

André Ricardo Damas Martinho

Novel tool use acquisition in human primates and the evolution of social learning: An experimental approach

Dissertação de Mestrado em Evolução e Biologia Humanas

Janeiro de 2017



Universidade de Coimbra

Department of Life Sciences, Faculty of Sciences and Technology, University of Coimbra

Novel tool use acquisition in human primates and the evolution of social learning: An experimental approach

Master's degree in Human Evolution and Biology Academic year 2016/2017

André Ricardo Damas Martinho

uc2013104376@student.uc.pt

Supervisors: Prof. Susana Carvalho / Prof. Sofia N. Wasterlain

Table of Contents

List of Figures iii
List of Tablesiv
Resumov
Abstractvii
Acknowledgementsix
$1-Introduction \dots 1$
1.1 – Tool use in humans and other animals1
1.2 – Stone tool use in wild primates
1.3 – Percussive behaviour in extant and extinct primates
1.4 – Social learning in chimpanzees and humans
2 – Material and Methods
2.1 – Study 1: Nut cracking experiment with human adults
2.1.1 – <i>Subjects:</i>
2.1.2 – Apparatus and methods
2.2 – Study 2: Nut cracking experiment in school-age subjects
9.2.1 – <i>Subjects:</i>
2.2.2 – Apparatus and method:
3 – Results
3.1 – Study 1: Nut cracking experiment in human adults
3.1.1 – Tool-use behaviour: Raw material selection, Tool features and Function
3.1.2 – <i>Time to select tools and time to complete task</i>
5.1.2 - 11me to select tools and time to complete task
3.1.2 – Time to select tools and time to complete task
-
3.1.3 - Nut cracking efficiency: Number of bouts to crack nut #1, #2 and #3
3.1.3 – Nut cracking efficiency: Number of bouts to crack nut #1, #2 and #3
3.1.3 – Nut cracking efficiency: Number of bouts to crack nut #1, #2 and #3133.1.4 – Subjects' behaviour143.2 – Study 2: Nut cracking experiment in school-age subjects14
 3.1.3 – Nut cracking efficiency: Number of bouts to crack nut #1, #2 and #3
3.1.3 – Nut cracking efficiency: Number of bouts to crack nut #1, #2 and #3 13 3.1.4 – Subjects' behaviour 14 3.2 – Study 2: Nut cracking experiment in school-age subjects 14 3.2.1 – Tool-use behaviour: Raw material selection, Tool features and Function 14 3.2.2 – Time to select tools and time to complete task 15
 3.1.3 – Nut cracking efficiency: Number of bouts to crack nut #1, #2 and #3

List of Figures

Cover: Photo taken by Catarina Coelho and courtesy of Professor Susana Carvalho.
Figure 1: Examples of the location where the matrix of stones was placed. Courtesy of Professor Susana Carvalho
Figure 2: Examples of the location where the matrix of stones was placed
Figure 3: Examples of the location where the matrix of stones was placed
Figure 4: Examples of the location where the matrix of stones was placed17
Figure 5: Examples of the location where the matrix of stones was placed
List of Tables
Table 1: Examples of the location where the matrix of stones was placed. 9
Table 2: Examples of the location where the matrix of stones was placed. 10
Table 3: Examples of the location where the matrix of stones was placed
Table 4: Examples of the location where the matrix of stones was placed

Resumo

Os seres humanos são conhecidos pela sua extensa capacidade de utilização e produção de ferramentas em comparação com os seus parentes mais próximos, os chimpanzés. A literatura mostra que a disparidade na aquisição de tais capacidades está relacionada com diferentes mecanismos de aprendizagem social: enquanto os seres humanos modernos utilizam, para adquirir novas capacidades, a imitação e o ensino ativo, os chimpanzés parecem depender da emulação e de uma aprendizagem por tentativa/erro para adquirir comportamentos de uso e manufatura de ferramentas. Em chimpanzés existe uma fase crítica de aprendizagem (período infantojuvenil) e os indivíduos tendem a ser conservadores uma vez passada essa fase, e raramente adquirem novos comportamentos tecnológicos. Em humanos, muito pouco é conhecido sobre: 1) A facilidade de aquisição de novos comportamentos tecnológicos em adultos; 2) As variáveis que influenciam a aprendizagem social durante a aquisição de um novo comportamento tecnológico em indivíduos no período infantojuvenil. O presente estudo trata-se de uma abordagem experimental com o objetivo de testar indivíduos humanos expostos a uma nova tarefa tecnológica, considerada simples e rudimentar ("nut cracking"), para a qual existem dados análogos relativamente aos chimpanzés de África Ocidental.

