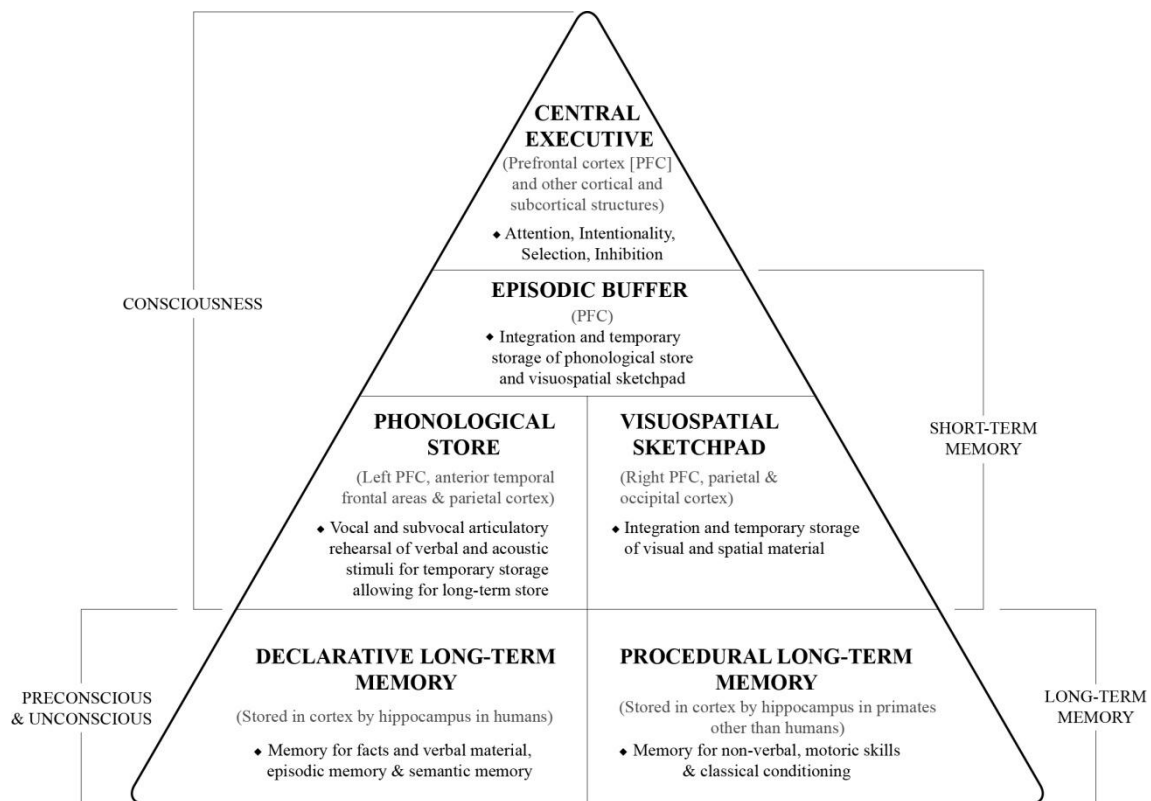
information in active attention (Wynn and Coolidge, 2010; 2011; Baddeley, 2012). The working memory model is not a simple, neural system but a complex neural network consisting of neural pathways that interlink much of the neocortex. As it stands, the model consists of an attentional pan model processor – the 'central executive' –, two subsystems – the 'phonological loop' and the 'visuospatial sketchpad' –, and a temporary memory store – the 'episodic buffer' (Baddeley, 2012).

The phonological loop is dedicated to auditory phenomena, and maintains and rehearses auditory information either vocally or subvocally. It may be the most neurological isolated component consisted of a specialized auditory-vocal sensoriomotor circuit connecting posterior temporal areas with the inferior parietal lobe and the ventrolateral prefrontal cortex (Aboitiz *et al.*, 2010). The visuospatial sketchpad is a distinct subsystem that processes and stores visual information (shapes and locations), allowing transfer for long-term memory. Its neural implications are not completely clear yet, but it may connect the right prefrontal cortex to the parietal and occipital cortex. These two can perform simultaneously. The episodic buffer holds information provided by the subsystems in active attention where it can be processed by the resources of the central executive. The central executive, on the other hand, performs most of the processing, including attention, active inhibition, decision making, planning, sequencing, temporal tagging and the updating of the information in the two subsystems. It also serves as the chief liaison to long-term memory. Both the

episodic buffer and the central executive are related to the prefrontal cortex (Wynn and Coolidge, 2010; 2011; Baddeley, 2012).

Long-term memory is the ability to store information for hours, days and years and it can be divided between declarative and procedural. Declarative memory matches consciously retrievable knowledge. In other words, it can be expressed (in humans) in words, while procedural memory corresponds to the physical 'know-how',

consisting on the ability to replay motor behaviours, techniques or procedures, which are often hard to verbalize (Wynn and Coolidge, 2010; 2011). Furthermore, the declarative memory depends on the hippocampus, while the procedural depends on the striatum (Burgess, 2008). This will be the most commonly used model throughout this essay. Figure 1 aims to clarify its different components.



**Figure 1. Major components of working memory and long-term memory according to Wynn and Coolidge (2010). This figure also includes general considerations by these authors, such as the localization in the brain of these components and of their correspondence to conscious or preconscious and conscious processes.**

As a final note, one common problem in models in the evolution of cognition is that they tend to take a linear approach, where all

types of behaviour that are not considered fully 'modern' assume a position at a lower level of cognition. However, the modern

biological model of human evolution is that of a branching tree. Considering this, it is likely that unique cognitive expressions existed throughout time and that two different kinds of *equal* complex cognition existed side by side (Langbroek, 2012). This is an interesting dilemma, which poses many methodological problems, but to which this work will try to remain attentive.

### **Spatial cognition in humans**

As defined by Hartley and Burgess (2003: 1) “spatial cognition covers processes controlling behaviour that must be directed at particular locations or responses that depend on the location or spatial arrangement of stimuli”. In other words, this capacity enables their possessors with the ability to distinguish one spatial arrangement of stimuli from another. It is easily deductible that this broad definition includes a wide range of behaviours and that is present in life forms as varied as insects, birds, fishes and mammals.

Although this might seem like a too broad of a definition, one must not forget that these concepts are, by definition, human-made. They do not translate directly into reality. Definitions are meant to help in understanding this nature but they do not correspond to necessary boundaries. Over the last century, more and more barriers of thought have been overcome while scientists come to the realization that too strict definitions might blur connections among different concepts. A neuron cannot be separated from the brain, which in turn, cannot be divided in extant units, and cannot

be considered without the developmental, ecological and in many cases social environment (Grove and Coward, 2008).

Spatial cognition in humans is believed to separate into two modes, which represent differently in the mammalian brain. In the first one, processes involved in action, attention and perceptual constancy involve the parietal neocortex. In the second one, processes involved in long-term spatial memory, orientation and navigation happen in the hippocampus and adjacent cortical and subcortical structures. The retrosplenial cortex and parieto-occipital sulcus, on the other hand, allow for both types of representation to interact. Again, this division of labour is somewhat artificial; most tasks don't fall exactly into one type or the other, but involve elements of both. Besides, the parietal neocortex and the hippocampus perform other tasks other than these and are involved in many neural processes (Hartley and Burgess, 2003).

What is of interest to this discussion is that, first, parietal processes concern short time scales and the space surrounding the body, while hippocampal processes are concerned with large distances and long timescales. Second, these processing modes demand different forms of spatial representation (Hartley and Burgess, 2003; Salas *et al.*, 2003). The first one uses egocentric representations where objects are referred to the self – example: the rock to my right. This can be used either when the observer remains stationary or when he/she moves and is able to keep track of the movement, a process known as ‘dead reckoning’. This type of egocentric

representation can be useful for guiding action on a short term basis. But on a long term basis, they would have to be constantly updated to reflect changes in the subject's location and heading. So, it most likely relates to object representation and manipulation. From the point of view of tool-making, it is also important to consider that mental rotation – an important part of object manipulation in humans – frequently also activates motor areas relevant to the hands (Wraga *et al.*, 2005).

Processes demanding long-term memory of a location benefit from a representational map that relates locations to each other and to landmarks in the environment. Such representations are deemed allocentric. They can be further divided into intrinsic, where objects are truly located in relation to each other (example: the big rock by the side of the river) or geocentric, where an absolute frame is used (example: the rock on the northwest corner). But, again, limits are not strictly defined, most actions should call for the coordination of different space representations, as they develop to demand coordination of many effectors in time and space (Hartley and Burgess, 2003; Gentner, 2007; Vasilyeva and Lourenco, 2012).

Another central issue in spatial cognition is the type of information used. This is usually divided between metric and categorical representations, where the first one can be seen as a spatial representation that specify distance and direction from a point of reference, while the second codes object locations with respect to a larger spatial region, without specifying exact coordinates

within that region (Vasilyeva and Lourenco, 2012)

Interestingly, in the archaeological context one has access to two types of spatial patterning. The first refers to patterns of activity in the site and patterns of sites on the landscape. The second type concerns the artefact itself and the organization of actions in space and time in order to obtain it (Wynn, 2010). Moreover, one must consider the already mentioned sliding scale of resolution in the archaeological record. As such, the first type of spatial patterning requires limited taphonomic effects and as such can only be used in relatively recent archaeological contexts or in very well preserved contexts (Wynn, 2010; Arbib, 2011). The second type, however, concerns a smaller scale of action and translates, for instance, in stone tools, those being the earliest and most widespread evidence of hominid behaviour (de Sousa and Cunha, 2012).

These two types of spatial patterning in the archaeological record roughly match the two modes of spatial cognition. The production of stone tools should be handled, at least partly, by the mode of spatial cognition that is located in the parietal neocortex. This was confirmed by Stout and Chaminade (2007) in a study that tests experimental Oldowan toolmaking by naive subjects. They found: 1) activation of an evolutionarily conserved object manipulation circuit including the rostral part of the dorsal intraparietal sulcus (IPS) and ventral premotor cortex (PMC); 2) bilateral recruitment of human visual specializations in a more evolutionary recent part of IPS; 3) modulation by practice of activity relating to

visual search (caudal intraparietal/transverse occipital sulci), object recognition (lateral occipital cortex), and grip selection (ventral PMC); 4) lack of any activation in dorsolateral prefrontal cortex (PFC) relating to strategic action planning. Based on these findings, Stout and Chaminade (2007) defend that simple stone tool making skills are related to perceptual-motor adaptation to task constraints and exploitation of object affordances, rather than with higher order strategic organization. They further suggest that the acquisition of sensorimotor capabilities, and not the executive capacities for strategic planning, provided the evolutive force in the initial development of complex tool use and tool making skills.

