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Evolution of Spatial Cognition in the *Homo* lineage

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Dissertação apresentada à Universidade de Coimbra para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Evolução e Biologia Humana, realizada sob a orientação científica da Professora Doutora Eugénia Cunha (Universidade de Coimbra) e da Professora Doutora Susana Carvalho (Universidade de Oxford)

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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 literature review yield a framework where important cognitive developments in spatial cognition provided possible cognitive mechanisms/changes that could explain technologies transitions on the archaeological record, namely by integration of metric and categorical information and by evolution of mental rotation. A methodological approach to test this hypothesis on stone tool analysis is proposed, which should be tested on subsequent work. The fascinating result of this literature review consists in suggesting and, to a certain point prove, that ontogenic data can be useful for understanding human cognitive evolution. Further investigation in this field would be required to achieve more conclusive results.

Key Words: Spatial Cognition; 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. Esta revisão da literatura científica deu origem a um quadro onde se correlacionam importantes desenvolvimentos na cognição espacial, os quais podem ter estado na origem de mecanismos/mudanças cognitivas, nomeadamente a integração de informação métrica e categorial e a evolução de rotação mental. Estas, por sua vez, podem explicar as transições tecnológicas observadas no registo arqueológico. Uma abordagem metodológica é proposta para testar esta hipótese em instrumentos líticos. 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: Cognição Espacial; Desenvolvimento Cognitivo; Evolução Humana; Instrumentos Líticos.

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1. INTRODUCTION

This essay falls within the scope of the Master Thesis on Human Biology and Evolution taught at the Faculty of Sciences and Technology of the University of Coimbra.

The general aim of this thesis is to shed some light on how the human mind evolved. 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. And, as Herbert Spencer stated in 1855: “Mind can be understood only by showing how mind is evolved” (*in* Huber, 2000: 23).

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 evolution of cognition becomes very hard to study on 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 approach of cognitive archaeology to focus on the evolution of spatial cognition across human evolution with a special emphasis on the *Homo* lineage. This tactic 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 inter relational 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 Léon, 2013). In other words, developmental and evolutionary accounts of cognition are complementary and can provide powerful insight into human history (Fiddick and Barrett, 2001). Others have already attempted this, e.g. Wynn, whom, in his article "Piaget, stone tools and the evolution of human intelligence" (1985), 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 is presented to test is: does child spatial cognitive development retrace the evolution of human spatial cognition? 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?

In order to achieve this goal of bringing together cognitive development and the evolution of spatial cognition, a thorough literature review is undertaken in order to framework the topic and to explore possible bridges between different fields of study, such as primatology, neuroscience and, obviously, archaeology.

Next, one must consider that lithic instruments have been widely used as a mean to study human evolution because they are the most widespread evidence of human evolution (de Sousa and Cunha, 2012) and because they allow for a glimpse of the early human mind, since they are, ultimately, its product. Stone tool technologies have been previously used to unravel phylogenetic relationships (Foley and Lahr, 1997). Following this reasoning, one could also use stone tool technologies to untangle some of the main knots in the evolution of cognition. So, as a result of the literature review a new method of lithic tools analysis will be proposed. One that encompasses pertinent developmental considerations and that is able to test the proposed framework, resultant from the literature review. In order to allow for a more straightforward reasoning this project will only focus on the African technologies.

The original project for this thesis included testing this new method on an adequate stone tool sample. Access to this sample was to be kindly conceded by Professor Marta Lahr and Professor Robert Foley, at the University of Cambridge. Unfortunately, it was not possible to accomplish this experiment in a timely fashion, and so, only the proposed methodology and not its results are included here.

This dilemma resulted in a somewhat skewed Thesis, since a much greater importance is given to the literature review, than to the method itself. Nevertheless, it was believed that this evolutive-developmental approach has the potential to give an important input into the subject of human evolution and that, as such, it was a fascinating theme on which to conduct this Master's Thesis.

As a final remark two points must be made. First, not all sorts of inferences regarding the evolution of spatial cognition can be made from stone tools. It has even been argued that stone tool patterning is simply a matter of raw material variability, reduction intensities and technological constraints (McPherron, 2000). Second, changes in behaviour not always match changes in biology, at least not archaeological visible changes and so evolution of spatial cognition must not be expected to necessarily follow phylogeny (Wynn and Coolidge, 2011; Shultz *et al.*, 2012). Hence, the special emphasize on the literature review that might allow for a correct redirecting of enquiry efforts, which will translate, hopefully, in as accurate as possible interpretations.

2. THEORETICAL CONTEXT

2.1. The *Homo* lineage

The first step of this literature review is to include a summary of human evolution, especially where the Genus *Homo* is concerned.

Human evolution discussions can be a true headache. Over the years, numerous scholars with an even more varied number of opinions and ideas have dealt with this issue and yet, the end is far from settled, and it will likely remain so for many years to come.

Over time there has been some consensus models regarding human origin. These, however, had a high turnover through time, one making the way for a new one, when too many weaknesses were pointed out on the standing model. This is not to say that developments have not been made. Each time one abandons a model breakthroughs follow. Everyday more and more is discovered, just not quite enough.

So, in a brief overview of past models, one can find changes in trends of thought throughout time. The human being has questioned its origins for a long time but from Aristotle and all through the Middle Ages, the standing belief was that the natural world had always existed exactly as it was. This belief was strongly enforced by church doctrine and their hold on science (Jacob, 1970).

Then, during the Renaissance, a discussion ensued to whether there were multiple origins for humanity – polygenism – or if it were the result of a single act of creation – monogenism. The church took the side of monogenism and there were severe consequences to anyone who dared to gainsay them. However, it is very important that this discussion even got to take place, because it testifies for thought paradigms (Le Douarin, 2005).

These changes were brought on, for the most part, by the development of some sort of scientific thought, the study of human anatomy by escolars such as Leonardo da Vinci and finally, the European discovery and exploration of the New World. These three factors allowed people to develop a sense of variation within the natural world, specifically within the human species (Jacob, 1970; Le Douarin, 2005).

During the seventeenth and eighteenth century, conversely, the ultimate biological origin of humans was pushed aside and classification took precedence, with Linnaeus creating the *Systema Naturae,* and coining the name *Homo sapiens* in 1758 (Linnaeus, 1758). But these naturalists did not part from the theological view of a static, unchanging world (Le Douarin, 2005).

Later, still in the end of the eighteenth and early nineteenth centuries, a number of natural historians contributed to the explanation of the diversity of flora and fauna and went on to strongly influence Darwin's thinking decades later. Some of those were Comte de Buffon, Georges Cuvier, Geoffroy Saint-Hilaire and Jean-Baptiste Lamarck. Finally in 1859, Charles Darwin published *The Origin of Species*. Darwin, and to same extent Thomas Huxley that was working on the same theory at about the same time, proposed an elegant mechanism to how evolution worked: natural selection (Darwin, 1871; Jacob, 1970; Le Douarin, 2005).

Rephrased in modern terms what they defended was that for natural selection to work, three preconditions must be met. First, the trait in question must be inherited, second, the trait must show variation among individuals and, third, the filter between the organism and its genetic makeup is the environment that must exert some pressure in order for natural selection to act. This discovery brought on a revolution in thought, since it provided a simple and effective mechanism for evolution to act through. Although some scientists had held evolutionary views for some time, it was difficult to defend their position without a reliable theory to support them (Darwin, 1859; Stanford *et al.* 2011).

Despite this major breakthrough, between 1860 and 1920, all evolution came to be seen as progressive, driven by orthogenetic processes, ending in modern humans. Key problems related to the existence and order of transitional steps in this ladder leading to human species – this included living human diversity, where different ethnic groups were ordered on the ladder. This gave rise to an idea of qualitative improvement from human ancestors until nowadays (Lewin and Foley, 2004).

In contrast, from 1900 to 1950, most fossils were seen as side branches away from the main line that gave rise to modern humans (single-species hypothesis), which meant that most similarities between African apes and humans were described as the result of parallel evolution. So, most of the discussions were related to which fossils belong to the human line of descent (Lewin and Foley, 2004).

Following, in the time period 1940-1990, it was recognized that variation within species and populations could occur, which, due to the pressures of selection, would lead to the appearance of new species. Emphasis was then put on continuous variation, gene flow and progressive adaptive change. This gave rise to the Multiregional Model, where humans were thought to have evolved in several places at the same time (Foley and Lahr, 1997).

From the 80's onwards, the focus turned once again towards taxonomically diverse models of evolution, due to the study of geographical variation, mechanisms of speciation and the role of isolation. Developments in genetics and dating methods led to a much more precise and justified chronologies. Hence, the Single Origin Model was developed, where Africa is regarded as the cradle of human evolution and through a branching model of evolution, several species appeared and disappeared and spread across the globe (Foley and Lahr, 1997; Lewin and Foley, 2004).

After this review of the main models that may have acted as motors for human origins research, the focus will now turn to the *Homo* lineage, since these hominins have the more well documented indications of tool production and are the only ones that have been found in context with lithic instruments (Hovers and Braun, 2009).

Not surprisingly, research on human origins is fraught with uncertainties and disagreements. These derive from the paucity of the fossil record, differences in species concepts – with splitters naming new species on the basis of small anatomical differences, and lumpers seeing these anatomical differences as intraspecies variation –, and the difficulty in applying a static classification system to the dynamic process of evolution – where species are continuous and not stable categories through time (Endersby, 2009; Kimbel, 2009).

But first things first: to start this analysis one must bear in mind that a species is, by definition, a group of individuals that are able to mate with each other, producing fertile offspring, while a genus implies a very recent common ancestor, with close phyletic relationships among the species in question and a shared adaptive strategy (Mayr, 1963; Wood, 1999; Wood and Baker, 2011).

These concepts are very hard to identify in the archaeological record because: 1) individuals obviously can no longer reproduce and, 2) there is only indirect evidence of both species relationships and adaptive strategies. Usually, in these cases, anatomical aspects are used to distinguish among different clades, since they are the most readily available information, but this might lead to severe misconceptions of events (Wood, 1999; Wood and Baker, 2011).

Anatomically, the genus *Homo* differs by having a larger braincase, a smaller, less projecting face, smaller teeth and jaw and possibly a larger body and more efficient/habitual bipedalism. These features may relate to a shift to an adaptive strategy that includes a more animal-based diet and a greater food processing through tool use, as well as a greater encephalization and an ability to use complex language (Kimbel, 2009; Wood and Baker, 2011).

To help clarify the different nomenclatures for the genus *Homo* and the way they relate to each other, Fig. 1 is included. It must be pointed out that this figure does not aim to represent phylogenetic relations but only to illustrate how can hominin species be lumped or split, so that the consequent text becomes more reader-friendly.