This experiment was later expanded by Stout *et al.* (2008) to include expert stone tool makers and Acheulean tool making. According to their expectations, expertise during Oldowan tool making was associated with increased inferior parietal lobe (IPL) activation – an area associated with tasks involving familiar tools (Lewis, 2006). This activation was bilateral, which was not expected, considering the common left hemisphere dominance for tasks involving familiar tools (Lewis, 2006). Stout *et al.* (2008) explain this result indicating that expert Oldowan tool making depends more upon enhanced sensorimotor representation of the ‘tool plus body’ system than upon stored action semantics of the kind recruited when planning the use of everyday tools. Also of interest is the unexpected bilateral supramarginal gyrus (SMG) activation, which supports that proper bimanual coordination, and particularly the left-hand support role,

only develops after consistent practice. There was also no evidence of engagement of PFC areas, suggesting that expert Oldowan tool makers also do not engage in strategic planning.

Where Acheulean tool making is concerned, there was an increase in right hemisphere activity, indicating a critical role for the right hemisphere-left hand system in handaxe production, as well as the involvement of more complex technical action sequences. There was also activation of ventrolateral, but not dorsolateral PFC indicating that Acheulean tool making is distinguished by cognitive demands for the coordination of ongoing, hierarchically organized action sequences, and not by the internal rehearsal and evaluation of action plans. The right hemispheric activation of ventrolateral PFC probably reflects demands for such action coordination that are particular to the left-hand core support and manipulation aspect of the task (Stout *et al.*, 2008). These two factors testify to the more complex, multi-level structure of Late Acheulean tool making, which includes the flexible interaction of multistep processes in the context of larger scale technical goals (Stout *et al.*, 2008).

These authors also found increased activation of ventral premotor and inferior parietal elements of the parietofrontal praxis circuits in both the hemispheres and of the right hemisphere homologue of Broca’s area, suggesting that toolmaking and language share a basis in more general human capacities for complex goal-directed action.



### Spatial cognition in other animals

When comparing spatial cognition across the animal kingdom, Salas *et al.* (2003) claim that there is a close functional similarity between spatial cognition mechanisms in different groups of vertebrates, mammals, birds, reptiles and teleost fish, which rely on homologous neural mechanisms.

Traditionally, cognitive mapping skills were seen as an exclusive attribute of vertebrate groups with more complex associational structures, such as mammals and birds, which have been shown to be capable of using allocentric representations of space for navigation and goal location (Jacobs, 2003). However, there is also evidence that reptiles and teleost fishes are also capable to use cognitive mapping strategies (Holtzman *et al.*, 1999). For instance, it appears that turtles and goldfish can navigate accurately and flexibly to a goal on the basis of information provided by an array of landmarks, by means of encoding their spatial relationships in a map-like representation that provides a stable frame of reference (Rodríguez *et al.*, 1994; López *et al.*, 2003; Broglio *et al.*, 2010). More, it seems that turtles and goldfish can choose the appropriate trajectory towards the goal from novel start locations in the absence of local cues, which rules out the hypothesis of exclusively-egocentric referenced orientation mechanisms (Rodríguez *et al.*, 1994; López *et al.*, 2003; Durán *et al.*, 2010). This data may suggest that the neural mechanisms for mental mapping were already present in the last common ancestor of teleosts and land vertebrates and have been retained throughout phylogenesis. (Salas *et al.*, 2003).

Although the underlying neural mechanisms may be the same, this does not mean that different species do not have different types of spatial cognitions. Elephants, for instance, are an interesting case study. As humans and great apes, they possess large brains, have a long life expectancy and their offspring requires long periods of dependency (Hart *et al.*, 2008). However, despite this characteristics and when comparing to great apes, elephants perform below expected in tasks such as tool use, visual discrimination learning and tests of 'insight' behaviour. Where elephants do seem to excel is in long-term, extensive and spatial-temporal and social memory (McComb *et al.*, 2000; Hart *et al.*, 2001; Bates and Byrne, 2007). They might even exhibit 'theory-of-mind' behaviours by the way they react to disabled or diseased conspecifics (Douglas-Hamilton *et al.*, 2006). Elephants may be specialized for cognitive mapping, since they need to remember spatial information over very long periods, for instance the locations of waterholes in a desert, which they may need to re-visit after many years of not doing so or the social interactions they take on over time (Byrne *et al.*, 2009).

Hart *et al.* (2008) suggest that the interactions between neurons of the cerebral cortex of these animals may be much less compartmentalized, with a bias toward maintaining global connections throughout the cerebral cortex, and the interaction times slower than in primates, putting elephants at a disadvantage in primate-like, time-sensitive or intricate tests of 'higher order' brain functions. But it may be, according to these

authors, an adaptation to other aspects of brain functions, namely long term, spatial-temporal and social memory, by allowing for an exceptional ability to integrate information from a wide variety of spatial-temporal and social domains.

Also of interest is the fact that several animals have been found to be capable of applying different strategies in different situations, encoding locations in different ways, depending on what information is available to them (Hribar and Call, 2011; Hribar *et al.*, 2011). For instance, it has been found that cats, dogs and great apes prefer allocentric over egocentric coding when they are forced to move, before attempting to find a given object (Burgess, 2006; Fiset and Doré, 1996; Fiset *et al.*, 2000). Moreover, there are proof that nonhuman primates readily use landmark cues to search for hidden food (Potì *et al.*, 2005; Dolins, 2009; Kanngiesser and Call, 2010). Hribar and Call (2011) tested chimpanzees, bonobos and orangutans and confirmed that great apes use landmark cues over spatial relations to find hidden food. They found no evidence for geocentric strategies.

These authors found two other interesting results. First, their subjects showed lower results when using two landmarks, instead of one. Having to encode a location in relation to two landmarks is cognitively more demanding than encoding that location in relation to a single landmark. Several studies have shown that while non-human animals readily use single landmarks to find food, they struggle when using multiple landmarks cues simultaneously (Potì *et al.*, 2005; Marsh *et al.*, 2011).

Even in humans, children more easily master their search behaviour in relation to one landmark – at around two years – than in relation to two landmarks – at four years of age – (DeLoache and Brown, 1983; Uttal *et al.*, 2006). This is especially intriguing when one considers that to be capable of analogical thinking animals would need to be capable of reasoning about the relation between two relations (Hribar *et al.*, 2011). More, considering the role of analogies in language acquisition and inductive inference or categorization, it has been wondered if the ability to recognize and respond to abstract relations within relations might be especially pronounced in humans (Hribar *et al.*, 2011).

The second interesting result of Hribar and Call (2011) lies in that chimpanzees and bonobos outperform orangutans in spatial cognition tasks that involve displacements (Herrmann *et al.*, 2007; Albiach-Serrano *et al.*, 2010). Hribar and Call (2011) suggest that the level of sociality and/or terrestriality might help explain the observed inter-species differences in spatial cognition. They suggest, although empirical verification is required, that bonobos and chimpanzees may have a greater capacity to keep track of the movements and locations of their conspecifics or to keep track of food sources on the ground, encoding them according to landmark.

This last hypothesis is fascinating in light of the proposition by Meulman *et al.* (2012) that terrestriality may have been of crucial importance for the innovation, acquisition and maintenance of ‘complex’ technological skills in primates. More exactly, within an initial context of tool use tendencies –

spurred by dexterous manipulative skills – and social tolerance, terrestriality would promote not only the acquisition, but also the transmission and complexity of such skills, through enhanced probability of innovation and of socially based learning. Meulman *et al.* (2012) base their statement in four lines of evidence. First, the only monkey population exhibiting habitual tool use seems to be particular terrestrial. Second, semi-terrestrial chimpanzees have more complex tool variants in their repertoire than does their arboreal Asian relative, the orangutan. Third, tool variants of chimpanzees used in a terrestrial setting tend to be more complex than those used exclusively in arboreal contexts. Fourth, the higher frequency in tool use among captive versus wild primates of the same species may be attributed in part to a terrestriality effect. It must be noted that the authors recognize the need for further investigation to support their theory, which proposes terrestriality as a ‘facilitating condition’ for ‘complex’ technology within a composite framework, and not as stand-alone evolutive pressure.

Another relevant fact is reviewed by Oleksiak *et al.* (2011). These authors concluded that monkeys do not process spatial information with different efficiency in the two hemispheres, suggesting that lateralization of spatial cognition in humans represents a relatively new feature on the evolutionary time scale, possibly developed as a by-product of the left hemisphere intrusion of language competence.

Cerebral lateralization is usually seen to ensure more efficient employment of neuronal processing space, paralleled by a

reduction of possible interference between concurrent processes (Bradshaw, 2001). This process most likely results from an increase in absolute brain size, coupled with a relatively lower increase rate of the number of callosal axons (Aboitiz *et al.*, 2003). This hemispheric independence holds true mainly for the prefrontal and temporo-parietal visual areas that execute ‘higher’ cognitive functions and are interhemispherically connected by slow-conducting, weakly myelinated fibres (Schuz and Preissel, 1996; Aboitiz *et al.*, 2003).

Oleksiak *et al.* (2011) gathered ample proof that, one, monkeys do not show a more severe neglect or a longer recovery after experimentally induced right- as opposed to left-hemisphere damage, as in humans. Two, recovery to this damage in monkeys is much faster than in human. Three, there was no evidence of lateralized distribution of spatial working memory in monkeys, which also differs from human right hemisphere superiority. There is very limited evidence where non-human primate did show a similar to human asymmetrical hemispheric advantage in a visuospatial task and these usually related to an evolutionary old subcortical structure (Baker *et al.*, 2006; Kagan *et al.*, 2010). This could mean that monkey subcortical brain regions should have clear homologues in *Homo sapiens*’ brain.

In sum, although spatial information processing capacity of nonhuman primates resembles that of humans, there is a strong lateralization in humans, where monkeys process spatial information in either the left or the right hemisphere. Now, one must consider that there is clearer evidence for

functional brain lateralization in monkeys concerning left hemisphere species-specific vocalization processing (Belin, 2006; Poremba, 2006; Poremba and Mishkin, 2007). Such vocalizations are often perceived to be analogous to some aspects of human language.

Furthermore, both monkeys and humans seem to have a right-hemisphere advantage in discriminating faces (Hauser and Akre, 2001). This gives a picture where hominins inherited right hemispheric dominance in the processing of faces and a left hemispheric specialization when handling meaningful vocalizations. This pattern, according to Oleksiak *et al.* (2011), evolved overtime in such a way that visuospatial working memory first became compartmentalized in the right hemisphere and then served as basis for verbal working memory and language acquisition in the left-hemisphere (Aboitiz *et al.*, 2006; Ray *et al.*, 2008).