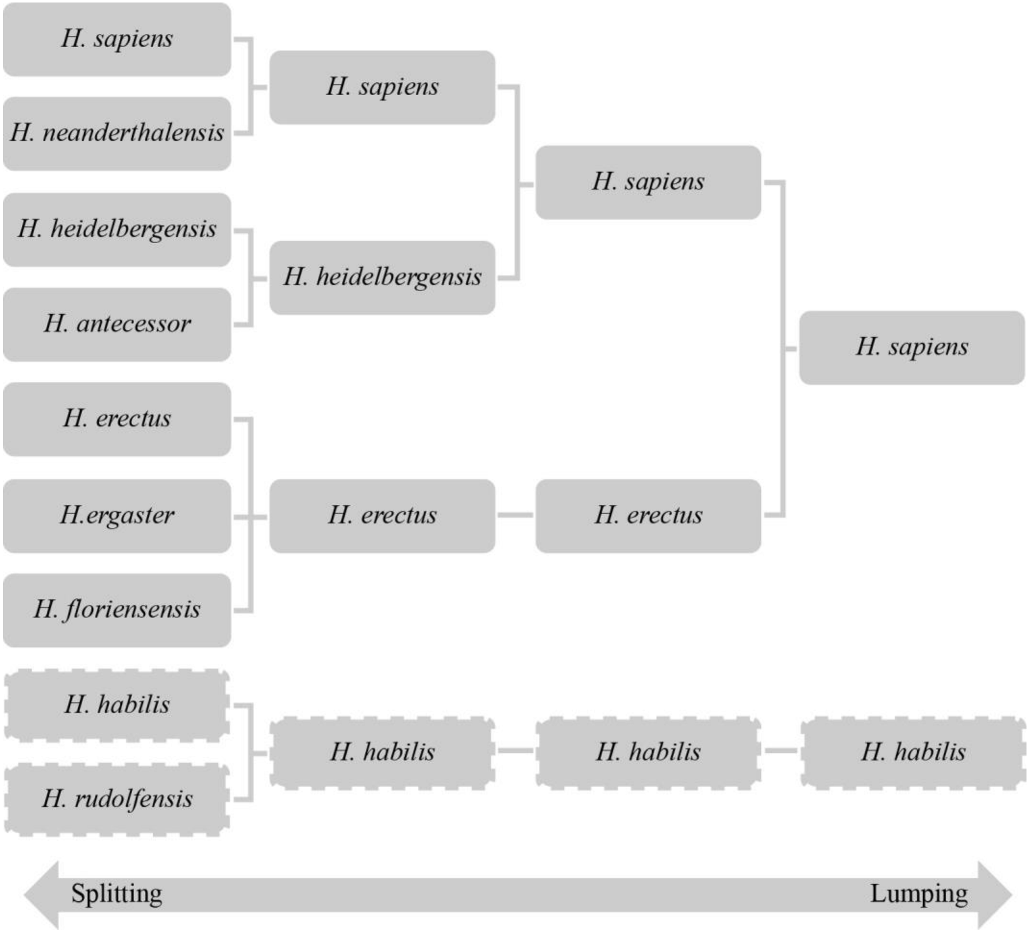

Fig. 1. Alternative nomenclatures for the genus *Homo*, adapted from Lewin and Foley (2004): 371 and updated according to Wood and Baker (2011). This figure does not aim to illustrate direct phylogenetic relationships but to clarify how the various taxa may be lumped or split. Dashed lines identify species that do not necessarily belong in the *Homo* genus, according to Wood and Baker, 2011.

What species should be included in Genus *Homo* is still a major issue. Wood (1999) and Wood and Baker (2011), for instance, defend that *Homo habilis* and *Homo rudolfensis* (or *Homo habilis, sensu lato*) are more closely related to *Austrolopiths* genera than to *Homo,* and as such should be included either in the earlier taxa and not the latter, or in anew genus. They make a compelling case, supporting their statement on evidence concerning body size and shape, posture and locomotion, size and shape of the bony labyrinth, brain size, dexterity, diet and teeth, genetics and life history. Here, however, *Homo habilis* and *Homo rudolfensis* will still be considered, given the lack of consensus on the subject.

If one considers tool production as the critical change that calls for a new genus, then *Homo* can be seen as differing from the *Australopithecus* sps. at around 2.6-2.5 million years ago (Ma) because the first stone tools are so dated, although the identity of their manufacturers is still unknown (Semaw, 2000). Tool production, however, may not be the best way to justify the inclusion of these fossils in the *Homo* genus, considering that tool production in earlier hominins is plausible, given the behaviour repertoire exhibited by non-human primates today. On the fossil record, a few specimens that have been attributed to *Homo* fall on the time frame 2.5-2.0 Ma, but most of these are fragmentary or their diagnostic value is questionable. The earliest well-sampled record that exhibits features only found in *Homo* date 1.7-1.8 Ma (Kimbel, 2009).

Homo habilis is a species discovered and named by Louis and Mary Leakey in the 70’s (Leakey *et al.*, 1964). They based the creation of the genus not only on an anatomical difference but on the already discussed behavioural switch, tool production. Nowadays, *Homo habilis* is distinguished by having a mean endocranial capacity of about 610 cm^3, thin vault bones, a forwardly placed *foramen magnum,* nasal bones that widen inferiorly, a relative narrow midface with a near-vertical malar region, overall reduction in tooth size in comparison to *Australopithecus* sps. and post-cranial adaptations to bipedalism (Rightmire, 2010).

Some researchers, however, divide this species into two, due to the great variation in cranial capacity and more elongated limbs– considered a primitive feature – on the termed *Homo habilis*. These are just two of the most important differences. Hence, some fossils are deemed *Homo habilis*, while others are *Homo rudolfensis* (Alexeev, 1986).

Homo habilis is, so far, restricted mostly to Eastern Africa, and its earliest appearance may be as early as 2.33 million years ago and lasted until maybe 1.6 million years ago. (Kimbel *et al*., 1996; Wood, 1999). They are also associated with the Oldowan technology – as already mentioned, the earliest ones are dated to 2.6-2.5 million years –, a stone tool industry that is thought to link to an increase in meat consumption. Again, while this is the standing paradigm, the role of *Homo habilis* as the first active producer of stone tools remains highly debatable (Barsky, 2009). More on the subject will follow on later chapters.

Following *Homo habilis sensu lato*, sometime around the Plio-Pleistocene boundary, at around 1.8 Ma, there was a major adaptive shift, which is reflected in a larger average brain and body size – much larger than between *Homo habilis* and *Homo rudolfensis* – and decrease in tooth size, giving rise to *Homo erectus* (Dubois, 1894; Asfaw *et al*., 2002). These changes might indicate an improvement in diet quality, with increased meat consumption and a larger home range requiring broader ecological adaptations (Isaac, 1978; Antón, 2003).

On a side note, at the same time, another genus, *Paranthropus*, also strived, although in a completely different fashion. Larger teeth and jaws characterize this parallel genus, which initially were thought to imply an increased specialization in tough food processing. Recent studies, however, have shown that different species of this genus followed very different diets and *P. boisei* had a rich diet in C_4 biomass such as grasses or sedges (Cerling *et al*., 2011).

Homo erectus was the first known hominin to leave Africa, dispersing into Asia and Southeast Asia around 1.7 million years ago. This dispersal has a series of implications because as it occurred, some changes also took place, leading many scientists to subdivide the species (Antón, 2003). The first division is between *Homo erectus* and *Homo ergaster* and is based on cranial morphology – *Homo ergaster* has thinner cranial bones and less pronounced browridges than *Homo erectus* – (Groves and Mazák, 1975; Wood, 1999). *Homo ergaster* is normally used to refer to early African forms of *Homo erectus*. Moreover, there are some who also consider the existence of *Homo georgicus*, which is very similar to *Homo ergaster*, albeit smaller (Gabounia, 2002).

A second splitting takes form with *Homo floresiensis*, a fossil whose anatomical characteristics place it with *H. erectus*, but that has a dwarf aspect, maybe due to the fact that he lived on an island – Flores in Indonesia, hence its name – (Brown *et al.*, 2004). These authors defend this hominin evolved from an ancestral *Homo erectus* population, which suffer endemic dwarfism, after long-term island isolation. Jungers (2009), on the other hand, defends that some very primitive characteristics, in foot morphology, for instance, might indicate that *Homo floresiensis* evolved from an earlier hominin, whose dispersal into Southeast Asia is not yet documented. Nevertheless, if one includes *Homo floresiensis* in the *H. erectus* clade, this would mean that this species spans from around 1.8 million years ago, as already mentioned, to as recently as 18 000 years ago (Brown *et al*., 2004; Lieberman, 2009).

Where stone industries are concerned, a new one appeared in this time period, the Acheulean technology. Together with Oldowan, these two stone technologies are usually regarded as belonging to Early Stone age. Acheulean is characterized by a quasi-standardized production of large flake-based bifacial handaxes and cleavers. These tools seem to retain their cutting edges longer and are easier to hold than simple flakes and may be adaptations to carcass processing (Lepre *et al.*, 2011). It is generally believed to have appeared at around 1.6 Ma, but recent findings have pushed back this boundary to around 1.75 Ma (Lepre *et al.*, 2011; Beyene *et al.*, 2013). It has been argued that a technological boundary, called 'the Movius Line', separates Acheulean technologies of early and middle Pleistocene Africa/ western Eurasia from simpler core-and-flake industries of equivalent age in eastern Asia. However, Lepre *et al.* (2011) defends that this phenomenon can be explained by coexistent groups of hominins with distinctive stone-tool-making behaviours and different dispersal strategies in Africa at that moment in time.

Brumm and Moore (2012), on the other hand, state that classifying a handaxe is not based exclusively on morphological attributes inherent to the artefact, but it includes contextual data such as age and geographical location, leading to a double standard, in which Asian handaxes are disregarded as the product of modern human cultures. To this bias, also concurs the lack of consistent study of the Asian territory.

Around the Middle Pleistocene, a new shift occurred. Many fossils from this period are classified as archaic *Homo sapiens*, since they exhibit some features that are considered as derived, but phylogenetic relationships among them are very difficult to discern, illustrating the transitional step that this fossils represent (Kimbel, 2009).

The main differences observed are a larger brain size than *H. erectus*, but without the characteristic angular shape, a more parallel sided vault and a supraorbital torus more double arched than bar-like. These specimens are sometime grouped under the name of *Homo heidelbergensis* (Schoetensack, 1908), in spite of the reservations concerning its validity as a cohesive species. Also, some scholars include just the European pre-Neanderthal lineages, while others include specimens from Africa and Asia (Smith, 2010).

As far as stone tool technologies from the Middle Pleistocene are concerned, those are characterized by the appearance of prepared core techniques, amongst which is the Levallois technique. Prepared core technologies require the toolmaker to pre-modify the original core by removing a certain number of flakes in order to prepare it to produce the desired flake of prescribed size and shape (Wynn, 2002; Wynn and Coolidge, 2010).

Middle Stone Age industries also used other flaking techniques, characterized by the introduction of the soft hammer percussion (where materials such as bone or soft stone are used to remove flakes), more retouched tools, and a larger variety of possibly stylizes tool shapes (Andrefsky, 2005). The first biodegradable tools are also known from this time period and indications of hunting also appear for the first time, as opposed to the scavenging practiced before (Thieme, 1997; Whiten *et al.*, 2009; Pante *et al.*, 2012; Pickering *et al.*, 2013).

The group of early hominins above referred are likely to be ancestors to later hominins in their regions. In Europe, to Neanderthals (or *Homo neanderthalensis*), and in Africa to modern humans. Another possible candidate for Neanderthals and modern humans' predecessor is *Homo antecessor* (de Castro *et al.*, 1997). These fossils are dated from around 1.0 Ma and they were found in Atapuerca Spain – Gran Dolina – (Berger *et al.*, 2008). Atapuerca has a longer period of occupation, however, and has yielded older fossils from a different site, named Sima del Elefante, which is dated to 1.3-1.2 Ma (Carbonell *et al*., 2008; de Castro *et al*., 2011). These fossils seem to be different from *Homo antecessor* and have not yet been classified, being referred by their investigators as *Homo* sps. Their relation to *Homo antecessor* is also unknown at the moment (de Castro *et al*., 2011; Mosquera *et al*., 2013).

Returning to Neanderthals, these hominins are characterized by large brain cases, with the greatest breadth in the middle of the parietal – long and low crania (King, 1864). A suprainiac fossa and an occipital bun are present, although an occipital torus is lacking. The midface is prognathic, with a sweptback cheek region and large nasal aperture. Browridges are large and double arched. A retromolar space is present in the mandible but there is a lack of chin. Postcranially they were robust, had barrel-shaped chests and were heavily muscled. Most of these seem to be adaptations to the intense cold they must have faced while living in a glacial period in Europe. The earliest specimens appeared in Western Europe around 250 thousand years ago (Ka) and lasted until around 30 Ka years ago, coexisting in the same time and space frame (Europe and Middle East) as *Homo sapiens* (Wood, 1999; Smith, 2010). It must be noted that although there is evidence for existence in the same space frame, there is no evidence of true cohabitation, although contact is most likely (Wang *et al*., 2013).

Since Neanderthal genome is relatively distinct from modern humans, it was usually thought that they did not contribute to recent human gene pool but a recent study by Green *et al.* (2010) showed that between 1 and 4 % of the genomes of people in Eurasia are derived from Neanderthals, which may indicate that Neanderthals could be considered as a sub-species of *Homo sapiens*. This issue, however, is quite controversial, due to data quality and insufficient sampling, especially about when and where the genetic admixture took place, and the direction of the assumed gene flow (Wang *et al.*, 2013). Moreover, Neanderthals exhibited a series of technological innovations such as the hearths, thrusting spears, and even projectile technology. They likely hunted and used a great deal of animal resources. They did not possess a lot in ways of symbolic behaviour but there is evidence that they buried their dead (Arsuaga, 2007; Smith, 2010).