There is, however, a major flaw on the review conducted by Oleksiak *et al.* (2010). The authors only included data from monkeys, and not apes. Amici *et al.* (2010) investigated differences in cognitive skills between monkeys and apes on their ability to remember object locations – memory task –, track object displacements – transposition task – and obtain out-of-reach rewards and found no significant differences on the first and third test. Those are not, obviously, the full range of cognitive skills of non-human primates. And also, where Amici *et al.* (2010) did found differences between apes and monkeys was on the object displacement task, which requires spatial cognitive skills. Considering this, further studies in apes'

lateralization of spatial functioning would be extremely useful to provide insight into this problem.

As a final point, it is of interest to know that chimpanzees seem to experience difficulties in learning social rules in the context of object manipulation. Although young chimpanzees learn object tasks through observation, it is not common for them to present their mothers with interesting or novel objects, seeking social reference, as it is not common to see active teaching of infants by part of the mothers on object manipulation. It may be difficult for chimpanzees to divide attention between two targets at the *same time*: the demonstrator and the object (Hayashi, 2010).

### **Evolution of human development and development of spatial cognition**

Now, one must bring to attention the importance that developmental studies may bring towards understanding evolution. First, development can evolve, because it is repeated from generation to generation with variation in the developmental trajectories, with some leading to increasing fitness features and/or skills, and others not (Fiddick and Barrett, 2001). And, second, as pointed by the same authors, many adult competences, although they appear to function seamlessly, are in fact composed of separate components, whose individual operation may be more readily observed in children. As an example, many animals orient themselves in space using allocentric representations. Adult humans, however, use many different spatial cues, among others, to

orient themselves, making it difficult to understand the components of this competence. This core representation is more readily observed in infants (Vasilyeva and Lourenco, 2012).

Fiddick and Barrett (2001) make two other pertinent observations for this study. First, cognitive *flexibility* may in fact be the result of selection for developmental efficiency. In other words, evolved skills may be designed to tolerate some kinds of variation in developmental inputs, especially if it is not relevant to the adaptive problem the mechanism resolves – for instance, the same cognitive features allow one to learn several different languages. The second relevant remark by Fiddick and Barrett (2001) is that the evolved design of an organism will reflect the sorts of problems his ancestors faced and not the problems that the organism faces today. This is crucial, since the goal of this study is to understand how and why humans evolved.

At this point, one must consider the relation between development and life history. Life history relates to the way individuals of a given species adapt to their environment by dividing their energy among the tasks of self-maintenance, growth, production of offspring and maintenance of said offspring prior to independence (Bogin, 2003; Wood and Baker, 2011).

Humans differ from other primates mainly in four life history traits; they have higher neonatal weight, higher age at first reproduction, shorter interbirth interval and longer life span (Zimmerman and Radespiel, 2007). There are two advantages to the

prolongation of development. First, it may lead to a shortening of the infancy period when mothers are lactating, allowing them to become again fertile more quickly and decreasing intervals between births (Aiello and Key, 2002; Bogin, 2003; Nowell and White, 2010). Second, the added years of slow growth allows for behavioural experience that enhances developmental plasticity (Kaplan *et al.*, 2000; Bogin, 2003).

The prolongation of development is the most interesting factor for this study. It is generally thought that the life histories of the Middle Pleistocene *Homo* already included a significantly expanded childhood (Bogin, 2003; Nowell and White, 2010). It is still under discussion whether an adolescence stage was part of *Homo erectus* life story, but skeletal evidence points for a certain adolescence stage in archaic *sapiens* (Tardieu, 1998; Antón and Leigh, 2003; Bogin, 2003; Nowell and White, 2010). This is extremely important, since for the first time, there was an additional time to learn and develop social, ecological and technical skills.

Despite this change in life history in the Middle Pleistocene with an increase in development time, it probably still didn't match modern patterns (Dean *et al.*, 2001). Brain growth pattern in *Homo erectus* was still closer to that of a chimpanzee than that of a human (Coqueugniot *et al.*, 2004). Based on the distinctively slow dental development seen in modern humans, it seems that modern life history can be traced back to 160 Ka, but no further (Smith *et al.*, 2007). Neanderthals also seem to have had a developmental tempo similar to *Homo sapiens* (Dean *et al.*, 2001) although there is

evidence for some subtle differences (de León *et al.*, 2008; Smith *et al.*, 2010). More exactly, although Neanderthal brain size was similar to human brain size – likely due to equivalent obstetric constraints –, early brain growth rates were higher in Neanderthals than in humans, resulting in bigger adult brains (de León *et al.*, 2008). Neanderthals also presented a significant faster dental maturation. It is not yet clear what the implications are of these differences (Smith *et al.*, 2010).

The hominin life history is most probably a mosaic evolution and several factors influenced it. Important factors are bipedal locomotion – *Homo erectus* is generally thought as the first obligate biped –, the extension of geographic range and a shift towards more meat in the diet (Tardieu, 1998; Aiello and Wells, 2002; Antón *et al.*, 2002; Krovitz *et al.*, 2003). As a side note, there is some evidence that earlier hominins, namely *Australopithecus afarensis*, also engaged in bipedal locomotion (Stern and Susman, 1983; Latimer and Lovejoy, 1989). This claim is still contentious and a mosaic of terrestrial and arboreal locomotion has been defended. Bottom line, *Homo erectus* remains the *uncontested* first fully bipedal hominin (Harcourt-Smith and Aiello, 2004). Regarding the increasing reliance on meat, this dietary change led to a greater reliance on true hunting – stimulating the increase of geographic range – and an increased use of fire, resulting in hominin body proportions around the modern human range. It also caused a reduction in gut size and a 20 to 60 % increase in brain size, relative to early *Homo* (Aiello and Wells, 2002). This, together

with the bipedal locomotion and its consequent narrower hips may have led to earlier births, with more secondarily altricial infants. This also relates to the already mentioned shorter interval between births (Trevantham and Rosenberg, 2000). This is a very good example of how different factors intertwine and exponent each other to produce a given evolutionary effect.

Developmental shifts in spatial cognition allow humans to solve spatial problems with a higher degree of flexibility and accuracy (Hermer-Vasquez *et al.*, 1999, 2001; Rosati and Hare, 2012).

Early allocentric coding can be found in as early as 8.5 month olds, when infants use close landmarks to as a cue to object location. Only at 12 months is there some evidence for farther landmarks. Interestingly, it is possible that the emergence of allocentric coding in infants may be related to the onset of crawling at 8-9 months (Vasilyeva and Lourenco, 2012). At around the same time that allocentric coding begins, there is some evidence for the development of dead reckoning, although 12 month olds performance doesn't reach the same level on dead reckoning they reach when using adjacent landmarks. In fact, dead reckoning doesn't show significant improvement between 16 and 26 months, perhaps reflecting stability in motor development during toddler years (Newcombe *et al.*, 2013).

In reorientation tasks, when one must rely on cues of the environment to reorient and establish position towards target, organisms can use two different strategies. Spatial

strategies rely on cues that are based on the spatial layout of a place like its geometry or its relation to a configuration of landmarks, whereas feature strategies rely on cues that are based on specific features, such as colour or shape (Kanngiesser and Call, 2010). Lee and Spelke (2010) suggest that individuals first reorient themselves by reference to a three-dimensional environment and later use associative processes to link two-dimensional features. Features are only used as direct indicators of the target location, rather than as a guide to reorientation. This change may be related to the acquisition of language (Haun *et al.*, 2006a). Another model suggests that geometric and nongeometric information depends on relative weights associated with available cues – for instance, more distal landmarks are usually more reliable (Newcombe *et al.* 2013). Despite disagreements on models, geometric information seems to be of major importance since a very young age.

Even though infants and toddlers are capable of using egocentric and allocentric representations, this early ability is quite limited. Infant's reliance on environmental landmarks depends on their salience and proximity, while toddlers' use of geometric cues for reorientation is not integrated with landmark cues (Vasilyeva and Lourenco, 2012). Development of spatial cognition in older children involves improvement in the use of individual spatial representational systems and in the ability to integrate them. For instance, only at six years old can children use the structure of the environment to infer the target location from a novel position (Nardini *et al.*, 2009). Also only at six years

old, do children learn to combine different types of cues, for instance, combining geometric and nongeometric cues (Hermer-Vazqu ez *et al.*, 1999). The ability to integrate allocentric and egocentric frames of reference only develops later, with younger children alternating between one and the other. This integration follows an extended course of development, but once completed, it provides its user with an advantage by reducing response variance and improving accuracy (Nardini *et al.*, 2008).

Where the type of information – metric or categorical – is concerned, it has been generally thought that children begin by using categorical cues, and then go on to master metric ones. Indeed 3-4 months olds form categories tied to the objects used during learning, while older children – 6-7 months – are capable of forming abstract spatial categories (Quinn *et al.*, 1999). However, young infants already seem to have some notion of metric cues.

Similarly to categorical coding, metric properties emerge early in development – around 4-5 months – and undergo developmental change, as representations become more precise in older infants, around 6-7 months (Baillargeon, 1991). There is also proof to sensitivity to angular size and to distance (Lourenco and Huttenlocher, 2008). These notions would enable an individual to identify object size, shape and location. However, most of these studies are based on looking times, which is not always a reliable method. Older children can be more easily tested through search tasks. Although they seem to readily use metric cues, their success seems to be dependent on whether the

object size can be coded to another object. In other words, young children may rely on relative cues in coding spatial space (Huttenlocher *et al.*, 2002; Frick and Newcombe, 2012).

Another remarkable feature of toddler's spatial cognition is their ability, albeit limited, to integrate categorical and metric cues. This is useful, considering that the use of categorical information is generally helpful in reconstructing locations since metric representations are imprecise and short-lived (Huttenlocher *et al.*, 1994). From four to 12 years old, the accuracy of performance in such tasks that require coding object size and location improves greatly. One of the reasons for this is the increased memory for metric information and the other, the development of a hierarchical coding system, which integrates metric and categorical information (Sandberg *et al.*, 1996; Newcombe and Huttenlocher, 2000).

Mental rotation is far from fully developed in infancy. Örnkloo and von Hofsten (2007) found that only at 22 months could infants mentally rotate objects to be fitted through an aperture in order to successfully fit objects through holes. Frick *et al.* (2013), on the other hand, found that 4-year-olds still performed at chance levels in mental rotation tasks, using a touch screen paradigm – a simplified version of the famous Tetris game. In this experiment only at 5-year-old did subjects showed some signs of successful mental rotation, although the results were still far from perfect. These authors suggest that precursors of mental rotation abilities, such as basic understanding of rotation processes and anticipation of object

movement, develop early, which then have to be coupled with manual dexterity, among other factors. In fact, mental rotations continues to strengthen through early childhood – long after manual dexterity stops being a limiting factor –, being accelerated by motor experience (Okamoto-Barth and Call, 2008; Frick *et al.*, 2013; Newcombe *et al.*, 2013)

Another significant spatial development around 6-7 years old and going on to about 12 years old concerns the ability to code location in relation to multiple distal landmarks, instead of only one. Thus, there appears to be a relatively long lag time between developing the ability to encode a location in relation to one landmark and then to more landmarks. This may be due to functional maturation of the hippocampus, as well as to experience with navigation and use of landmarks (Newcombe and Huttenlocher, 2000; Leplow *et al.*, 2003).