Where stone technology is concerned most Neanderthals are found with Middle Palaeolithic – Middle Stone Age – industries, although in a later period there is some association with Upper Palaeolithic industry – termed Later Stone Age in Africa. This later stone industry appeared around 40 000 years ago, although some defend that it’s even more ancient, beginning substantially earlier than 46 000 years ago (Ambrose, 1998; Kuhn *et al.*, 2001). This industry is characterized by microliths, which are small, shaped flakes that probably were once attached to wood or bone to make composite tools, and it includes many more tool types and regional specialization than earlier technologies (Hublin *et al.*, 1996; Bar-Yosef, 2002).

At the same time that Neanderthals were making their living in Europe, *Homo sapiens* were evolving in Africa. The earliest appeared about 195 Ka years ago (McDougall *et al.*, 2005). Modern human beings are characterized by a more vertical forehead, the presence of chin, a reduced facial size, a reduced brow size, the presence of canine fossa and a more gracile skeleton (Wood and Baker, 2011). This new species diverged to the Near East around 100 000 years ago, into Southeast Asia and Australasia by 50 Ka years ago and into Europe by 40 Ka years ago. *Homo sapiens* appears initially associated with Middle Stone technologies and then with Later Stone Age (Bar-Yosef, 2002). *Homo sapiens* is also associated with the appearance of what is often called "Behavioural Modernity" whose most striking feature is the appearance of signs of symbolic reasoning.

In Europe the shift to Upper Palaeolithic is often thought to be the result of a behavioural or cultural revolution that took place when modern humans replaced Neanderthals. However, it is possible that these changes occurred gradually through time in Africa and where then exported to Europe (McBrearty and Brooks, 2000). Zilhão (2007), for instance, defends that symbolic behaviour, such as the production of figurine, arose when there was the need for systems of social identification/differentiation. Need that, in turn, is a consequence of adaptive success, with technological innovation leading to demographic growth and to increased intergroup competition and consequent regulation of that competition.

In other words, according to Zilhão (2007) the increase in population led to intergroup strains that were solved through ceremonial behaviours addressing issues of property and rights over resources. However, and again, according to this author, the cognitive processes that allowed for these behaviours were already in place long before the appearance of their proof on the archaeological record, both in Neanderthals and in modern humans. He bases this idea on the fact that there are several indications of symbolic behaviour throughout the late Middle and early Upper Pleistocene, both in Europe and Africa. For a review of the archaeological evidence for the emergence of symbolism, consult d'Errico *et al.* (2003).

Mellars (2005), on the other hand, continues to defend a much more rapid emergence of the hallmarks of modern behavioural patterns in Africa. This author states that although the appearance of symbolic behaviour took place earlier than initially thought, it can still be associated with a significant “revolution” in human behavioural and cognitive patterns, associated closely with the biological and evolutionary emergence of *Homo sapiens*.

As one can rapidly perceive by this very brief summary, there are many ifs in these sentences, and the certainties are very sparse. Many more species have been proposed, numerous phylogenies trying to correlate them, and a vast amount of inferences concerning behaviour, cognition and environment. This review aimed to give a general, but as accurate as possible, idea of the evolution of the *Homo* genus. This will be crucial throughout this Thesis, although the discussion of all the dilemmas this theme faces exceeds the scope of the study.

2.2. Evolution of Human Cognition

An overview of the evolution of human cognition in general reveals itself essential, which will be included, with a special emphasis on what the problems and advantages of cognitive archaeology contributions are.

As stated in the Introduction, cognition can 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, are 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, but are usually very fractioned, suffer from a sliding scale of resolution – in other words, the older the site, the worst its preservation (Foley, 1996) and are strongly subjected to the investigator’s interpretation (d’Errico *et al.*, 2003; Wynn, 2010). Also, this same investigator is strongly influenced by his field of study and although there has been an increasing strive for multidisciplinarity, 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).

Over the last 25 years, research in evolutionary psychology has been dominated by a model based on a human mind consisting of several distinct “modules”, evolved to solve specific problems posed to our ancestors. Cosmides and Tooby (*in* Mithen, 1996) mostly promoted this theory and their most commonly known metaphor for this reasoning is the Swiss Army knife. This theory has remained dominant, although other theories have been proposed such has the cathedral metaphor used by Mithen (1996), where the different modules would be linked by a cognitive ‘fluidity’ whose advance would mark modern human cognition.

More recently, a hand metaphor was proposed, where the mind is seen as capable of performing “a wide and open-ended variety of technical and social functions” (Heyes, 2012: 2092).

Without a nice metaphor, Wynn and Coolidge (2011) and several other authors support a working memory model, initially constructed by Baddeley. 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. Baddeley’s current 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’.

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 sensiromotor 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. The following Fig. aims to clarify its different components.

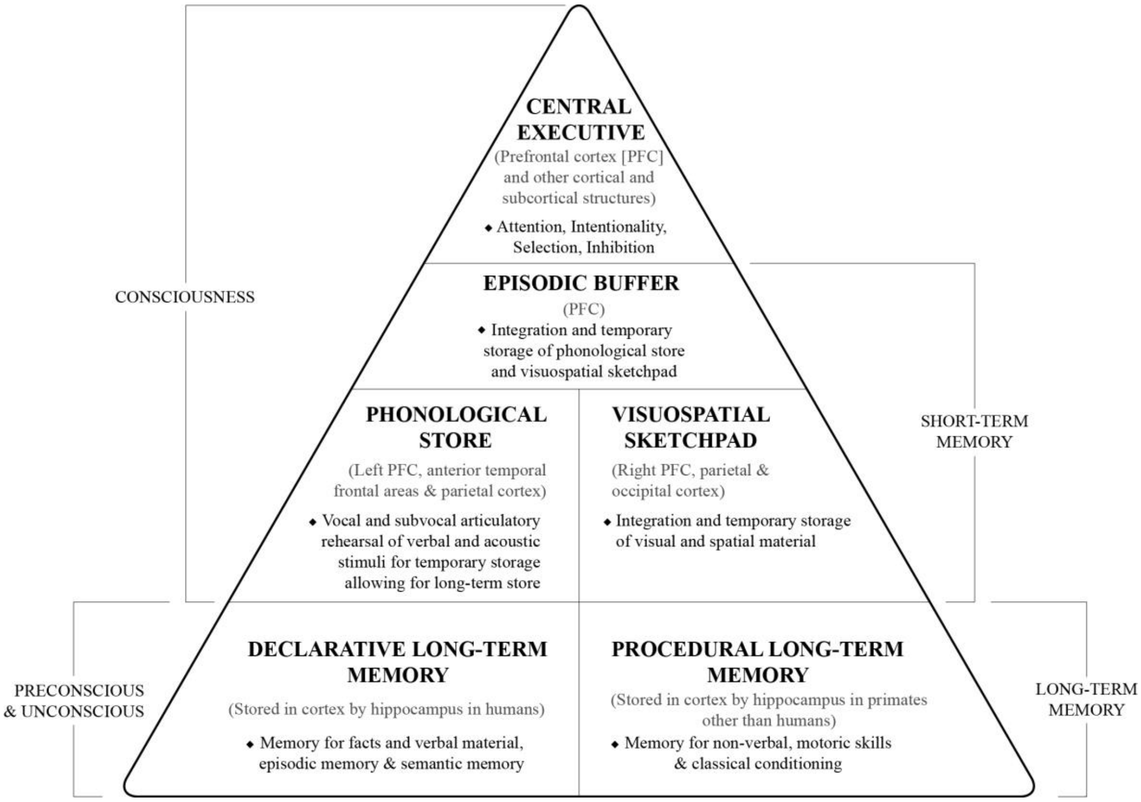

Fig. 2. Major components of working memory and long-term memory according to Wynn and Coolidge (2010). This figure also includes general considerations by these authors, such as the localization in the brain of these components and of their correspondence to conscious or preconscious and conscious processes.

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.

2.3. 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 into the reality. Nature does not fall into neat packages. Each element of the universe makes its existence among other elements with whom it interacts. 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. On the cognition field, Cosmides and Tooby’s Swiss Army knife model, where the mind is seen as a series of modules that are independent and perform specific tasks, dominated scientific thought over the last 25 years (Heyes, 2012). Nowadays, this approach is being gradually abandoned in favour of a more inclusive point of view. 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).

Back to the original topic, at the moment, 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.

Also of interest are the sex differences that can be found in humans in spatial tasks. Men are usually found to perform consistently and cross-culturally better than women in at least three areas: 1) mental rotations – to imagine an object from a different point-view; 2) spatial perception – to identify horizontal and vertical despite competing cues and 3) targeting – to hit or intercept moving objects (Kimura, 2000; Silverman *et al.*,2000; Cashdan *et al.*, 2012). Women, on the other hand, seem to perform better at spatial location memory – to remember the location of objects (Kimura, 2000; Silverman *et al.*, 2007). These sex differences may also be associated with the choice of navigational strategies. Women are more likely to use landmarks and directional cues, while men include more Euclidean cues such as distance and cardinal directions (Ward *et al*., 1986; Dabbs *et al.*, 1998; Kimura, 2000). In other words, one could say that women tend to use intrinsic mental maps while men use geocentric ones.

It has been argued that these differences can be related to our evolutionary history, more exactly by ranging patterns in ancestral hominins. Supposedly, good spatial ability and attention to Euclidean cues in men were favoured because they moved more in their environment, either due to a mating-system model of polygyny (Gaulin, 1992) or due to the demands of hunting mobile prey (Eals and Silverman, 1994; Kimura, 2000) or of way finding in a landscape (Silverman *et al*, 2000). On the other hand, a navigational strategy based on landmarks in women might be an adaptation to gathering activities (Kimura, 2000; Ecuyer-Dab and Robert, 2004). Cashdan *et al*. (2012) have tested this hypothesis for a modern hunter-gatherer population and found that men performed better in Euclidean tests, but also in the object location memory task. Also, older women were consistently nominated by peers as the best at finding bush foods, although women’s performance at object location memory task deteriorated with age.

The authors present several explanations for this latter result. First, it is possible that gathering takes place on a spatial scale too large to be aided by object location memory. Second, gathering in groups may compensate individual spatial cognition deficits with experience becoming the differentiating factor. Third, short-term and working memory decline with age, while long-term memory doesn’t, which may be more important in successful gathering. And, fourth, older women may be relying less on object location memory and more on Euclidean spatial skills.

Interestingly, this can be related to lower estrogen levels associated with menopause, since estrogen appears to improve performance on short-memory games, but reduces performance on Euclidean spatial tasks (Hampson, 2002). This result can also be found in ovariectomized female Rhesus monkeys, where prolonged absence of ovaries, prevents or lessens age-related decline in certain aspects of spatial memory (Lacreuse *et al.*, 2000). These last data seem to be consistent, according to Cashdan *et al*. (2012), with the 'fertility' hypothesis from Sherry and Hampson's (1997), which defends that selection has led to reduced mobility and spatial ability in reproductive-aged women in order to minimize their energetic costs and the risks associated with travel, constraint to be lifted in older, post reproductive women with consequential increase in spatial abilities.

Controversially, Wynn *et al*. (1996) defend that sex differences on spatial cognition are an evolutionary by-product. According to these authors, these sex differences appear through selective forces operated on the timing of fetal development, which, in turn, would affect the hormonal milieu of cerebral growth, and hence, the effect of testosterone on cerebral asymmetry and co-related cognitive skills. Selective forces on the timing of fetal development would be put in place by mechanisms such as the increase or decrease of fetus viability or through maternal viability.

According to Wynn *et al*. (1996), hypothesis that emphasize selection for female cognitive abilities are handicapped, given the probable source of the neurological sex difference in the timing of fetal testosterone. On the other hand, hypothesis favouring male hunting mobile prey and mating strategies do not hold when evaluated in light of the timing of the evolution of spatial cognition. In other words, according to these authors, archaeological evidence for the proposed selective behaviours and for the spatial abilities in question do not correspond in a way that would permit a link between them.