An important factor in the development of spatial cognition is symbolic representation, which allows one to acquire and communicate information about space beyond that available from direct experience (Vasilyeva and Lourenco, 2012). Generally speaking, the ability to solve mapping tasks on the basis of object correspondence appears at 2.5-3 years of age, but the ability to use spatial relations in mapping emerges later and initially manifests itself only in limited contexts (DeLoache, 1995). At around four years, children are able to use distance cues and, at 5-6 years, they start using angular relations in simple map tasks, although they keep improving depending on accumulating experience with maps (Spelke



*et al.*, 2011). In fact, accuracy in spatial scaling – a very important part of using maps – undergoes the most marked development between 3-5 years. Moreover, the youngest children in the test group were the ones who showed the higher variability in performance and that most profited from landmark information, indicating a developmental progression from treating the referent space as homogenous toward a more fine-grained response (Frick and Newcombe, 2012). Finally, Frick and Newcombe (2012) found that participants encoded relative rather than absolute distances.

Language is also likely to be a very important factor. For instance 8 year-olds performed best at spatial tasks on the reference frame favoured by their language as Gentner asserts (2007). This author goes on to propose that developmentally, humans begin by using an allocentric bias that is shared with great apes and then, by late childhood, give way to the bias characteristic of the language they speak. Language may also play a causal role in allowing humans to rapidly form novel representations of space that combine both geometric and non-geometric – feature – information (Haun *et al.*, 2006a; Kanngiesser and Call, 2010). Finally, Balcomb *et al.* (2011) suggest that the emergence of place-based searching when locating hidden targets may be correlated with the acquisition of spatial prepositions in the second year of life. However, it is not yet clear, whether language facilitates, is correlated, or is necessary for these ontogenetic changes to occur.

The age-related changes in spatial cognition are usually seen as a result of the

interaction between biological and experimental factors. There is no systematic study, however, that allows understanding of how do these factors interact. Biological factors are usually associated with the maturation of specific brain regions. The maturation of the hippocampus between 18 and 24 months of age may be related to the increase in the durability of location memory. At 4-5 years, the growth of the hippocampus-mediated ability to encode relations among multiple objects may allow children to increase the range of stimuli they rely on during reorientation and navigation tasks (Sluzenski *et al.*, 2004; Newcombe *et al.*, 2013).

An example of an experimental factor may be the emergence and development of allocentric coding which begins with the onset of self-locomotion and further develops according to it. These may be related, if increases in self-mobility and other experiences lead to hippocampal and other biological changes (Woollett and Maguire, 2011).

At this point, it's important to see how does spatial cognition develops in non-human primates, not only because they are the closest living relatives of human beings, but also because spatial cognition and memory are critical cognitive skills underlying foraging behaviours for all primates (Rosati and Hare, 2012).

By comparing humans with non-human primates, one can pinpoint which aspects of spatial cognition may be relatively independent from language acquisition and understand which traits are derived and

which are not. Chimpanzees can use small-scale models to infer the location of hidden targets, suggesting that some basic form of 'map-reading' is independent of spatial language (Kuhlmeier and Boysen, 2002). On the other hand, apes are more dependent on spatial information than feature information, similar to that seen in younger children (Haun *et al.*, 2006a), although they are able to use feature information when there is a need to it (Kanngiesser and Call, 2010).

Also, apes show a preference for using an allocentric strategy when operating with spatial relations, once again as seen in younger children (Haun *et al.*, 2006b). Although there are not many studies on the cognitive development of apes, Rosati and Hare (2012) compared chimpanzees and bonobos and found that chimpanzees have more accurate spatial memory than bonobos, in particular in their ability to recall multiple target locations. More exactly, these species showed similar spatial memory abilities in infancy, but older chimpanzees showed significant improvements, while bonobos did not. Rosati and Hare (2012) suggest that these differences in cognitive development may be related to differences in feeding ecology. In fact chimpanzees depend on more seasonably variable food sources, face more competition for less-abundant food, engage in more risky hunting behaviours and use tools for extractive foraging.

Considering that human hunter-gatherer use far larger home ranges and daily ranging patterns than other apes, and exhibit a unique pattern foraging, where individuals return to a centralized location with food (Marlowe, 2005; Hill *et al.*, 2009), has led

these authors to propose that these unique features of human foraging may have spurred derived cognitive traits to solve more complex spatial problems. These authors also suggest that heterochrony, or differences in developmental timing, is the evolutionary mechanism underlying some differences in chimpanzee and bonobo traits. In particular, the paedomorphism hypothesis – development delays in acquisitions of traits – defends that bonobos will retain more juvenile-like traits in adulthood, relative to chimpanzees (Wobber *et al.*, 2010; Hare *et al.*, 2012). Moreover, although Rosati and Hare (2012) recognize the important role that language may play in spatial abilities development, they suggest that maturational changes in certain brain regions may also be an important intrinsic factor, as above mentioned.

Gunz *et al.* (2010) suggest that there were significant differences in post-natal brain development between modern *Homo sapiens* and Neanderthals. In fact, it appears that most endocranial shape differences develop postnatally, testifying for an important brain reorganization. As any cognitive differences these ontogenetic differences should express themselves behaviourally – as in the example described above between chimpanzees and bonobos.

In sum, Gunz *et al.* (2010) defend that a shift away from the ancestral pattern of brain development occurring in archaic *Homo sapiens* underlies brain reorganization and that the associated cognitive differences made this growth pattern a target for positive selection in modern humans.

### Tool use and tool production

One of the best definitions of tool use is the updated version of Beck's 1980's one:

“the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates or carries the tool during or prior to use and is responsible for the proper and effective orientation of the tool”(Shumaker *et al.*, 2011: 5)

Where “manipulable attached environmental object” cannot be an attached part of the user's body. Although Beck's definition may seem complex, it covers most, if not all, behaviours that imply tool use and it has, with minor modifications, survived the test of time.

But this discussion is not over. What exactly is tool use is still under debate, contributing greatly for many of the confusions found on this field of study (Shumaker *et al.*, 2011). One may also call upon on the very general definition of tool – and not tool use – by Toth and Schick (2009: 290), which reads that a tool is “an object, modified or unmodified, that is used by an animal for a purpose or objective”. This is not an as complete definition but it helps to clarify matters and is entirely applicable to the topic under discussion.

When analysing complete revisions on the use and manufacture of tools in the animal kingdom, such as the ones compiled by Bentley-Condit and Smith (2010) or by Shumaker *et al.* (2011) one finds that this

sort of behaviour occurs in a wide variety of species and in a diversity of contexts. Bentley-Condit and Smith (2010), for instance, classified tool use into ten categories – Food preparation, food extraction, food transport, food capture, physical maintenance, mate attraction, nest construction, predator defence, agonism and other – and found evidence of tool use in three phyla – *Arthropoda*, *Mollusca* and *Chordata* – and in seven classes – *Insecta*, *Malacostraca*, *Gastropoda*, *Cephalopoda*, *Actinopterygii*, *Aves* and *Mamallia* – of the animal kingdom.

Moreover, *Aves* and *Mammalia* completely overlap in tool use categories, namely food extraction, food capture and agonism, giving the idea that to explain *Primate* tool use, there's no need to invoke special skills. But taking a closer look, these investigators found that almost 85% of tool users use tools in only one of the tool use categories, while only members of the *Passeriformes* and *Primates* orders have been observed to use tools in four or more of the ten categories. Finally, although there are similarities between *Aves* and *Mammalia*, and *Primates* and *Passeriformes*, primate tool use is qualitatively different because approximately 35% of the entries for this order exhibit a breadth of tool use (i.e. three or more categories by any one species), compared to other mammals (0%), *Aves* (2.4%) and *Passeriformes* (3.1%).

The greater breadth in tool use by *Primates* may reflect a bias that resulted from differences in length and intensity of observation (McGrew, 1992). On the other hand, it may also involve phylogenetic or

cognitive differences. Namely, Lefebvre *et al.* (2002) stated that independent parallel evolution of tool use may have not only arisen in different vertebrate lines but as much as six times in different avian taxa.

In *Primates*, tool use may have arisen three different times – on the great ape/human branch, the macaque/baboon branch, and the capuchin branch (van Schaik *et al.*, 1999; Panger, 2007 in Bentley-Condit and Smith, 2010). Moreover, Lefebvre *et al.* (2002) also found a positive correlation between brain size and true tool use in birds, providing independent evidence for a role of tool use in brain evolution. Also of interest is another study by Lefebvre *et al.* (2004), whom found that innovation rate is also positively correlated to the taxonomic distribution of tool use, as well to interspecific differences in learning in birds.

Thus, some features of cognition may have evolved in a similar way in primates and some birds and may have played a role in evolutionary diversification, considering its impact on groups' ecological niches, which, in turn, impacts evolutionary trajectories (Lefebvre *et al.*, 2004; Bentley-Condit and Smith, 2010).

Also, one must consider manual dexterity, a common feature of primates, as a major advantage towards manipulation of objects. A primate can hold an object with the five digits of the hand, considered to be an adaptation to an arboreal life that requires holding on to branches. This, together with opposable thumbs, allows a fine control of hands to hold or grasp objects (Craist *et al.*, 2009; Hayashi, 2010).

However, considering the erratic distribution of tool use in living great apes, it is unlikely that the intellectual capacity for tool use itself provided the only selective force that produced more generalized cognitive skills (van Schaik *et al.*, 1999). Van Schaik *et al.* (1999) propose a model where tool use in the wild depends on suitable ecological niches – especially extractive foraging –, the manipulative skills to go with them, a measure of cognition skills that enables rapid acquisition of complex skills – both through invention and observational learning –, and social tolerance in a gregarious setting.

More, the evolution of high cognitive skills in primates may be a byproduct of selection on abilities for socially biased learning that are needed to acquire important skills (van Schaik and Pradhan, 2003). Culturally-transmitted behaviour can also be observed in other species, even in tool use. In Shark Bay (Western Australia), wild bottlenose dolphins (*Tursiops* sp.) use marine sponges as foraging tools (Mann *et al.*, 2012). Krützen *et al.* (2005) found that this behaviour cannot be explained by genetic or ecological reasons. More, *sponging* shows an almost exclusive vertical social transmission from mother to female offspring and female *spongers* more likely associate with other *spongers*, than with *non-spongers* (Krützen *et al.*, 2005; Mann *et al.*, 2012).