On a later article, Wynn (2010) addresses the 'way finding' theory, defending that although there are early evidences of hunting, it were more likely opportunistically. Hunting such as seen in modern hunter-gatherer populations, with long distance hunting trips, managed landscape hunting or large scale cooperative hunts, most likely appeared too late in human evolution to provide a reasonable selective force on spatial cognition differences observed today. Wynn *et al.* (1996) points out that the abstract nature of the skills tested, as opposed to real world problem associated skills further sustain that sex-related spatial abilities are an evolutionary by-product. Cashdan *et al.* (2012) rather ambiguous results when testing a modern hunter-gatherer population, using real world problem tasks, further support this claim. Burke *et al*. (2012) also found no sex-based differences in a real world way finding task. They suggest that differences in spatial abilities consistently reported in the literature are the result of gender bias in training opportunities. Nevertheless, Burke *et al*. (2012) recognize that the subjects in their experiment could have been using different spatial strategies. They just point out that these hypothetical differences on spatial strategies do not seem to handicap any of the genders in way finding tasks, further disclaiming the Hunter-Gatherer hypothesis for spatial cognition.

As for the "fertility" hypothesis, Sherry and Hampson's (1997) are the first ones to recognize two main problems within the theory. First, natural selection has no effect on the direct fitness of post-reproductive individuals because, by definition, there can be no raising or lowering of their reproductive success. And, second, survival beyond middle age may be very recent in human history and show minimal effects of natural selection.

The Grandmother hypothesis could sway these arguments, since it defends that *Homo erectus* were the first whose life expectancy extended beyond menopause, with grandmothers and great aunts involved in the rearing of young offspring, thus increasing their indirect fitness (Aiello and Key, 2002; Hawkes, 2004). Krovitz *et al*. (2003) disagree defending that there is no fossil evidence to support this hypothesis.

In summary, it is very hard to find conclusive evidences for the evolutive explanation of sex-based differences in spatial cognition, if there are any.

2.4. Spatial Cognition in other Animals

When comparing spatial cognition across the animal kingdom, Salas *et al*. (2003) claims 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). Recent studies have, however, provided strong evidence that reptiles and teleost fish 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 Dore, 1996 and Fiset *et al.*, 2000 *in* Hribar and Call, 2011). 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 2 years – than in relation to two landmarks – at 4 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. Meulman *et al*. (2012) base their statement in four lines of evidence. First, the only monkey population exhibiting habitual tool use seem 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.

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 review, 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).

2.5. Evolution of Human Development

In this chapter, one must bring to attention the importance that developmental studies may bring towards understanding evolution. First, as already mentioned in the introduction, 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, as already described, 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, considering that they have higher neonatal weight, higher age at first reproduction, shorter interbirth interval and longer life span (Zimmerman and Radespiel, 2007). As a result, human life history consists of five stages: infancy, which goes from birth to weaning; childhood, from weaning to the eruption of the first molar, juvenile, adolescence and adulthood. 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 became 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). 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 still some debate over this (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). 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 (Trevanthan and Rosenberg, 2000). This is a very good example of how different factors intertwine and exponent each other to produce a given evolutionary effect.

2.6. Development of Spatial Cognition

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, it has been suggested that 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 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 6 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 6 years old, do children learn to combine different types of cues, for instance, combining geometric and nongeometric cues (Hermer-Vazquéz *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 4 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 4 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). Generally speaking, accuracy in spatial scaling – a very important part of using maps – undergoes the most marked considerable development between 3-5 years. More, the youngest children showed the higher variability and most profited from landmark information (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 being, 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. For instance 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 led to 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.

A final relevant point is made by Gunz *et al.* (2010) when suggesting 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.

2.7. Tool Use and Tool Production

One of the best definitions of tool use is the updated version of Beck’s 1980’s one, where tool use is seen as:

> “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

Here, one must underline, as the authors did, that “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.

This is not to say that this discussion is 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 breath 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 (Crast *et al.*, 2009; Hayashi, 2010).

However, at this point in reasoning, one must understand that, considering the erratic distribution of tool use in living great apes, it is unlikely that the intellectual capacity for tool use itself provided the selective force that produced more generalized cognitive skills (van Schaik *et al.*, 1999). Instead, as always in an evolutive context, it is likely that there were several elements into play. Van Schaik *et al.* (1999), for instance, proposed 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, it has been suggested that 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). This does not means that other animals, besides primates, are not capable of exhibiting culturally-transmitted behaviour, even where tool use is concerned. For instance, in Shark Bay (Western Australia), wild bottlenose dolphins (*Tursiops* sp.) have been found to 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, consisting on a true cultural behaviour. 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. More exactly, 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 is 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, it has been stated that these attempts made by bonobos lack future action planning, such as to 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 statement 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) goes 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 *in* Boesch *et al.*, 2009) 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, and so they did not used them, or because they used tools made of organic materials, which do not preserve. If one follows the first scenario, then it is 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, for instance, 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 came 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.

2.8. Evolution of Tool Use and Tool Production in Human Ancestry

During the course of human evolution, temporal progression does not go necessarily in the direction of greater sophistication. In other words, there is no linear line leading from simple to ever increasing complex tools (Roche *et al.*, 1999). Nevertheless, some major shifts can be pinpointed, as will be explored in this chapter.

According to Delagnes and Roche (2005), there are only about a dozen of reliable sites that have yielded stone artefacts produced by earlier hominins. Those are: Hadar and Gona (Harris 1983; Kimbel *et al.*, 1996; Semaw, 2000; Corvinus and Roche, 1980 and Roche and Tiercelin, 1980 *in* Delagnes and Roche, 2005); Omo (Chavaillon, 1976 and Merrick and Merrick, 1976 *in* Delagnes and Roche, 2005); West Turkana (Kibunjia *et al.*, 1992; Kibunjia, 1994; Roche *et al.*, 1999) and Kanjera (Plummer *et al.*, 1999). Of these, only in Hadar AL 666 have stone artefacts been associated with hominid fossil remains (Kimbel *et al.*, 1996).

However, the earliest *evidence* for stone tool-use is found in Dikika, Ethiopia and it dates back to 3.39 Ma. This evidence is indirect, since what was found were cut-marks in bones, presumably made by stone tools, but the stone tools themselves were not found. More, it is not possible to know if these stone tools were naturally sharp-edged stones or if they were modified in any way. In other words, it is not possible to know if the producers of these cut marks were engaged in tool production or only in tool use (McPherron *et al.*, 2010). Finally, these results have been strongly challenged by Domínguez-Rodrigo *et al.* (2010)

The earliest known stone tools date back to around 2.6-2.5 million years ago and they were found in Gona, Ethiopia (Semaw, 2000).These early stone tools are included into Oldowan, which spans from 2.5 Ma to around 1.5 Ma, considered by some researchers as a long period of stasis in stone technology (Semaw, 2000; Semaw *et al*, 2003) de la Torre *et al.*, 2003). Also, some authors have doubted of the intentionality of these early stone tool makers (de Sousa and Cunha, 2012).

Those two last affirmations have been much contested. Although these early tools were quite simple, they seem to imply an empirical understanding of the mechanics of fracture of hard rocks, with the production of sharp edged implements as the goal for the process (Delagnes and Roche, 2005; Wynn, 2010). Also, these hominids seem to have moved beyond the unintentional production of debris, such as that resulting from the accidental breakage of hammer stones at the nut-cracking loci of chimpanzees (Mercader *et al.*, 2002). However, there was no concern with final shape, as inferred from the absence of further modification of flakes (Wynn, 2010).

Where the claim for homogeneity in Oldowan is concerned, sites like Lokalalei 2C (West Turkana) have changed this picture of overall simplicity. In this site it seems that unidirectional or multidirectional removals are flaked on a single debitage surface from natural to prepared platforms (Roche *et al.*, 1999; Delagnes and Roche, 2005). Roche *et al*. (1999) state that the repeated application by the knappers of the same technical principles to several cores, and during the reduction of each one, indicate an elaborate debitage scheme, as well as motor precision and coordination. These principles include appreciation of good fracture qualities in raw materials, exploitation of the natural morphology of cores and maintenance of adequate flaking angles throughout the process (Roche *et al*, 1999; Wynn, 2010). This does not mean that the hominins at Lokalalei 2C had completely mastered stone knapping but they seem to have had the cognitive abilities to exploit pre-existing angles, although not to create new ones (Delagnes and Roche, 2005).

These authors go on to defend that a similar level of sophistication such as the one observed in Lokalalei 2C has not, of yet, been observed in other sites older than 2 Ma. Nevertheless, Carbonell *et al.* (2009) suggest that the technology used by Gona hominins, mainly directional and recurrent flaking – repeatedly from the same edge of the core – was systematic and well-mastered. Due to the predominant use of these unifacial, unidirectional methods, these first assemblies only *appear* homogeneous and simple, when in fact they are quite variable. Carbonell *et al.* (2009) go as far as to propose that, due the lack of homogeneity at sites older than 2 Ma, a new technological tradition should be created, which would precede Oldowan and would indeed be characterized by homogeneity.

Finally, later forms of Oldowan are also diverse with some technological innovations being introduced such as bifacial knapping, configuration of small flakes by retouch and standardization of some tools like polyhedrons (Carbonell *et al.*, 2009). This later form of Oldowan characterizes, for instance, the stone technology of *Homo floresiensis* (Moore and Brumm, 2009).

Considering the evidence above, which tell us that those early stone tool makers displayed distinct levels of technological skill, leads to the presumption that different hominin species and even genera could have produced those tools (Delagnes and Roche, 2005; Carbonell *et al.*, 2009). For instance, the only hominin present in Dikika, Ethiopia at 3.39 Ma was *Au. Afarensis*. And so, the most likely responsible for the cut marks found by McPherron *et al*. (2010). Also, Semaw *et al*. (2003) upholds that the 2.5 Ma Gona stone tools should be credited to *Au. garhi*. More, the earliest possible known occurrence of the genus *Homo* in the fossil record dates to about 2.33 Ma and so, the earliest evidence of stone tools cannot, at this moment, be credited to this genus (Kimbel *et al.*, 1996; Prat *et al.*, 2003). In the end, different species of three genera (*Paranthropus*, *Australopithecus* and *Homo*) lived contemporaneously or appeared successively during the time period that Oldowan span, and are potential producers of stone tools. However, it is very difficult to determine the makers with precision because their remains were never found in context with these lithic instruments – with the exception of *Homo floresiensis* and their stone technology and of Hadar AL 666 – (Kimbel *et al*., 1996; Delagnes and Roche, 2005; Carbonell *et al.*, 2009; Moore and Brumm, 2009).

Concluding, a linear technological evolution or a long lasting static Oldowan implies a single tool making species or shared techno cultural traditions with intergroup transmission of technical knowledge, all of which seems most unlikely at this time. So, in front of the evidence of both technological and paleoanthropological diversity, one should expect a mosaic evolution of stone technology with different tool making species, where there is a greater continuity between non-human apes and hominin tool makers than was previously thought (Delagnes and Roche, 2005; Whiten *et al*., 2009). Finally, Oldowan sites are commonly found in association with permanent water and animal bones, some of which exhibit cut marks. This led scientists to believe that these earlier stone tools were used for butchery and bone breaking for access to the marrow.

Also the body parts represented and the presence of carnivore gnawing marks indicates scavenging, as opposed to hunting (Wynn, 2010).

Then, at about 1.7 to 1.8 million years ago, a new species arose in East Africa: *Homo erectus*. This new species expanded rapidly – they can be found in Asian Georgia and Southeast Asia by 1.6 Ma –, continued to rely on meat although evidence for hunting is not conclusive, and learned to use and, maybe, even control fire. It is possible that these changes are due to some cognitive developments associated with cultural developments (Wynn, 2010).

Presumably, *Homo erectus* was the producer of this new stone technology that first appeared at 1.75 Ma (Lepre *et al.*, 2011; Beyene *et al*., 2013). It was named Acheulean and is characterized by the production of an overall two-dimensional shape: the biface. Detaching a large flake from a boulder-sized core, whose edges were then trimmed, made these (Lepre *et al.*, 2011). This stone technology, as the Oldowan, is also commonly described as more or less stagnant over a period of one million years and thousands of kilometres and across a number of varied environmental settings. Nowell and White (2010) defend that this pattern may be the result of poor chronological control, low-resolution signatures and the patchy, palimpsest nature of the data.

These authors recognize that there is an overall stasis in the technological system, but sustain that variation within Middle Pleistocene technology is actually more dynamic than the popular belief. There seems to be a far greater geographic and temporal variability when one views the Acheulean from a continental, regional or site/assemblage scale. If not for any other reason, tools were modified for a number of different reasons, which entails some degree of ‘inventiveness’.

Nowell and White (2010) go on to suggest that some observed stasis did not necessarily relate to cognitive shortcomings but to social or socioeconomic questions. For instance, it is possible that populations were just too small for any innovations to spread, although theoretically, this did not stopped changes into Oldowan and from Oldowan into Acheulean. Another hypothesis is that these tool makers lived a short childhood among small groups with limited number of peers, which would compromise innovative behaviour. A third hypothesis claims that this childhood period could have led to a standardization of material culture across generations. Where youngsters learned specific stone tool techniques and continued to apply them in adulthood without change.

Later, sometime between 500 and 200 thousand years ago, modern cognition must have evolved but unfortunately this is one of the most complex periods of human history to understand. Starting from before 500 Ka, hominid fossils diversified, leading to a diversification of clades exhibiting ever increasing modern anatomical features (Schwartz and Tattersall, 2010; Wood and Baker, 2011). Behaviourally, this time period is also characterized by a number of innovations, although it is not possible to observe complete modern human behaviour – art and burials are lacking, for instance – (Wynn, 2010).

On stone tool accounting, this was a time of great change. One of the main innovations was Levallois, which is not a type of stone tool but a reduction procedure, where a core is prepared for the ultimate removal of one or several flake blanks, which then may or may not be further modified (Wynn and Coolidge, 2004). Although there is no need for a final image of the flake, Boeda (1995) as argued that a "volumetric conception of the core" should be present (*in* Wynn and Coolidge, 2004: 474).

Wynn and Coolidge (2010) sustain that Levallois is proof of increased expertise of their toolmakers. Within the working memory model, these authors defend that, by this time, retrieval structures had evolved, either by increasing long-term memory capacity, speed of access or working memory capacity – the amount of information one can held in attention and process simultaneously. Nevertheless, not depreciating the complexity of core preparation techniques, the clearest inferences for spatial cognition can be made through bifaces.

Here, three novelties can be seen. First, some of these later bifaces show signs of congruency, i.e. mirroring sides are not just qualitative reversals, but quantitative duplicates, as far as possible. Second, three-dimensional symmetry appears, that is bifaces showed symmetry in plan, profile and cross section. Third, broken symmetry appears where an initially symmetric object is altered into a non-symmetrical shape that still maintains a regular shape. It must be pointed that not all bifaces found show these signs, some quite crude artefacts are also produced (Wynn, 2002).

2.9. Handedness

A final important feature relevant to spatial cognition and that can translate in the archaeological record is handedness, which strongly relates to brain lateralization. Due to the specificity of this subject, all the information concerning it is included in this single chapter.

Human hand patterns can be characterized as complementary role differentiation (CRD). In this model one hand executes high frequency tasks, involving finer temporal and spatial resolution, while the other hand performs low frequency tasks, such as supporting an object. This means that both hands have different but equally important and complementary roles. In this context, right and left-handed refers to the hand that adopts the high frequency role (Uomini, 2009). A hand preference appears to emerge quite early in human development. In fact it may appear as soon as voluntary grasping, between seven and thirteen months of age (Kimmerle *et al*., 1995; Fagard, 2009; Uomini, 2009). Also, a bias for right-handed CRD pattern is found at the species level in modern humans (Llaurens *et al*., 2009).

When looking at apes, one finds that individuals often have task-specific hand preferences, while populations can be right-handed, left-handed, evenly divided between the two or comprised of ambidextrous individuals (Fletcher, 2006; Hopkins, 2006). This, obviously, means that no species level of handedness can be found in apes. Interestingly, the tasks that elicit the strongest laterality are usually related to manual skill, tool use, bimanual complementarity, or sequence length (Uomini, 2009). It seems that the sorts of tasks that usually exhibit handedness are the most *complex* ones. Uomini (2009) includes these tasks within the framework of complexity as defined in prehistoric activities: the execution of elementary gestures through physical motor know-how and the realisation of the chaîne opératoire, through operative ideational know how.

Unfortunately, evidences of handedness in the archaeological record are hard to proof. Handedness markers can be found in material culture from the actions of lateralised tool manufacture and use that leaves traces on objects, and in fossil skeletal asymmetries resulting from asymmetric use of the upper limb over an individual’s lifetime (Uomini, 2009). The most robust evidence for population level handedness in prehistory belongs to Neanderthals (Cashmore *et al*., 2008). However, Toth (1985) suggest that handedness could have been present as early as 1.9 to 1.4 Ma. This means that handedness could have been present since *Homo habilis*. His method, however, has not been validated, and so there is no certainty of the results (Uomini, 2009).

At this point, one should, once again, consider Stout *et al*. (2008) results, where bilateral brain activation in expert Oldowan tool makers and Acheulean ones support a right-hemisphere-left hand system in handaxe production. This could support the evolution of the CRD model, where the role of support of the left hand played an important role on the evolution of handedness. This also implies that tools may have played an important role in the evolution of handedness and, consequently in the evolution of brain lateralization with language and handedness on the left hemisphere and visuo-spatial cognition on the right. Interestingly, if one agrees with Uomini (2009) and Cashmore and colleagues and supports that Neanderthals were right-handed, then it is possible, although the proof is indirect, that they possessed the cognitive mechanism for language.

2.10. Stone Tools and the Evolution of Spatial Cognition

Stone tools are one of the few ways one has to access early human minds. In the centre of this debate is the interrogation of whether stone tool is a result of, or a stimulus to a more flexible intelligence. These are not mutually exclusive (Grove and Coward, 2008).

The changes seen in the archaeological record leads to the conclusion that there must have been selective pressures that stirred new, if subtle cognitive skills. These don’t need to have appeared abruptly, but could have been the result of cumulative changes through time. Through the analysis of the stone tools produced by early hominids, it is possible to make some inferences about the cognitive abilities of their makers. Always taking into account that what one searches to infer is the *minimal* skills that these people had to possess to produce such artifacts (Wynn, 1985).

Here, it will only be included the inferences that can be made concerning spatial cognition. First, some hypothesis by different authors will be considered and then, these will be analysed in light of the literature review gathered above. Some of this hypothesis will be directly related to spatial cognition, but some consideration from other relevant theories will also be considered.

Thus, according to some authors, there seems to be no hominin-specific cognitive demands to produce Oldowan tools. These tool makers were able to direct action on the spatial field of an object, following a spatial boundary – applying blows on both sides of a boundary –, using proximity –applying blows one next to the other – and even ordering action in space. But the spatial repertoire of apes also includes these abilities (Wynn and McGrew, 1989). It is possible that there was some improvement in the detection of *flakeable* edges on cores, but has far as spatial cognition goes, this is as much as can be said. In fact, it is possible that other apes are not performing as these early hominins due to bio-mechanical constraints, like the shape of their arms and shoulders, or because there are no ecological demands to do so. In which case, it is an anatomical rubicon that had to be overcome and not a cognitive one. So “the Oldowan was not a new adaptive grade but a variation on an old one” (Wynn *et al.*, 2011: 195).

Here, one must point out that, on the other side of the argument, some researchers claim, that Oldowan stone tool makers indeed had a sophisticated understanding of stone fracture mechanisms, namely conchoidal fracture and a high level of motor control, not seen in apes (Semaw, 2000; de la Torre, 2010). Also, variability in late Oldowan in above mentioned sites such as Lokalalei 2C and Gona testify for a more complex scenario in Oldowan, than the previously thought stagnant one.

De la Torre *et al.* (2003) goes so far as to state that the late Oldowan tools found at Peninj – estimated to be about 1.6 Ma-1.4Ma – exhibit a knapping that indicates planning and template structuring, whose subjacent cognitive abilities, technical knowledge and manual dexterity equalled the ones necessary to produce Levallois tools. More than cognitive skills implied in later changes in Oldowan, de la Torre (2010) still defends that early stone tool assemblages – dated to 2.6-2.5 Ma – already show a good technical control of concepts, principles and methods associated with the mechanisms of conchoidal fracture and, so, show a mastering of the basic principles of stone flaking and an exponential qualitative leap over the use of tools by other animals.

If one assumes that ape spatial thinking was enough to enable these early hominids to carry on their activity, when one considers the increasing amount of evidence for flexible ape use of tools, then one must realize that for a long period of time no major evolutionary developments occurred in spatial cognition.

Then, according to the theory most developed by Wynn and colleagues, at around 1.5 Ma, something changed (Wynn, 2010; Wynn *et al.*, 2011). Early Acheulean tools, in fact, strongly resembled Oldowan's. With the exception of one new tool: the biface (Wynn, 2002). Bifaces exhibit one characteristic that is essentially novel. They are tendentially symmetrical. Davidson and Noble (1993) argue that biface shape is simply a bi-product of the application of a bifacial technology and Asthon and McNabb (1994) assert that it is no more than a function of raw material (*in* McPherron, 2000). However, most archaeologists believe the symmetry was intentional. They present three main supporting arguments. First, the most symmetrical examples are also the most trimmed, as there was more time devoted to production. Second, on some bifaces the trimming mirrors a natural shape on the other side. Third, symmetry brings no functional benefit for butchery, which is seen as the most likely purpose of stone tools (Wynn, 2002; 2010).

These authors claim that this new development – the imposition of shape on objects – represents the first clear indication of an evolutionary step away from an ape-like spatial cognition. Wynn (2010) suggested that a possible explanation for this change consisted on a coordination in the visuospatial sketch pad – within the working memory model – of two previously separate neural pathways: shape recognition and spatial cognition. In other words, *Homo erectus*, was the first to, not only recognize symmetry, but to consciously apply it to exterior objects.

Finally, Wynn suggests a new cognitive innovation in spatial cognition at around 500-200 Ka. This innovation is not made based on the Levallois flaking techniques but on novelties seen on bifaces, described on the prior chapter. As also explained above, Wynn and Coolidge (2010) see the Levallois technique as a consequence of improvements in cognitive skills related to expertise, and not to spatial cognition.

The cognitive requirements of innovations seen on bifaces imply two new spatial abilities. On one hand, the three dimensional symmetry calls for perspective coordination, in which the knapper would be able to coordinate perspectives in order to bring to mind points of view that are not readily available, such as cross-sections. That is, these hominins developed mental rotation. On the other hand, these stone tool makers should have some perception of space quantity in the notion of shape. In other words, knappers perceived, imagined and worked with spatial quantity in a shape (Wynn, 2001; Wynn, 2002; Wynn, 2010).

It seems that these hominids could manipulate perspectives, produce congruent symmetries and even distort these principles, if wanted. This indicates that they had a Euclidean understanding of space, where the surrounding universe is perceived in a three dimensional fashion. Thus, they had developed the cognitive mechanisms that enable them to use this conception to control their action, imposing shapes on the exterior field of action (Wynn, 2002; 2010). This author attributes this change to a possible enhanced capacity of the visuospatial sketch pad or to a nascent phonological loop where shapes and images could be held and processed as semantic, declarative categories. He even suggests that the visuospatial sketch pad preceded the phonological loop, presumably associated with the emergence of language.

So, according to Wynn (2010), two major leaps can be inferred from the archaeological record. The first occurred at around 1.5 Ma and relates to coordination of spatial cognition and shape recognition. The second is placed after 500 Ka and encompassed coordination of mental rotation and size constancy into a Euclidean understanding of spatial relationships.

Moore (2010), on the other side, presents a theory, where stone tools are by-products of *action grammars* that track the evolutionary history of hominin cognition. *Grammars of action* reflect the basic similarity between speech structure and motor skills in human infants and primates. This ontogenetic model was initially developed by Greenfield (1991), where she links developmental changes in brain anatomy with changes in the hierarchical organization of speech and motor skills. Greenfield (1991) identifies three strategies for ordering motor actions in human infants: 1) pairing strategy – where a single active object acts on a single static one to create the final structure, involving a one chain-like combination; 2) pot strategy – where multiple active objects act on a single static one to create the final structure, involving longer chains combinations; 3) subassembly strategy – where multiple active subjects are combined to form a subassembly, which is in turn combined with a static object or another subassembly to create the final structure, involving an hierarchical two-level combination.

These strategies are related to the way children organize nested cups and emerge sequentially between eight to twenty months. This progression is similar to the way children combine sounds and words. Then, at about two years, the way children combine objects diverge from the way they combine words and sounds. At this point in development, complex syntactical rules have no analogues in motor actions and new grammars of action have no analogue in linguistic grammars.