Following these considerations, one can turn to tool manufacture. According to Beck's classification (1980), there are four types of tool manufacture: 1) detaching, which involves separating or disconnecting a tool from a substrate or another object; 2) subtracting consists in the removal of

something from the object so that it is a more useful tool; 3) adding/combining takes place when two or more objects are put together to make a tool; and finally, 4) reshaping is a fundamental restructuring of an object. Critical to these categories is that each requires an active act of creation instead of a simple acquisition of the object. The production of stone tools by early hominins falls under the category of reshaping, but is most often described by the term knapping.

Knapping refers to the act of hitting, breaking apart, chipping or flaking stone, which mainly consists of striking a rock core with another object, termed hammer, breaking off a small piece termed a flake. Either the shaped core or the flakes produced may be used for a variety of different purposes (Savage-Rumbaugh *et al.*, 2007; Wynn, 2010; Finlay, 2013).

There is no evidence for flaked stone technologies in any known wild primate population. In captivity, however, there is some evidence for intentional stone knapping by bonobos. A long-term research project, showed that Kanzi, the first bonobo subject in this experiment, learned both the flaking and the cutting tasks through observation of a human tool maker, began using flakes the first day of the experiment, and made his first tool within the onset of the experiment. He has now been flaking stone for two decades, with shows of increased ability, and his sister, Panbanisha, is now also a practiced tool maker (Schick *et al.*, 1999; Savage-Rumbaugh *et al.*, 2007; Toth and Schick, 2009).

Still, these attempts made by bonobos may lack future action planning, such as search for acute angles on cores – from which to detach flakes with higher success –, and blow accuracy, likely due to biophysical constraints such as the inadequate shape of arm or hand (Schick *et al.*, 1999; Wynn, 2010). The first is most likely untrue, considering that there is evidence, in chimpanzees, for complex tool use in activities such as termite-fishing and honey-gathering, where individuals follow a hierarchical sequence of steps within sequential organization in tool use (Boesch *et al.*, 2009; Sanz and Morgan, 2009; Sanz *et al.*, 2009). Lower levels of complexity, but also involving sequential processes have been found in both nut-cracking and hunting tools (Pruetz and Bertolani, 2007; Carvalho *et al.*, 2008).

So, most non-human primates do not engage in at least *basic* stone knapping, not because they lack the cognitive and minimal motor abilities for it, but, most likely, because they don't have the need for it (Wynn, 2010; de Sousa and Cunha, 2012). It is possible that this can be explained by the fact that no food-getting or other activity in non-human primates requires reliance in cutting activities, for instance (Schick *et al.*, 1999; Toth and Schick, 2009).

Boesch *et al.* (2009) go on to suggest that the sequential actions observed by his team in honey gathering by chimpanzees are reminiscent of those proposed for early hominin tool use during the Early and Middle Stone Age. This includes appreciation of the quality of the raw material, material selectivity, transport of raw materials and tools, reduction and shaping of raw material

prior to use, retouching during usage, a notion of order when using sequential tools, a notion of geometry, uniformity of tool forms and an important cultural component in tool use.

Considering this, it is safe to say that non-human primates have an understanding of the object as a tool, and some form of mental representation of these objects, at least in some of the tasks performed. This said, while tool use can be found across the animal kingdom, flexible and complex tool use distinguishes humans and some great apes from other animal species (Boesch and Boesch-Achermann, 2000) On the other hand, where tool production is concerned, most examples in non-human primates use organic products, which cannot be found in the archaeological record. Also, there is still no evidence for the use of tools to make other tools in wild living non-human primates, which in turn, can be observed in Early and Middle Stone Age hominins (Boesch *et al.*, 2009).

Following this, one can say with some certainty that hominins that had the cognitive skills to use and produce tools prior to the earliest evidence of flaking artefacts, dated to 3.39 Ma (McPherron *et al.*, 2010). It has been assumed by some authors that modified stones were indeed used prior to this time (Delagnes and Roche, 2005). Although this is the most likely scenario, it is also possible that they have not been found in the archaeological record because they did not have the need for them or because they used tools made of organic materials. In the first scenario, it's possible that archaeological excavations have not used the correct

approaches to find them, or that not enough attention has been paid to this time period (Boesch *et al.*, 2009; Haslam *et al.*, 2009). Primate archaeology promises to shed new light on this problem, by combining techniques from both primatology and archaeology (Carvalho *et al.*, 2008; Haslam *et al.*, 2009)

Also, one must question, considering that the cognitive skills for tool use and tool production are not exclusive of *Homo*, why did this lineage come to depend so heavily on tools? And why did they come to make such an *apparently* different living from other primates?

Sometime during human history selective pressures must have appeared that selected for expert and highly consistent production of stone tools. With time, the minor shortcomings seen in other apes were overcome, most likely involving cognitive innovations (Wynn, 2010). This way, throughout technological history hominids acquired new techniques, employed new materials and produced an increasingly large range of final products (Wynn, 2010; Finlay, 2013). These changes and its evolutive implications will be explored in the following chapters.

## Discussion

The sort of approach used here fits with a new discipline termed 'Evo-Devo' or evolutionary developmental biology, which is in the process of producing a new model of evolution that integrates developmental science with evolution to explain and define the diversity of life on Earth and their

evolutionary path. So far this discipline has been concerned with genetics and how changes in the development can create the diverse variation that natural selection can act on (Gilbert, 2010). However, there is no reason why this discipline could not stray from genetics in the future and attempt approaches such as the one explored here.

The initial proposal that human development could retrace human evolution seems to recall the well-known Ernest Haeckel's theory that the major way to evolve was to add a step to the *end* of embryonic development. It turned out that there were so many exceptions to this rule that it fell into disrepute (Le Douarin, 2005; Gilbert, 2010). Despite this, during the last two decades many proofs have been found for a deep homology. This means that organisms share many regulatory pathways, as well as many of the transduction pathways. This principle is also known as molecular parsimony (Le Douarin, 2005; Gilbert, 2010). This does not mean that human development does indeed retrace human evolution, but only that development shows a deep homology that testifies for common evolutionary pathways that construct on pre-existent structures.

More recently, Mithen (2005) suggests that there is a broad compatibility between evolutionary history and brain structure. Although this author does not discuss this idea in depth, he suspects that there is a close similarity between infant-directed speech and proto-language, for instance. This is only an example of how the idea that human development may make some

contribution towards the understanding of human evolution is gaining strength.

It would not be possible to create a grade of equivalence between the development of a child and human evolution. But this still leaves a lot of ground to cover on the crossing between development and evolution. General inputs on the order and processes of evolutive innovations are potential contributions from this new area.

Turning now to the discussion of the selective forces behind changes in spatial cognition, it would seem that the selective forces behind changes on object recognition and manipulation could have been the stone tools themselves, but the most likely scenario is that a number of factors such as the developing of language or the application of social rules in the context of object manipulation also came into play. In fact, given the significant amount of gathered evidence relating tool use and production, spatial cognition and language, it seems that there was a strong interdependence on the role those two elements might have played on the evolution of the latter and vice-versa. Continued work on the precise ways of these relations would be fascinating.

An important limitation of this study relates to the amount of literature not covered. Due to the complexity of the subject it was impossible to include all data existent. One of the main areas overlooked concerned genetics, which could be of great interest to this discussion. Neurobiology of the processes discussed is also grossly overlooked. A few remarks on this last subject follow but they are only a minor

attempt, considering the amount of work existent. Later investigation should explore these approaches as well.

Considering the results of Stout *et al.* (2008) suggesting that Acheulean toolmaking, but not Oldowan toolmaking, activated prefrontal cortex areas, then it is possible that spatial cognition changes stimulated first brain reorganization and then brain expansion. This may be related to procedural and declarative long-term memory, possibly by the division between motor know-how in the first and operative ideational know-how, on the second, just as proposed by Uomini (2009). It would also be interesting to study which brain areas are activated during the production of three-dimensional symmetric objects.

Moreover, brain reorganization probably stimulated brain lateralization, with specialized brain areas. For instance, by opening the way for a left-hemisphere specialization in language. This hypothesis is promising in view of research by Holloway *et al.* (2003) where it is found that brain reorganization did indeed precede brain expansion in early hominid evolution. In fact, because large brains impose specific constraints on neuroarchitectural organization, the evolutionary enlargement of hominin brains will always entail brain reorganization (Zollikofer and de León, 2013).

Another interesting study in neurobiology reveals that ape differences in behaviour, including adaptations for imitation and social learning of tool use, which has been mentioned as very important on the evolution of modern cognition, may be

related to differences on the mirror system. More exactly, humans exhibit more substantial temporal-parietal and frontal-parietal connections, while macaques and chimpanzees present a preponderance of the frontal-parietal connections (Hecht *et al.*, 2013).

Interestingly, this could be related to previously discussed study by Arbib (2011) that defends that Oldowan tool making relates to simple imitation, while the Acheulean relates to complex imitation. Hecht *et al.* (2013) also lend indirect support to the idea that many of the cognitive innovations seen in the *Homo* lineage are, not the result of completely new neurological mechanisms, but the result of integration of pre-existent neuronal pathways, through a bigger connectivity between brain areas, for instance, just as suggested on the proposed framework

A final important study is the one by Hill *et al.* (2010), which proves that the pattern of human evolutionary brain expansion is remarkably similar to the pattern of human postnatal brain expansion. They hypothesize that it is beneficial for regions of recent evolutionary expansion to remain less mature at birth, perhaps to increase the influence of postnatal experience on the development of these regions or to focus prenatal resources on regions most important for early survival. This is a very strong argument in support of the role of developmental science on the study of human evolution.

Nevertheless, when studying the evolution of the human brain, one should be careful at



what one reads into brain extension proof, since it's very hard to know what exactly are the cognitive implications of having a brain of 600 cm<sup>3</sup> or of 900 cm<sup>3</sup> (Wood and Baker, 2011). Continued work on the neurological arena is of grave importance to understand paleo-minds.

Also a novel and fascinating field of research is the study of ape development. By understanding ape development, one might be able to better understand unique forms of their cognition and to attempt to stop considering their cognition from a uniquely human point-of-view, but from a truly ape point-of-view. Moreover, studies on primate archaeology should also contribute to this new view of ape cognition (Carvalho *et al.*, 2008; Haslam *et al.*, 2009)

Following this, one should always keep in mind that evolution works by chance and so, it didn't developed straightforward in the modern human direction but passed by many different stages that may be quite different from our current understanding of intelligence, but not inferior (Langbroek, 2012).

Development data cannot yield a complete account of the evolution of spatial cognition. Most likely, other spatial cognitive skills arose through time that cannot be perceived through development and were not discussed here.

A final point regarding human spatial cognition relates to its presupposed *uniqueness*. This requires several points to be taken into consideration. First, as mentioned above, humans are able to amplify their skills of spatial cognition through cultural artifacts

– maps and compasses, for instance. Second, human languages are also a rich source of spatial knowledge, exposing children to the habitual ways their communities' space is structured. Third, human adult cognitive skills not possessed by other primates can be due to children's early development traits for accumulating skilful practices and knowledge of their social groups (Hare, 2011). And finally, natural, technological and social environment is a significant structuring element in terms of brain development and adult cognitive style (Grove and Coward, 2008).