While studying primates, Greenfield (1991) concludes that the pairing, pot, and a rudimentary version of the subassembly strategies, with the overlapping neural wiring for action and linguistic grammar, were shared by the last common ancestor and allowed language and tool use to coevolve, through shared brain structures, leading to an expansion of the prefrontal cortex and stimulating an increase in hierarchical combined motor actions. Moore (2010) proposes, following Greenfield's model, that changes in early stone flaking should reflect the evolutionary development of an action grammar through subassemblies and combinations of subassemblies of ever-increasing complexity.

Given this, Moore (2010) proposes his model of the 'design space' of knapping. According to this model, knapping began in prehistory with the serial combinations of basic flake units. This basic flake unit is the result of multiple actions carried out sequentially on the static object, Greenfield's pot strategy. The key breakthrough here was probably ideational, based on the simple algorithm 'identify high mass → apply flake unit', and it most likely emerged early in hominin history. A subsequent evolutionary step involved adding a second layer to the basic flake unit, creating the complex flake unit. The complex flake unit reflects the recognition that platform arrangements could be modified by anticipatory flaking on the observed core face prior to removing the objective flake from the reverse face.

This was further elaborated by the addition of another layer of complexity to grind platform edges. This relates to Greenfield's subassembly strategy. Complex flake units were in place by late Middle Pleistocene and elaborated flake units by the Late Pleistocene, although Moore (2010) recognizes that it is possible that both were used to produce Acheulean handaxes. This author defends that subsequent innovation in lithic technology steam from the development of ever-more complex hierarchical arrangements of flake units. This study is quite interesting because, although it does not address spatial cognition directly, it points to an evolution in cognition that relates to increased complexity through integration of simple thought processes in multiple chain reactions.

There are many more studies that link spatial cognition with higher cognitive abilities specifically language, as already discussed. Such an example is the previously discussed study conducted by Stout and co-workers (2008), where it is shown, through positron emission tomography (PET) scans, conducted in both novice and expert modern toolmakers, that the neural circuits supporting Oldowan and Acheulean tool making overlap language circuits, suggesting that these behaviours share foundations and that they are "likely to have evolved in a mutually reinforcing way" (Stout *et al.*, 2008:1947).

Arbib (2011), in turn, argues that Oldowan tool making corresponds to a simple imitation and ape gestural communication, and that Acheulean tool making parallels with complex imitation and protolanguage, whereas the explosion of innovations in tool making and social organization of the past 100 000 years correlates with the emergence of language.

Uomini (2009) also brings an interesting suggestion to the table, proposing that the execution of elementary gestures takes place through physical motor know-how, which involve implicit learning and are responsible for precision and accuracy, while the realisation of the chaîne opératoire, or sequence implies operative ideational know-how. This seems to relate to the procedural and declarative long-term memory discussed on Baddeley's model above.

More related to spatial cognition, Gentner (2007) also suggests that humans begin, during child development, with an ape-like spatial reference frame and diverge later owing to the influence of language and culture. It is suggested that the early divergence of human from apes could be related to different experiences with objects. Besides, it is also possible, according to this author that noun learning drives the early shift from coding by location to coding by object features and that the learning and entrenchment of relational terms drives the shift from an allocentric to a language-consistent bias in frame of reference.

Langbroek (2012) also makes a fascinating suggestion when he states that in Pleistocene Europe, the producers of European Acheulean – presumably *Homo* *heidelbergensis* – and Late Pleistocene Neanderthals employed mobility systems that involved the creation reconstructed of pre-planned itineraries through the landscape, but without evidence that these originated in a *central place*. This author claims that these individuals moved from one sleeping local to another sleeping local on a near daily basis along itineraries during which they procured material resources and food resources in a spatio-temporal planned fashion.

This model was based on aspects of their lithic technology and raw materials management, which were tied into that mobility strategy, with the creation and employment of a transported core/tool component, extending and fluidly evolving along the chosen itinerary. According to this author, this mobility system is unknown among either modern hunter-gatherers, or extant apes. The intricate ways in which raw materials procurement, tool creation, fluid change of tool character and tool use are embedded within these itineraries, attest to a complex cognition, resulting in complex behaviour of a unique kind. More exactly, it is possible that these individuals possessed some particular form of spatial cognition. Studies such as this, although extremely provocative, are very difficult to reproduce in other contexts, where spatial-temporal sequences of action are hard to retrace.

3. MATERIAL AND METHODS

The method used was a literature review. As such, the material used consisted of papers searched using databases sites such as Web of Knowledge® and B-On®, as well as relevant books and publications found on University of Coimbra’s libraries. The methods included search by relevant key terms or by significant authors of the field. Also, many articles were read under guidance of supervisors or other investigators whose advice was invited, following a request for personal article. The results from the literature were then compiled and led support to a framework for the evolution of spatial cognition in the *Homo* lineage. Following, appropriate methods to test this framework were researched, giving rise to the proposed methodology in the next chapter.

4. RESULTS

4.1. Proposed Framework

Taking all of this into account, one can now turn to the initial hypothesis of if child cognitive development can somehow retrace the evolution of spatial cognition.

On a general take, it’s hard to believe that cognitive development can retrace spatial cognition evolution *exactly*, due to problems of mosaic evolution. However some trends can be pinpointed.

Even looking at ape’s spatial cognition, particularly that of chimpanzees, it seems that at least some rudimental form of all of the spatial processes seen in humans are already present. What seems to differ between apes and humans is the *integration* of cognitive processes.

On navigational skills, it seems that early hominins, just as their fellow apes, could have begun with predominately allocentric thought processes, although egocentric perspectives were possible when demanded. Later, there was an improvement in the integration and use of spatial systems, such as the one seen in children. At around the same time, or even earlier, hominins begun to integrate geometric and non-geometric information, as well as to use several landmarks, as opposed to only one.

This gives way to a scheme where navigational skills in hominins evolved through *gradual* integration of spatial traits that, in the end, enabled them to explore their environment much more efficiently, simply by being aware of greater spaces around them. It is possible that the selective force behind this was feeding ecology, just as Rosati and Hare (2012) proposed. The greater reliance on meat, through scavenging, and later, on hunting, could have given rise to a positive feedback loop where the better navigational skills allowed better scavenging/hunting skills, by allowing them to track migratory routes, for instance, and increased scavenging/hunting skills further stimulated evolution of navigational skills. Although Wynn (2010) defends that consistent hunting has not existed for a time period long enough to act as a selective force – for sexual differences in spatial cognition, it his paper –, scavenging may require similar spatial cognitive skills – in tracking herds, for instance – and has been in place long enough to act as a selective force.

Also important would be the brain evolution consequences of a greater reliance on meat. The most plausible cognitive innovation follows the model proposed by Wynn (2010) and consists in an increase in working memory capacity, which allowed individuals to hold and process more information in attention at the same time, resulting in integration of allocentric and egocentric perspectives and of geometric and nongeometric information and on reliance on more than one landmark. On the other hand, an increase in long-term memory capacity is also likely, considering that individuals might have to recall different locations not visited for long periods of time – in a somewhat similar way to elephants.

Interestingly, this development in integration of navigational skills might have been what allowed hominins to explore new territories and to expand beyond Africa, maybe even leading to unique forms of mobility such as the one proposed by Langbroek (2012) for *Homo heidelbergensis* and Neanderthals. Better forms of communication and later language could also have played a role, by allowing individuals to communicate about the way to follow prey, or the way to return home.

A key aspect of this process is that it was gradual, and as such, it would be very hard to pinpoint a specific hominin or a specific time when modern navigational skills came to be. Nevertheless, according to current archaeological data, and crossing information with Wynn's proposal (2001; 2002; 2010), it may be safe to assume that at least an incipient form of these navigational skills were already in place by 1.7 million years ago, with the appearance of *Homo erectus*, the first hominin to leave Africa, whom also exhibited signs of a greater reliance on meat and a larger home range (Aiello and Wells, 2002; Antón *et al*. 2002; Antón, 2003). Adequate methodology for this will be discussed ahead.

On object representation and manipulation a scheme of integration of cognitive skills also emerges. This is the theme of most interest, since its implied cognitive skills are the ones with most significance in stone tools. The first such integration would be between categorical and metric information. As discussed in the chapter Spatial Cognition in Humans this could take place through an increased memory for metric information, allowing individuals to retain such information for a longer time in attention, and/or through the development of a hierarchical coding system, which integrates metric and categorical information (Sandberg *et al*., 1996; Newcombe and Huttenlocher, 2000).

The second important innovation would be the advent of mental rotation, which implies the ability to integrate several view-points simultaneously. Once again this seems to fit with the model proposed by Wynn (2002; 2010), where the integration of shape recognition and spatial cognition corresponds to the integration of metric and categorical information. Hominins integrated the ability to recognize metric cues on a shape with the ability to impose these metric cues on a categorical space. The only point to add to Wynn's hypothesis is that this process took place not only through coordination of two neural pathways within the visuospatial sketchpad – in other words through a hierarchical coding system –, but also, through enhanced metric memory.

The second change also translates directly into Wynn's model, who suggests that coordination of mental rotation and size constancy into a Euclidean understanding of spatial relationships. The improvement in mental rotations in human children relate to exposure to object manipulation. It is possible that the increasing importance of tools in hominin lifestyle led to the positive-feedback development of mental rotations, through enhanced capacity of the visuospatial sketchpad or through enhanced working memory, which allowed holding different points of view in attention simultaneously. Wynn (2002; 2010) also proposes that a nascent phonological loop could have played a role in this process. That is, language, by allowing individuals to communicate about objects, might have allowed them to develop spatial skills related to them. Moreover, the improvement of navigational skills most likely also played a role in the ability to understand spatial relationships in a Euclidean framework.

Considering all of the above, and based on current archaeological data, crossed with Wynn's model (2001; 2002) a framework emerges where the advent of Oldowan at 2.5 Ma doesn't indeed imply for any special spatial cognitive skills. Perhaps the key breakthrough was ideational, based on the simple algorithm 'identify high mass → apply flake unit', just as proposed by Moore (2010). Following this, the emergence of the Acheulean at 1.75 Ma implies the coordination of metric and categorical information discussed above. Then at about 500 Ka, mental rotations in a Euclidean framework appeared leading to the changes in the archaeological record described by Wynn. Once again, methods to test this hypothesis will be included further ahead.

The developmental science doesn't seem to give any sort of information on the Levallois technique, although it is likely that mental rotation was required to produce these objects. The only possible connection consists in that the development of navigational skills most likely contributed to the increase of both working memory capacity and long term memory capacity.

The main difficulty in this image is to identify selective forces behind these changes. It is possible that they were the result of cumulative changes that, once a certain threshold was surpassed, led to a new technology. Another possibility is that stone tools themselves were an evolutive drive, which, once again through a positive feedback loop led to the successive appearance of new technologies.

On the other hand, it is also possible that completely different aspects came into play. For instance, an important step in cognitive evolution took place when hominins were able to surpass the ape pattern that prevented them to integrate social rules in the context manipulation, giving place for active teaching and for an increased role of socialization within stone tool production. Interestingly, this would require an enhancement of working memory capacity, since the handicap in apes seems to be that they are unable to hold the demonstrator and the object in attention at the *same* time. The most likely scenario is that all the above are true, giving rise to a true complex view of cognitive evolution.

4.2. Proposed Methodology

At this point, a methodology capable of testing the proposed framework is required.

First, when studying stone tools, or more exactly when trying to study a new approach/method for analysing stone tools, one must came to terms with the complex picture of such objects that the archaeological record can yield. Concerning the stone tool analysis, the Fig. illustrates the diversity of artefacts derived from an original stone that one can finds in the archaeological record.

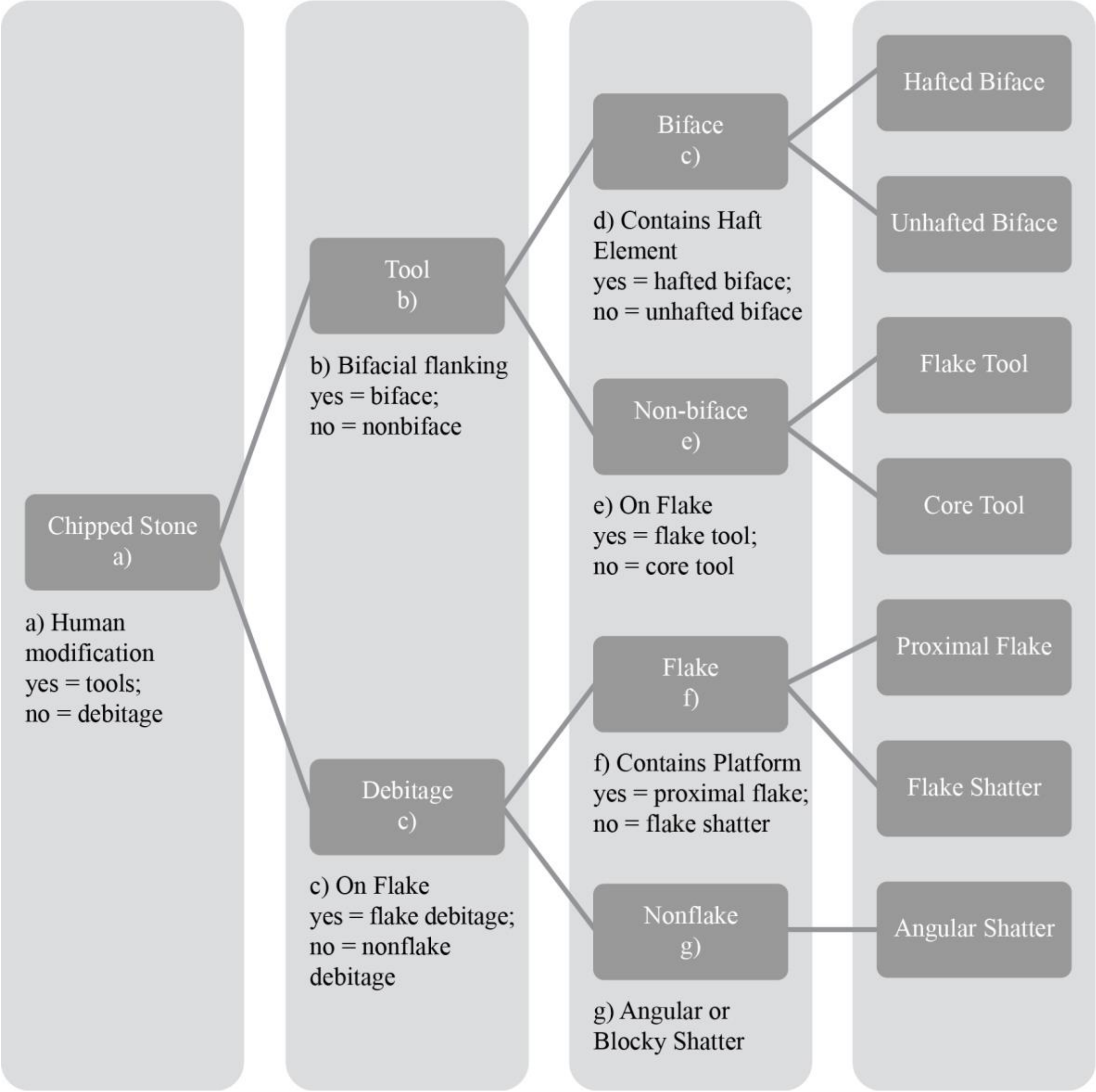

Fig. 3. Generalized morphological typology for chipped stone tools adapted from Andrefsky (2005). There are further subdivisions on this flow chart, according to additional refinements of classification, but these were not included for graphic clarification. They will be discussed when deemed necessary.

From the stone artefacts depicted above, this study focuses on stone tools, as mentioned numerous times. Inside tools, hafted pieces will also be disregarded, since hafting, although a technological revolution does not imply a spatial cognition innovation and are, by standard, relatively recent in the archaeological record (Wynn, 2002; Wadley *et al.*, 2009).

Considering that there are a number of factors that influence the range of stone tool types found in a given archaeological site, methodology will have to be adjusted according to artefacts provenience site and known deposition story. For instance, it has been shown that raw material abundance, quality and size play a major role in the technological procedure used. Even the lifeway of the hominin population has been shown to play a role. Using an example, there seems to be a preference for bifacial cores in mobile populations. Bifacial core have detached pieces from several directions in both faces of the specimen. This preference is consistent with the idea that mobile populations favour tools that are multifunctional, readily modifiable and portable, decreasing the uncertainty risk (Andrefsky, 2005).

There are, however, some general definitions of tool types and some descriptive measures that can be used as a first approach to stone tool analysis. The items here included were based on the book by Andrefsky (2005) "Lithics – Macroscopic Approaches to Analysis".

The first tools to be considered are cores. Cores can be considered primarily as objective pieces that are used as raw material source, although other functions might be possible. They represent the end product of a sequence of objective piece preparation, reduction of detached pieces and continued preparation and reduction. There are two main categories of core tools. The unidirectional cores usually have a single striking platform (or flat surface), from where pieces are detached in one direction. On multidirectional cores, on the other hand, the removal of flakes is done in more than one direction and, therefore, using more than one striking platform.

The second tool type, flakes, show evidence of modification either by intentional retouch of edges or from use wear along the margins and tend to have only two primary surfaces: dorsal and ventral. Functional requirements, tool use life and raw material differences are the three main causes of the wide range of variability seen in flake tool morphology, making it difficult to create extant categories of classification.

Biface tools can be defined as pieces with two sides that meet to form a single edge that circumscribes the entire artefact. Bifacial production is usually seen as comprising five stages, the first being the blank; the second, the initial edging, which produces an irregular bifacial edge that has few flake scars removed past the center of the piece; the third consists mainly on the thinning of the biface, where humps, ridges and previous step fractures are removed; the fourth stage includes the secondary thinning of the biface, when stage flake scars may be patterned and striking platforms are prepared by grinding; finally, fifth stage is the final shaping of the biface before notching or hafting. However, some authors do not recognize actual stages of bifacial production and instead conceive it as a continuum from raw-material acquisition to a final product (Muto 1971 *in* Andrefsky, 2005).

Table 1. Common descriptive features of stone tools and their formulas, according to Andrefsky (2005).

Description Features	Formula	Notes
Cores		
Weight	—	—
Maximum Linear Dimension	greatest linear dimension × weight	other measurements are hard to define but not greatest linear dimension; provides uniform measure of size
Flakes		
Maximum Length	straight line distance from the proximal to the distal end of the flake (perpendicular to the wide axis of the striking platform – at the center)	only for whole or unbroken pieces
Maximum Width	straight line distance perpendicular to ML (intersects the flake at its widest point)	
Maximum Thickness	distance from the dorsal to the ventral side of the flake (perpendicular to length)	
Weight	—	both whole and broken pieces
Size	ratio that relates two measurements (e.g. length and weight); diameter of the circle objects fit into	
Tool edges	number, localization, outline morphology, edge angle and edge length	proximal end oriented downward; ventral surface facing the observer
Bifaces (non-hafted)		
Maximum Length	distance of line perpendicular to pattern of flake scars across surface	common organization by reduction stage (but some authors defend production as a continuous process undividable into stages)
Maximum Width	distance from one lateral edge to the other (perpendicular to length)	
Maximum Thickness	distance from one surface to another (perpendicular to length)	
Weight	—	
Size	ratio that relates two measurements (e.g. length and weight)	

Table 1 includes descriptive general features of stone tools, according to Andrefsky (2005).

The descriptive features included above do not permit to take any direct cognitive inferences concerning spatial cognition. However through them, it is possible to compare lithic instruments in a way that could allow for inferences. More exactly all approaches used with cognition in mind must rely on a reconstruction of the steps that lead to the production of any given lithic instruments (Wynn, 1985; 2002, McPherron, 2000; Stout *et al.*, 2008). It is by analysing these consecutive changes that is possible to infer the cognitive abilities needed to perform such tasks.

Based on cognitive development, the previous chapter draw a picture where one would expect stone tools to first exhibit integration of metric and categorical information. This could show in the archaeological record through one dimensional symmetry, once again just as suggested by Wynn (2001; 2002). Three-dimensional symmetry should not be expected, considering that complete perspective coordination is only expected to arise later through evolution of mental rotation. This second type of symmetry could be related to overall regularity of the object. In other words, once this cognitive skill was in place, one should expect for roughness of artefacts to decrease and, so, for regularity to increase, given a stronger concern with the overall shape of the object.

One dimensional symmetry and roughness – as indicative of three-dimensional symmetry – can be measured quantitatively through a new method proposed by Saragusti *et al*. (2005). The quantitative approach is very important because it allows to compare different collection with different spatio-temporal differences with a lower degree of errors. Qualitative approaches on the other hand, although important on the general description of the sample are usually ambiguous and too dependent on observant judgement. Saragusti *et al*. (2005) use mathematical methods for the analysis of curves to study different artefacts. They propose a family of functions that store the entire information about the curve associated with the artefact. However, each function emphasizes different features by giving them more weight than others. The choice of function should be dictated by the specific application/problem in question and on the features of the curve that are of relevance. This is where archaeological considerations and constraints play a role.

Briefly reviewing Saragusti *et al*. (2005) method, one starts by defining a curve in the plane by providing the coordinates of each point on the curve $\big(x(s), y(s)\big)$, where s denotes the arc-length along the curve. As the parameter s changes, the point moves along the line. So, each artefact is represented by a single curve of length L that does not intersect itself. From this initial premise, Saragusti *et al.* (2005) deduce four different representations of the curve: the Cartesian, the polar, the tangent and the curvature representation. The Cartesian and the polar representations provide the large-scale features of the curve. A small indentation that changes the curve locally will appear as a small perturbation in these representations. The tangent representation depends more strongly on local features, and so, local changes of the line will show up. Finally, the curvature is very sensitive to local variations. The features of the line that provide information on the gross properties of the curve will be hardly shown.

Addressing mirror symmetry or one-dimensional symmetry, these authors define that a curve in the plane is symmetric if there is a line – symmetry axis – that divides the curve into two parts, which are mirror images of each other with respect to the symmetry axis. What they look to measure is the value of the minimal difference from perfect symmetry for a given object, which means their method provides a measure of *asymmetry*. In application to a sample of handaxes, these authors use the tangent representation, since this type of representation is medium-sensitive to changes in the curve and the general appearance of the line is an important factor. Here, the residual differences in the formula provide the deviation of the shape from perfect symmetry. They found that the mean, as well as the standard deviations of the asymmetry values tend to decrease over time in their sample, just as proposed by the literature.

In their paper, Saragusti *et al*. (2005) define regularity as a measure of directional changes in the object's surface in three dimensions. Analogously to the method used for mirror symmetry, their method, to establish regularity, quantifies the degree of concavity of an object's contour. In other words, the smoothest curves on objects are usually convex and so roughness can be determined by the frequency and amplitude of the transitions between convex and concave sections along the curve. In terms of the curvature function, the concavity can be defined as the sum of all the deflection along concave sections. An important element to take into consideration is the scale, since roughness is a relative term, and it depends on the scale at which it is defined and measured. A given curve may appear smooth on one scale and rougher as resolution increases. This is important for comparative studies, where the same scale should be used. An appropriate scale should filter all oscillations deemed too small and leave those of interest. When analysing the same sample used in the symmetry test, these authors found a similar trend of reduction in mean levels and standard deviation levels of roughness.

Saragusti *et al.* (2005) did not explore an asynchrony in timing of increase in symmetry and decrease of roughness, but it would be of interest to see if this trend is found on larger samples of tools, representative of several tool making periods, since it would testify for the different time periods of spatial evolution proposed on this essay.

Although not mentioned on the proposed framework, handedness may be an important factor for spatial cognition since it testifies for brain lateralization and its consequent division between hemispheres and spatial and linguistic cognition, among others. So, this trait would not testify for spatial cognitive skills *per se* but to an increased brain lateralization, which in turn, constitutes proof of a more complex brain organization and increased specification of spatial skills. Despite the somewhat circular reasoning, it would be helpful to determine when did handedness arose in the archaeological record.

However, it is very hard to identify proofs of handedness on stone tool analysis. While studying Oldowan and Acheulean flakes from Koobi Fora (Kenya), Toth (1985) created a method that is based on the preferential direction of flaking along the perimeter of the platform during single-platform flaking for the production of Karari scrapers (a type of core scraper). Through his own replications of the process, Toth (1985) concluded that right handers prefer to flake to the right of previous removals and left handers prefer to flake to the left of previous removals. Uomini (2009), however, criticizes that, if each flake is determined by the previous one, this would mean that all the flakes knapped from a single platform core should constitute one single data point. But this is usually very hard to find in the archaeological record due to difficulties of core reconstruction, considering time changes on the record. Considering this, the method requires further validation in order to be applicable to other collections.