So, it would appear that each primate, whether human or non-human, is born with the potential for a range of cognitive abilities, but that the specific set of cognitive abilities that he exhibits depend not only on the existing limits, but also on the exact combination of ecological environments, epigenetic influences and social and cultural learning context. This could mean that, not only are differences in human cognition due to minor cognitive changes, such as the integration of neural pathways, but initial cognitive differences themselves may be close to non-existent in some aspects and only due to the rich environment in which humans grow. This same reasoning could be applied to other aspects of cognition, further closing the gap between humans and non-human primates.

A proposed framework for how the development of spatial cognition may relate to the evolution of spatial cognition, in a translatable way to the archaeological record, will follow in later articles.

## Conclusion

Developmental data is indeed relevant to the study of human evolution and may provide an interesting new area of inquiry.

The work presented here also reinforces the idea that ape and human spatial cognition is not as different as initially thought. In fact, human apparent *uniqueness* may start from minor cognitive skills that then “snow-ball” into current human complexity by ecological environments, epigenetic influences and social and cultural learning context.

## References

- Aboitiz, F.; Aboitiz, S.; García, R. R. 2010. The Phonological Loop: A Key Innovation in Human Evolution. *Current Anthropology*, 51(S1): S55-S65.
- Aboitiz, F.; García, R. R.; Bosman, C.; Brunetti, E. 2006. Cortical memory mechanisms and language origins. *Brain and Language*, 98: 40-56.
- Aboitiz, F.; López, J.; Montiel, J. 2003. Long distance communication in the human brain: timing constraints for inter-hemispheric synchrony and the origin of brain lateralization. *Biological Research*, 36(1): 89-99.
- Aiello, L. C.; Key, C. 2002. Energetic Consequences of Being a *Homo erectus* Female. *American Journal of Human Biology*, 14: 551-565.
- Aiello, L. C.; Wells, J. C. K. 2002. Energetics and the Evolution of the Genus *Homo*. *Annual Review of Anthropology*, 31: 323-38.
- Albiach-Serrano, A.; Call, J.; Barth, J. 2010. Great Apes Track Hidden Objects After Changes in the Objects' Position and in Subject's Orientation. *American Journal of Primatology*, 72: 349-359.
- Amici, F.; Aureli, F.; Call, J. 2010. Monkeys and Apes: Are Their Cognitive Skills Really So Different? *American Journal of Physical Anthropology*, 143(2): 188-197.
- Antón, S. C.; Leigh, S. R. 2003. Growth and Life History in *Homo erectus*. In: Thompson, J. L.; Krovitz, G. E.; Nelson, A. J. (eds.) *Patterns of Growth and Development in the Genus Homo*. Cambridge, Cambridge University Press: 219-245.
- Antón, S. C.; Leonard, W. R.; Robertson, M. L. 2002. An ecomorphological model of the initial hominid dispersal from Africa. *Journal of Human Evolution*, 43: 773-785.
- Arbib, M. A. 2011. From Mirror Neurons to Complex Imitation in the Evolution of Language and Tool Use. *Annual Review of Anthropology*, 40: 257-273.
- Baddeley, A. 2012. Working Memory: Theories, Models and Controversies. *Annual Review of Psychology*, 63: 1-29.
- Baddeley, A.; Hitch, G. 1974. Working Memory. *The Psychology of Learning and Motivation – Advances in Research and Theory*. 8:47-89. DOI: 10.1016/S0079-7421(08)60452-1.
- Baillargeon, R. 1991. Reasoning about the height and location of a hidden object in 4.5- and 6.5-month-old infants. *Cognition*, 38: 13-42.
- Baker, J. T.; Patel, G. H.; Corbetta, M.; Snyder, L. H. 2006. Distribution of Activity Across the Monkey Cerebral Cortical Surface, Thalamus and Midbrain during Rapid, Visually Guided Saccades. *Cerebral Cortex*, 16: 447-459.
- Balcomb, F.; Newcombe, N. S.; Ferrara, K. 2011. Finding where and saying where: developmental relationships between place learning and language in the second year. *Journal of Cognition and Development*, 12: 315-331.
- Bates, L. A.; Byrne, R. W. 2007. Creative or created: Using anecdotes to investigate animal cognition. *Methods*, 42: 12-21.
- Beck, B. B. 1980. *Animal Tool Behavior: The Use and Manufacture of Tools by Animals*. New York, Garland STPM Publishing.
- Belin, P. 2006. Voice processing in human and non-human primates. *Philosophical Transactions of the Royal Society – Biological Sciences*, 361: 2091-2107.
- Bentley-Condit, V.; Smith, E. O.; 2010. Animal tool use: current definitions and an updated comprehensive catalog. *Behaviour*, 147(2): 185-221.
- Boesch, C.; Boesch-Achermann, H. 2000. *The Chimpanzees of the Tai Forest – Behavioural Ecology and Evolution*. Oxford, Oxford University Press.
- Boesch, C.; Head, J.; Robbins, M. M. 2009. Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution*, 56: 560-569.
- Bogin, B. 2003. The Human Pattern of Growth and Development in Paleontological Perspective. In: Thompson, J. L.; Krovitz, G. E.; Nelson, A. J. (eds.) *Patterns of Growth and Development in the Genus Homo*. Cambridge, Cambridge University Press: 15-44.

- Bradshaw, J. L. 2001. Asymmetries in preparation for action. *Trends in Cognitive Science*, 5: 184-185.
- Broglio, C.; Rodríguez, F.; Gómez, A.; Arias, J. L.; Salas, C. 2010. Selective involvement of the goldfish lateral pallium in spatial memory. *Behavioural Brain Research*, 210: 191-201.
- Burgess, N. 2006. Spatial memory: how egocentric and allocentric combine. *Trends in Cognitive Science*, 10(12): 551-557.
- Burgess, N. 2008. Spatial Cognition and the Brain. *Annals of the New York Academy of Sciences*, 1124: 77-97.
- Byrne, R.; Bates, L. A.; Moss, C. J. 2009. Elephant cognition in primate perspective. *Comparative Cognition & Behavior Reviews*, 4: 65-79.
- Carvalho, S.; Cunha, E.; Sousa, C.; Matsuzawa, T. 2008. Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal of Human Evolution*, 55: 148-163.
- Coqueugniot, H; Hublin, J.; Veillon, F.; Houët, F.; Jacob, T. 2004. Early brain growth in *Homo erectus* and implications for cognitive ability. *Nature*, 431: 299-302.
- Crast, J.; Frigaszy, D.; Hayashi, M.; Matsuzawa, T. 2009. Dynamic In-Hand Movements in Adult and Young Juvenile Chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology*, 138: 274-285.
- d'Errico, F.; Henshilwood, C.; Lawson, G.; Vanhaeren, M.; Tillier, A.; Soressi, M.; Bresson, F.; Maureille, B.; Nowell, A.; Lakarra, J.; Backwell, L.; Julien, M. 2003. Archaeological Evidence for the Emergence of Language, Symbolism, and Music – An Alternative Multidisciplinary Perspective. *Journal of World Prehistory*, 17(1): 1-70.
- de León, M.; Golovanova, L.; Doronichev, V.; Romanova, G.; Akazawa, T.; Kondo, O.; Ishida, H.; Zollikofer, C. 2008. Neanderthal brain size at birth provides insights into the evolution of human life history. *Proceedings of the National Academy of Sciences of the United States of America*, 105 (37): 13764-13768.
- de Sousa, A.; Cunha E. 2012. Hominins and the emergence of the modern human brain. *Progress in Brain Research*, 195: 293-322.
- Dean, C.; Leakey, M. G.; Reid, D.; Schrenk, F.; Schwartz, G. T.; Stringer, C.; Walker, A. 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature*, 414: 628-631.
- Delagnes, A.; Roche, H. 2005. Late Pliocene hominid knapping skills: The case of Lakalalei 2C, West Turkana, Kenya. *Journal of Human Evolution*, 48: 435-472.
- DeLoache, J. S. 1995. Early Symbol Understanding and Use. *Psychology of Learning and Motivation*, 33: 65-114.
- DeLoache, J. S.; Brown, A. L. 1983. Very Young Children's Memory for the Location of Objects in a Large-Scale Environment. *Child Development*, 54(4): 888-897.
- Dolins, F. L. 2009. Captive Cotton-Top Tamarin's (*Saguinus Oedipus Oedipus*) Use of Landmarks to Localize Hidden Food Items. *American Journal of Primatology*, 71:316-323.
- Douglas-Hamilton, I.; Bhalla, S.; Wittemyer, G.; Vollrath, F. 2006. Behavioural reactions of elephants towards a dying and deceased matriarch. *Applied Animal Behaviour Science*, 100: 87-102.
- Durán, E.; Ocaña, F. M.; Broglio, C.; Rodríguez, F.; Salas, C. 2010. Lateral but not medial telencephalic pallium ablation impairs the use of goldfish spatial allocentric strategies in a "hole-board" task. *Behavioural Brain Research*, 214: 480-487.
- Fiddick, L.; Barrett, H. C. 2001. Evolution of Cognition. In: Smelser, N. J.; Baltes, P. B. (eds.) *International Encyclopedia of the Social and Behavioral Sciences Vol. 7*. New York, Elsevier: 4996-5000.
- Finlay, N. 2013. Gender and Lithic Studies in Prehistoric Archaeology. In: Bolger, D. (ed.) *A Companion to Gender Prehistory*. West Sussex, John Wiley & Sons, Inc.
- Fiset, S.; Doré, F. 1996. Spatial Encoding in Domestic Cats (*Felis catus*). *Journal of Experimental Psychology: Animal Behavior Processes*, 22(4): 420-437.
- Fiset, S.; Gagnon, S.; Beaulieu, C. 2000. Spatial Encoding of Hidden Objects in Dogs (*Canis familiaris*). *Journal of Comparative Psychology*, 114(4): 315-324.
- Foley, R.A. 1996. Measuring Cognition in Extinct Hominids. In: Mellars, P.; Gibson, K. (eds.) *Modelling the early human mind*. McDonald Institute Monographs: 57-63.
- Frick, A.; Ferrara, K.; Newcombe, N. S. 2013. Using a touch screen paradigm to assess the development of mental rotation between 3½ and 5½ years of age. *Cognitive Processing*, 14: 117-127.
- Frick, A.; Newcombe, N. 2012. Getting the big picture: Development of spatial scaling abilities. *Cognitive Development*, 27(3): 270-282.
- Gentner, D. 2007. Spatial Cognition in apes. *Trends in Cognitive Sciences*, 11(5): 192-194.
- Gilbert, S. F. 2010. *Developmental Biology*. 9<sup>th</sup> edition. Massachusetts, Sinauer Associates, Inc.