Another possible approach to determine handedness is the Cone of Percussion method developed by Rugg and Mullane (2001). These authors carried out an experiment with four left-handed knappers and four-right handed ones and found strong correlations between the direction of skew in a flake's cone of percussion and its knapper's hand preference. When applying this method to lithic instruments, they found a weak bias towards right skewed flakes. There were some problems with this method, namely 67% of flakes were unscorable. Nevertheless, this method could be extremely useful as a universally applicable tool for determining the ratio of right- to left-knappers in all industries that contain flakes, including the earliest knapped stone. By applying it to large samples, a general picture of the evolution of handedness could arise (Rugg and Mullane, 2001; Uomini, 2009).

In summary, to study possible evolutive changes connected to the development of spatial cognition in the archaeological record, one would have to, first, gather several samples spanning most of the period of hominin evolution. It would also be of interest to span a vast amount of space. In other words, to consider samples from several continents. Nevertheless, this first attempt concerned itself with evolution on the African context and, as a result, only samples from this origin should be considered at first.

The second step of analysis would be to analyse the sample as to their general descriptive features, in order to support or disclaim future allegations on parallelisms.

The third and most important step would be to study mirror symmetry and roughness on the sample, through the method developed by Saragusti *et al.* (2005), followed by the study of handedness on flakes using the method developed by Rugg and Mullane (2001).

Only after the completion of this steps could one have some verification, or disclaim, of the framework of evolution of spatial cognition through first, integration of metric and categorical information, and then through mental rotation.

On the account of navigational skills, these would be very hard to test, if not impossible exclusively using stone tools. A thorough study of the patterns of occupation in Africa during significant time periods would be more useful. This is very difficult to do, considering that the spatial patterning across a landscape is severely disturbed by taphonomic effects, as already discussed, and that there is a lack of systematic study of the African territory. This them is also beyond the scope of this Thesis.

5. DISCUSSION

Following advice by Humphrey (2011), the three main questions to be answered by the literature review are: What is (are) the existing theoretical framework(s) most prevalent in this research space? How can the existing research be organized? And what are the next steps for this research space? In order to answer the first question, an as complete as possible compilation of all research relevant to the topic underhand was gathered on the chapters above. Next, to achieve the second goal, a framework was created to help make sense of the literature and a methodology to study such framework on the archaeological study was proposed. Finally, the third question aims to recognize the limitations of existing research and identify potential space and underexplored fields to where the literature should proceed (Humphrey, 2011). The present discussion addresses this last question.

To begin with, one must understand the current raise of 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 on this thesis.

In fact, the initial proposal that human development could retrace human evolution seems to recall 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 where 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, but also many of the transduction pathways. Moreover, in different organisms, these pathways are composed of homologous proteins arranges in a homologous manner. 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.

However, it is quite naïve to think that human spatial development retraces human spatial cognition evolution exactly, mainly due to the problem of mosaic evolution. 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.

Concerning the results of this Thesis, taking into account all of the available information on cognition, spatial behaviours, development, evolutionary pathways, lifestyles and selective forces, a general framework emerged, where different steps in the evolution of spatial cognition take place.

Actually, when taking into account the literature review, the first step in the evolution of spatial cognition could have taken place before the beginning of the *Homo* lineage. It would have been brought upon by an increased terrestriality and/or sociality. This aspect should be present on the last common ancestor between humans and chimpanzees and might have led to an increased long term memory, in order to keep track of interspecific interaction and/or of food locations. This is would be similar to what Hribar and Call (2011) proposed for the outperformance of orangutans by chimpanzees and bonobos. It would be interesting to test this hypothesis considering archaeological data on future studies.

Following this, the advent of Oldowan itself at 2.6-2.5 Ma doesn’t indeed imply for any special spatial cognitive skills. Perhaps the key breakthrough was ideational, based on the simple algorithm ‘identify high mass → apply flake unit’, just as proposed by Moore (2010).

On the other hand, the emergence of the Acheulean at 1.75 Ma may imply the coordination of metric and categorical information discussed above, which would allow hominins to start applying shapes to objects, leading to the appearance of the first mirror symmetries. This would be accomplished through an increased memory for metric information and/or through the development of a hierarchical coding system, which integrates metric and categorical information – allowing individuals to retain such information for a longer time in attention – (Sandberg *et al.*, 1996; Newcombe *et al.*, 2013).

Then, at about 500 Ka, a third change took place, which consisted on the appearance of accomplished mental rotations in a Euclidean space that allowed for the appearance of three-dimensional symmetries. This could have taken place through enhanced capacity of the visuospatial sketchpad – due to a nascent phonological loop – or through enhanced working memory, which allowed to hold different points of view in attention at the same time.

The developmental science doesn't seem to give any sort of information on the Levallois technique, although it is likely that mental rotation was required to produce these objects. The only possible connection consists in that the development of navigational skills most likely contributed to the increase of both working memory capacity and long term memory capacity.

This brings us to the subject of navigational skills. Most of the above changes concerned inferences on object recognition and manipulation, but the other important side of spatial cognition, navigation has also evolved. Although it was not the original goal of this study, since it's hard to infer navigational skills from stone tools characteristics, although their distribution through space and time could give important clues, forms another future avenue of study. As already discussed, this approach faces the problem of serious taphonomic alterations on the archaeological record and of the lack of consistent studies of territories at the present moment.

Based on the literature reviewed here, it would seem that early hominins begun with allocentric thought processes – although egocentric perspectives were possible – and then proceed to integrate both spatial systems. At around the same time, or even earlier, hominins begun to integrate geometric and non-geometric information, as well as to use several landmarks, as opposed to only one. This would allow them to better explore their environment and its resources, which would show on the archaeological record by a bigger reliance on meat and an increase in home range and of migratory expansions, perhaps even leading to the expansion out of Africa. This would also act as a selective pressure to improve navigational skills, giving way to positive-feedback loop.

The most plausible cognitive innovations is an increase in working memory capacity, which allowed individuals to hold and process more information in attention at the same time or an increase in long-term memory capacity, which permitted individuals to recall different locations not visited for long periods of time – in a somewhat similar way to elephants. Better forms of communication and later, language could also have played a role, by allowing individuals to communicate about the way to follow prey, or the way to return home, once again lending support to the role of language on the evolution of human cognition.

Some form of these navigational skills could have been in place by 1.7 million years ago, with the appearance of *Homo erectus*, the first hominin to leave Africa, whom also exhibited signs of a greater reliance on meat and a larger home range (Antón *et al*. 2002; Aiello and Wells, 2002; Antón, 2003).

The evolution of handedness, on the other hand, although it would have strong implications for the evolution of spatial cognition due to its relatedness to stone tool working and to brain lateralization is still too hard to analyse on the archaeological record. Continued works, perhaps through application of Saragusti *et al*. (2005) method should provide useful information considering this question.

When confronting this framework with the one proposed by Wynn (2002; 2010), there are main criticisms can be found. First, the date proposed here for the first change in spatial cognition in the *Homo* lineage – on object recognition and manipulation – took place is different from the one proposed by this author. 1.75 Ma for the first and 1.5 Ma for the latter. This can be explained by the updated account of human evolution used in this Thesis or by the gradual change of these skills throughout time. This lends support to the idea that a consistent study of stone tool samples, through a methodology such as the one proposed here, would be most beneficial for the advancement of this subject. Second, it seems that the coordination of allocentric and egocentric spatial systems in navigation, strongly relates to mental rotation skills, on object representation and manipulation, which also implies coordination of perspectives. However, the times proposed for the development of these two are too different – 1.7 Ma for the first and 500 Ka for the second. Possible explanations for this are, that coordination of perspective on a small space – the size of a stone tool – is more cognitively demanding than the coordination of perspectives on a grand scale – such as a landscape, or that mental rotation needs several different perspectives to be hold in attention at the same time, and not only to be integrated. This would maybe call for a more enhanced working memory than navigation tasks. Further investigation should be concluded to solve this problem.

Another important consideration concerns the cognitive framework used throughout this work. Wynn's view of the working memory model was strongly used for no other reason that it satisfactorily explained the results found. It would be interesting, in the future, to try to use other cognitive frameworks. Interestingly, some of these models seem to mesh rather well with the used model. For instance, Mithen's (1996) model of cognitive fluidity translates into an increase in working memory which leads to the increase of amount of information one can hold in attention and operate on.

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.

First, considering that the proposed paths for evolution of spatial cognition were usually related to integration of pre-existent cognitive traits or increase in memory capacities, then, most likely, these processes were more related to brain reorganization than to brain expansion. On the other hand, 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^3 or of 900 cm^3 (Wood and Baker, 2011). Continued work on the neurological arena is of grave importance to understand paleo-minds.

Another important arguable point is the defence on the proposed framework that there is no significant difference between the cognitive implications of Oldowan stone knappers and great apes, then it is curious to try to understand why does the bonobo Kanzi doesn't exhibit equal accuracy to the one seen in Oldowan (Schick *et al*., 1999; Toth and Schick, 2009). Part of these differences is probably explained by the biophysical constraints alleged by the authors. But another factor may be developmental change. Considering the differences found by Rosati and Hare (2012) on the developmental change of spatial cognition between chimpanzees and bonobos, it would be interesting to see if chimpanzees developed a higher accuracy in stone tools knapping, once taught. Although this is plausible, it is not certain, since the differences in spatial cognition found by Rosati and Hare (2012) were related to spatial memory capacity, and not to object manipulation tasks.

This presents a fundamental new field of study. 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).

Nevertheless, despite the considerable amount of evidence lending support to the contribution of developmental science, it would be wrong to base an entire evolutionary framework on developmental data, given the risk of overlooking important factors or important changes taking place. In other word, developmental data should never be considered in isolation. This becomes more and more important as researchers realize that the only way to do science is to take an as multidisciplinary approach as possible.

In fact, 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.

This Thesis attempted to take such a multidisciplinary approach, by including as much as possible relevant literature on other subjects, besides development. But, in fact, due to the partiality of this approach, a major criticism towards this Thesis is that it follows a *bottom down*, as opposed to *bottom up* perspective, since it starts from a theoretical point of view towards the archaeological record, instead of beginning from the archaeological record towards a theoretical framework. This critique can also be made for many cognitive archaeology papers, since this branch of study presupposes looking at the archaeological record within a psychology framework.

The initial idea was to overcome this unbalance by analysing a sample of stone tools in order to create the framework. Unfortunately, this was not possible, as already mentioned, due to time constraints, and, so, it was opted to create the framework and explore the contribution of developmental science to the evolution of spatial cognition. Later work, namely carrying on and testing the proposed methodology on an adequate sample would be most valuable to overcome this problem.

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.

6. CONCLUSION

The general conclusions resulting from this essay are as follow.

First, developmental data is indeed relevant to the study of human evolution and may provide an interesting new area of inquire.

Second, it is possible that changes in the archaeological record seen at 1.75 million years ago and 500 thousand years ago may be related to ontogenic changes in hominins, resulting in new object representations and manipulation skills, namely the ability to produce first, mirror symmetry and then, three dimensional symmetry. These changes would have been brought upon by integration of metric and categorical information for the first transformation and by development of mental rotation for the latter.

Subsequently, these spatial cognitive changes can be explained by an increase in working memory capacity, among others, which would allow for the integration of metric and categorical information and integration of different spatial systems, namely allocentric and egocentric ones. The selective forces behind this process are hard to determine, but it is likely that the experience with tool use and production elicited a positive-feedback loops that led to an ever increasing complexity of spatial cognitive skills and of tools.

Navigational skills might have also profited from developmental changes, once again by ever increasing integration of allocentric and egocentric points of view, which would allow a more efficient exploration of the environment and its resources. For this, not only a development in working memory capacity was needed but also an increase in long-term memory capacity in order to recall long-visited locations. The most likely selective force for this change was feeding ecology, which led to greater reliance on meat and greater home ranges, once again giving rise to a positive-feedback loop. This should have been relatively well in place by 1.7 million years ago when hominins first left Africa.

Finally, 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.

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