- Grove, M.; Coward, F. 2008. From Individual Neurons to Social Brains. *Cambridge Archaeological Journal*, 18(3): 387-400.
- Gunz, P.; Neubauer, S.; Maureille, B.; Hublin, J.-J. 2010. Brain development after birth differs between Neanderthals and modern humans. *Current Biology*, 20(21): R921-R922.
- Harcourt-Smith, W.; Aiello, L. 2004. Fossils, feet and the evolution of human bipedal locomotion. *Journal of Anatomy*, 204 (5): 403-416.
- Hare, B. 2011. From Hominoid to Hominid Mind: What Changed and Why? *Annual Review of Anthropology*, 40: 293-309.
- Hare, B.; Wobber, V.; Wrangam, R. 2012. The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, 83, 573-585.
- Hart, B. L.; Hart, L. A.; Pinter-Wollman, N. 2008. Large brains and cognition: Where do elephants fit in? *Neuroscience and Behavioral Reviews*, 32: 86-98.
- Hart, B. L.; Hart, L. A.; McCoy, M.; Sarath, C. R. 2001. Cognitive behaviour in Asian elephants: use and modification of branches for fly switching. *Animal behaviour*, 62: 839-847.
- Hartley, T.; Burgess, N. 2003. Models of Spatial Cognition In: Nadel, L. (ed.) *Encyclopedia of Cognitive Science*. London, Macmillan.
- Haslam, M.; Hernandez-Aguilar, A.; Ling, V.; Carvalho, S.; de la Torre, I.; DeStefano, A.; Du, A.; Hardy, B.; Harris, J.; Marchant, L.; Matsuzawa, T.; McGrew, W.; Mercader, J.; Mora, R.; Petraglia, M.; Roche, H.; Visalberghi, E.; Warren, R. 2009. Primate archaeology. *Nature*, 460: 339-344.
- Haun, D. B. M.; Call, J.; Janzeon, G.; Levinson, S. C. 2006a. Evolutionary psychology of spatial representations in the Hominidae. *Current Biology*, 16, 1736-1740.
- Haun, D. B. M.; Rapold, C. J.; Call, J.; Janzen, G.; Levinson, S. C. 2006b. Cognitive cladistics and cultural override in Hominid spatial cognition. *Proceedings of the National Academy of Sciences*, 103(46), 17568-17573.
- Hauser, M. D.; Akre, K. 2001. Asymmetries in the timing of facial and vocal expressions by rhesus monkeys: implications for hemispheric specialization. *Animal Behaviour*, 61: 391-400.
- Hayashi, M. 2010. Using an Object Manipulation Task as a Scale for Comparing Cognitive Development in Chimpanzees and Humans. In: Lonsdorf, E. V.; Ross, S. R.; Matsuzawa, T. (eds.) *The Mind of the Chimpanzee: Ecological and Experimental Chimpanzees*. Chicago, The University of Chicago Press.
- Hecht, E. E.; Gutman, D. A.; Preuss, T. M.; Sanchez, M. M.; Parr, L. A.; Rilling, J. K. 2013. Process Versus Product in Social Learning: Comparative Diffusion Tensor Imaging of Neural Systems for Action Execution – Observation Matching in Macaques, Chimpanzees, and Humans. *Cerebral Cortex*, 23: 1014-1024.
- Hermer-Vasquez, L.; Spelke, E. S.; Katsnelson, A. S. 1999. Sources of flexibility in human cognition: dual-task studies of space and language. *Cognitive Psychology*, 39:3-36.
- Hermer-Vazquez, L.; Moffet, A.; Munkholm, P. 2001. Language, space, and the development of cognitive flexibility in humans: the case of two spatial memory tasks. *Cognition*, 79: 263-299.
- Herrmann, E.; Call, J.; Hernández-Lloreda, M. V.; Hare, B.; Tomasello, M. 2007. Humans Evolved Specialized Skills of Social Cognition: The Cultural Intelligence Hypothesis. *Science*, 317:1360-1366.
- Hill, J.; Inder, T.; Neil, J.; Dierker, D.; Harwell, J.; Essen, D. V. 2010. Similar patterns of cortical expansion during development and evolution. *Proceedings of the National Academy of Sciences*, 107(29). 13135-13140.
- Hill, K.; Barton, M.; Hurtado, M. 2009. The emergence of human uniqueness: characters underlying behavioral modernity. *Evolutionary Anthropology*, 18: 187-200.
- Holloway, R. L.; Broadfield, D. C.; Yuan, M. S. 2003. Morphology and Histology of Chimpanzee Primary Visual Striate Cortex Indicate That Brain Reorganization Predated Brain Expansion in Early Hominid Evolution. *The Anatomical Record Part A*, 273A: 594-602.
- Holtzman, D. A.; Harris, T. W.; Aranguren, G.; Bostock, E. 1999. Spatial learning of an escape task by young corn snakes, *Elaphe guttata guttata*. *Animal Behaviour*, 57: 51-60.
- Hribar, A.; Call, J. 2011. Great apes use landmarks cues over spatial relations to find hidden food. *Animal Cognition*, 14 (5): 623-635.
- Hribar, A.; Haun, D.; Call, J. 2011. Great apes' strategies to map spatial relations. *Animal Cognition*, 14(4): 511-523.
- Huber, L. 2000. Psychoplylogogenesis: Innovations and Limitations in the Evolution of Cognition. In: Heyes, C.; Huber, L. (eds.) *Evolution of Cognition*, Cambridge, MIT Press: 23-41.
- Huttenlocher, J.; Duffy, S.; Levine, S. 2002. Infants and toddlers discriminate amount: Are they measuring? *Psychological Science*, 13(3): 244-249.
- Huttenlocher, J.; Newcombe, N.; Sandberg, E. H. 1994. The coding of spatial location in young children. *Cognitive Psychology*, 27: 115-148.

- Jacobs, L. F. 2003. The evolution of the Cognitive Map. *Brain, Behavior and Evolution*, 62: 128-139.
- Kagan, I.; Iyer, A.; Lindner, A.; Andersen, R. A. 2010. Space representation for eye movements is more contralateral in monkeys than in humans. *Proceedings of the National Academy of Sciences*, 107(17): 7933-7938.
- Kanngiesser, P.; Call, J. 2010. Bonobos, chimpanzees, gorillas, and orangutans use feature and spatial cues in two spatial memory tasks. *Animal Cognition*, 13: 419-430.
- Kaplan, H.; Hill, K.; Lancaster, J.; Hurtado, A. M. 2000. A Theory of Human Life History Evolution: Diet, Intelligence, and Longevity. *Evolutionary Anthropology*, 9(4): 156-183.
- Krovitz, G. E.; Thompson, J. L.; Nelson, A. J. 2003. Hominid Growth and Development from Australopithecines to Middle Pleistocene *Homo*. In: Thompson, J. L.; Krovitz, G. E.; Nelson, A. J. (eds.) *Patterns of Growth and Development in the Genus Homo*. Cambridge, Cambridge University Press: 271-294.
- Krützen, M.; Mann, J.; Heithaus, M. R.; Connor, R. C.; Bejder, L.; Sherwin, W. B. 2005. Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences*, 102(25): 8939-8943.
- Kuhlmeier, V.A.; Boysen, S. T. 2002. Chimpanzees' recognition of the spatial and object similarities between a scale model and its referent. *Psychological Science*, 13: 60-63.
- Langbroek, M. 2012. Trees and ladders: A critique of the theory of human cognitive and behavioural evolution in Palaeolithic archaeology. *Quaternary International*, 270: 4-14.
- Latimer, B.; Lovejoy, C. 1989. The Calcaneus of *Australopithecus afarensis* and its implications for the evolution of bipedality. *American Journal of Physical Anthropology*, 78 (3): 369-386.
- Le Douarin, N. 2005. *Quimeras, Clones e Genes*. Lisboa, Fundação Calouste Gulbenkian.
- Lee, S. A.; Spelke, E. S. 2010. A modular geometric mechanism for reorientation in children. *Cognitive Psychology*, 61:152-176.
- Lefebvre, L.; Nicolakakis, N.; Boire, D. 2002. Tool and brains in birds. *Behaviour*, 139: 939-973.
- Lefebvre, L.; Reader, S. M.; Sol, D. 2004. Brains, Innovations and Evolution in Birds and Primates. *Brain, Behavior and Evolution*, 63: 233-246.
- Lepow, B.; Lehnung, M.; Pohl, J.; Herzog, A.; Ferstl, R.; Mehdorn, M. 2003. Navigational place learning in children and young adults as assessed with a standardized locomotor search task. *British Journal of Psychology*, 94: 299-317.
- Lewis, J. W. 2006. Cortical Networks Related to Human Use of Tools. *Neuroscientist*, 12(3): 211-231.
- López, J. C.; Vargas, J. P.; Gómez, Y.; Salas, C. 2003. Spatial and non-spatial learning in turtles: the role of medial cortex. *Behavioural Brain Research*, 143:109-120.
- Lourenco, S. F.; Huttenlocher, J. 2008. The representation of geometric cues in infancy. *Infancy*, 13:103-127.
- Mann, J.; Stanton, M. A.; Patterson, E. M.; Bienenstock, E. J.; Singh, L. O. 2012. Social networks reveal cultural behaviour in tool-using dolphins. *Nature communications*, 3: 980. DOI: 10.1038/ncomms1983.
- Marlowe, F. W. 2005. Hunter-gatherers and human evolution. *Evolutionary Anthropology*, 14: 54-67.
- Marsh, H. L.; Spetch, M. L.; MacDonald, S. E. 2011. Strategies in landmark use by orangutans and human children. *Animal Cognition*, 14: 487-502.
- McComb, K.; Moss, C.; Sayalel, S.; Baker, L. 2000. Unusually extensive networks of vocal recognition in African elephants. *Animal behaviour*, 59: 1103-1109.
- McGrew, W. C. 1992. Tool use by free ranging chimpanzees – the extent of diversity. *Journal of Zoology*, 228: 689-694.
- McPherron, S. P.; Zeresenay, A.; Marean, C. W.; Wynn, J. G.; Reed, D.; Geraads, D.; Bobe, R.; Béarat, H. A. 2010. Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature*, 466: 857-860.
- Meulman, E. J. M.; Sanz, C., M.; Visalberghi, E.; van Schaik, C. P. 2012. The Role of Terrestriality in Promoting Primate Technology. *Evolutionary Anthropology*, 21: 58-68.
- Mithen, S. 2005. *The Singing Neanderthals – The Origins of Music, Language, Mind and Body*. London, Orion Books Ltd.
- Nardini, M.; Jones, P.; Bedford, R.; Braddick, O. 2008. Development of cue integration in human navigation. *Current Biology*, 18: 689-693.
- Nardini, M.; Thomas, R. L.; Knowland, V. C. P.; Braddick, O. J.; Atkinson, J. 2009. A viewpoint-independent process for spatial reorientation. *Cognition*, 112: 241-248.
- Newcombe, N. S.; Huttenlocher, J. 2000. *Making Space: The Development of Spatial Representation and Reasoning*. Cambridge (MA), MIT Press.
- Newcombe, N. S.; Uttal, D. H.; Sauter, M. 2013. Spatial Development. In: Zelazo, P. (ed.) *Oxford Handbook of Developmental Psychology*. Oxford, Oxford University Press: 564-590.
- Nowell, A.; White, A. 2010. Growing Up in the Middle Pleistocene – Life History Strategies and Their Relationship

- to Acheulian Industries. In: Nowell, A.; Davidson, I. (eds.) *Stone Tools and the Evolution of Human Cognition*. Boulder, University Press of Colorado: 67-81.
- Okamoto-Barth, S.; Call, J. 2008. Tracking and Inferring Spatial Rotation by Children and Great Apes. *Developmental Psychology*, 44(5): 1396-1408.
- Oleksiak, A.; Postma, A.; van der Ham, I. J. M.; Klink, P. C.; van Wezel, R. J. A. 2011. A review of lateralization of spatial functioning in nonhuman primates. *Brain Research Reviews*, 67: 56-72.
- Örnkloo, H.; von Hofsten, C. 2007. Fitting objects into holes: On the development of spatial cognition skills. *Development Psychology*, 43: 404-416.
- Poremba, A. 2006. Auditory Processing and Hemispheric Specialization in Non-human Primates. *Cortex*, 42: 87-89.
- Poremba, A.; Mishkin, M. 2007. Exploring the extent and function of higher-order auditory cortex in rhesus monkeys. *Hearing Research*, 229: 14-23.
- Poti, P.; Bartolommei, P.; Saporiti, M. 2005. Landmark Use by *Cebus apella*. *International Journal of Primatology*, 26(4): 921-948.
- Pruetz, J. D.; Bertolani, P. 2007. Savanna Chimpanzees, *Pan troglodytes verus*, Hunt with Tools. *Current Biology*, 17: 412-417.
- Quinn, P. C.; Norris, C. M.; Pasko, R.; Schmader, T. M.; Mash, C. 1999. Formation of categorical representation for the spatial relation between by 6- to 7-month-old infants. *Visual Cognition*, 6(5):569-585.
- Ray, M. K.; Mackay, C. E.; Harner, C. J.; Crow, T. J. 2008. Bilateral Generic Working Memory Circuit Requires Left-Lateralizes Addition for Verbal Processing. *Cerebral Cortex*, 18(6): 1421-1428.
- Rodríguez, F.; Durán, E.; Vargas, J. P.; Torres, B.; Salas, C. 1994. Performance of goldfish trained in allocentric and egocentric maze procedures suggests the presence of a cognitive mapping system in fishes. *Animal Learning & Behavior*, 22 (4): 409-420.
- Rosati, A.; Hare, B. 2012. Chimpanzees and bonobos exhibit divergent spatial memory development. *Developmental Science*, 15(6): 840-853.
- Salas, C.; Broglio, C.; Rodríguez, F. 2003. Evolution of Forebrain and Spatial Cognition in Vertebrates; Conservation across Diversity. *Brain, Behavior and Evolution*, 62: 72-82.
- Sandberg, E. H.; Huttenlocher, J.; Newcombe, N. 1996. The development of hierarchical representation of two-dimensional space. *Child Development*, 67: 721-739.
- Sanz, C. M.; Morgan, D. B. 2009. Flexible and Persistent Tool-using Strategies in Honey-gathering by Wild Chimpanzees. *International Journal of Primatology*, 30: 411-427.
- Sanz, C.; Call, J.; Morgan, D. 2009. Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biology Letters*, 5: 293-296.
- Savage-Rumbaugh, E. S.; Toth, N.; Schick, K. 2007. Kanzi Learns to Knap Stone Tools. In Washburn, D. A. (ed.) *Primate Perspectives on Behavior and Cognition*, Washington, American Psychological Association: 279-291.
- Schick, K.; Toth, N.; Garufi, G.; Savage-Rumbaugh, E.; Rumbaugh, D.; Sevcik, R. 1999. Continuing investigations into the stone tool-making capabilities of a Bonobo (*Pan paniscus*). *Journal of Archaeological Science*, 26, 821-832.
- Schuz, A.; Preissel, H. 1996. Basic Connectivity of the Cerebral Cortex and some Considerations on the Corpus Callosum. *Neuroscience and Behavioral Reviews*, 20(4): 567-570.
- Shumaker, R. W.; Walkup, K. R.; Beck, B. B. 2011. *Animal Tool Behavior: The Use and Manufacture of Tools by Animals*. Baltimore, John Hopkins University Press.
- Sluzenski, J.; Newcombe, N. S.; Satlow, E. 2004. Knowing where things are in the second year of life: implications for hippocampal development. *Journal of Cognitive Neuroscience*, 16(8):1443-1451.
- Smith, F. H. 2010. Species, Populations, and Assimilation in Later Human Evolution. In: Larsen, C. S. (ed.) *A Companion to Biological Anthropology*. Chichester, Blackwell Publishing Ltd.: 357-378.
- Smith, T. M.; Tafforeau, P.; Reid, D. J.; Pouech, J.; Lazzari, V.; Zermeno, J. P.; Guatelli-Steinberg, D.; Olejniczak, A. J.; Hoffman, A.; Radovčić, J.; Makaremi, M.; Toussaint, M.; Stringer, C.; Hublin, J.-J. 2010. Dental evidence for ontogenetic differences between modern humans and Neanderthals. *Proceedings of the National Academy of Sciences*, 107(49): 20923-20928.
- Spelke, E. S.; Gilmore, C. K.; McCarthy, S. 2011. Kindergarten children's sensitivity to geometry in maps. *Developmental Science*, 14: 809-821.
- Spencer, H. 1870. *The Principles of Psychology*. 2<sup>nd</sup> Edition. London, Williams and Norgate.
- Stern, J.; Susman, R. 1983. The Locomotor Anatomy of *Australopithecus afarensis*. *American Journal of Physical Anthropology*, 60 (3): 279-317.
- Stout, D.; Chaminade, T. 2007. The evolutionary neuroscience of tool making. *Neuropsychologia*, 45: 1091-1100.

- Stout, D.; Toth, N.; Schick, K.; Chaminade, T. 2008. Neural correlates of Early Stone Age toolmaking: technology, language and cognition in human evolution. *Philosophical Transactions of the Royal Society of London – Series B*, 363: 1939-1949.
- Tardieu, C. 1998. Short Adolescence in Early Hominids: Infantile and Adolescent Growth of the Human Femur. *American Journal of Physical Anthropology*, 107: 163-178.
- Thornton, C. 2012. Renewing the link between cognitive archaeology and cognitive science. *Journal of Archaeological Science*, 39: 2036-2041.
- Toth, N.; Shick, K. 2009. The Oldowan: The Tool Making of Early Hominins and Chimpanzees Compared. *Annual Review of Anthropology*, 38(1): 289-305.
- Trevarthen, W.; Rosenberg, K. 2000. The shoulders follow the head: postcranial constraints on human childbirth. *Journal of Human Evolution*, 39: 583-586.
- Uomini, N. 2009. The prehistory of handedness: Archaeological data and comparative ethology. *Journal of Human Evolution*, 57: 411-419.
- Uttal, D. H.; Sandstrom, L. B.; Newcombe, N. S. 2006. One Hidden Object, Two Spatial Codes: Young Children's Use of Relational and Vector Coding. *Journal of Cognition and Development*, 7(4): 503-525.
- van Schaik, C. P.; Deaner, O.; Merrill, M. Y. 1999. The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution*, 36(6): 719-741.
- van Schaik, C. P.; Pradhan, G. R. 2003. A model for tool-use tradition in primates: implications for the coevolution of culture and cognition. *Journal of Human Evolution*, 44: 645-664.
- Vasilyeva, M.; Lourenco, S. 2012. Development of Spatial Cognition. *Wiley Interdisciplinary Reviews: Cognitive Science*, 3: 249-362.
- Vieira, A. B. 2010. Grammatical equivalents of Palaeolithic tools: a hypothesis. *Theory in Biosciences*, 129: 203-220.
- Wobber, V.; Wrangham, R.; Hare, B. 2010. Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. *Current Biology*, 20: 226-230.
- Wood, B.; Baker, J. 2011. Evolution in the Genus *Homo*. *Annual Review of Ecology, Evolution and Systematics*, 42 (1): 47-69.
- Woollett, K.; Maguire, E. A. 2011. Acquiring "the knowledge" of London's layout drives structural brain changes. *Current Biology*, 21: 2109-2114.
- Wraga, M.; Shepard, J. M.; Church, J. A.; Inati, S.; Kosslyn, S. M. 2005. Imagined rotations of self versus objects: an fMRI study. *Neuropsychologia*, 43: 1351-1361.
- Wynn T. 2010. The evolution of human spatial cognition. In: Dolins F. (ed.) *Spatial Perception, Spatial Cognition*. Cambridge, Cambridge University Press: 213-236.
- Wynn, T. 1985. Piaget, Stone Tools and The Evolution of Human Intelligence. *World Archaeology*, 17(1): 32-43.
- Wynn, T. 2002. Archaeology and cognitive evolution. *Behavioral and Brain Sciences*, 25: 389-438.
- Wynn, T.; Coolidge, F. L. 2010. How Levallois Reduction Is Similar to, and Not Similar to, Playing Chess. In: Nowell, A.; Davidson, I. (eds.) *Stone Tools and the Evolution of Human Cognition*. Boulder, University Press of Colorado: 83-103.
- Wynn, T.; Coolidge, F. L. 2011. The Implications of the Working Memory Model for the Evolution of Modern Cognition. *International Journal of Evolutionary Biology*. [Published online: 18-01-2011]. DOI: 10.4061/2011/741357.
- Zimmerman, E.; Radespiel, U. 2007. Primate Life Histories. In: Henke, W.; Tattersall, I. (eds.) *The Handbook of Paleoanthropology – Primate Evolution and Human Origins (Vol.2)*. Berlin, Springer-Verlag: 1163-1205.
- Zimmerman, E.; Radespiel, U. 2007. Primate Life Histories. In: Henke, W.; Tattersall, I. (eds.) *The Handbook of Paleoanthropology*. Berlin, Springer-Verlag: 1163-1205.
- Zollikofer, C. P.; de León, M. S. P. 2013. Pandora's Growing Box: Inferring the Evolution and Development of Hominin Brains from Endocasts. *Evolutionary Anthropology*, 22: 20-33.