O presente trabalho consiste em dois estudos experimentais, ambos incidindo sobre os estágios iniciais da aprendizagem do uso de ferramentas: Estudo 1) Testa a eficiência em adultos ocidentais (com idades entre os 19 e 30 anos) numa nova tarefa "nut cracking"; Estudo 2) Testa a eficiência na mesma tarefa em pares de crianças de um contexto cultural diferente (África Oriental) em idade escolar (entre os 4 e 15 anos), perante diferentes condições experimentais: 1) sem modelo humano; 2) com um vídeo modelo de 15 segundos em que chimpanzés executam "nut cracking"; 3) com um modelo humano a realizar "nut-cracking" antes do teste.

Os resultados do presente estudo mostram que a escolha de ferramentas para a execução da tarefa é baseada nas suas características morfológicas. Estes resultados têm paralelo com estudos em chimpanzés. O estudo também indica diferenças importantes no desempenho de "nut cracking" entre primatas humanos e não-humanos. À semelhança do que a literatura nos mostra sobre diferenças entre sexos no desempenho desta tarefa em chimpanzés (em que as fêmeas são mais eficientes do que os machos), a análise dos dados dos dois estudos experimentais em primatas humanos demonstram que o sexo dos indivíduos também tem preponderância no desempenho da tarefa, contudo, os resultados

indicam que indivíduos do sexo masculino são mais eficientes do que os indivíduos do sexo feminino, necessitando de menos tentativas para serem bem-sucedidos. Os resultados mostram ainda que, ao executar uma nova tarefa, os primatas humanos tendem a adquirir e aprender a melhorar as suas capacidades significativamente mais rápido que os primatas não-humanos. Todavia, comparando com o que a literatura nos indica sobre a proficiência de primatas não-humanos em "nut cracking", neste estudo os indivíduos humanos necessitaram de, em média, significativamente mais tentativas para abrir uma noz.

Em relação ao Estudo 2, os resultados mostram que a idade dos indivíduos parece ter um papel preponderante na capacidade de execução da tarefa: indivíduos mais jovens têm mais dificuldades para desempenhar a tarefa que indivíduos mais velhos. Relativamente aos padrões comportamentais demostrados pelos indivíduos, o estudo mostra que existe uma tendência para "over-imitation" por parte de indivíduos mais velhos. Por outro lado, indivíduos mais jovens tendem a observar os seus pares com mais frequência. Assim, o Estudo 2 parece indicar que a transmissão de novos comportamentos via horizontal poderá ser um importante mecanismo para a aprendizagem social.

Este estudo também corrobora que a aquisição de novas capacidades, tais como em tarefas percussivas, pode compartilhar paralelos com as espécies do género *Pan*, não sendo necessários mecanismos complexos para a transmissão cultural.

Palavras-chave: Aprendizagem social; Utilização de ferramentas líticas; Comportamento de percussão; Primatas humanos e não-humanos.

Abstract

Human primates are known for their extensive capability to tool use and tool making compared with their closest relatives, the chimpanzees. Literature shows that the disparity in the acquisition of such capacities is related to different mechanisms of social learning: while modern humans use imitation and active teaching to acquire new capacities, chimpanzees seem to rely on emulation and trial / error learning to acquire behavioural use and tool manufacturing. In chimpanzees, there is a critical phase of learning (juvenile age), and individuals tend to be conservative after this phase, and rarely acquire new technological behaviours. In humans, very little is known about: 1) Acquiring new technological behaviours in adults; 2) The variables that influence social learning during the acquisition of a new technological behaviour in individuals in the period of childhood. The present study is an experimental approach with the intent of testing human individuals exposed to a new technological task, considered simple and rudimentary (nut cracking), for which there are similar data regarding the chimpanzees from West Africa.

The present work consists of two experimental studies, both focusing on the initial stages of learning the use of tools: Study 1) Tests the efficiency in western adults (between 19 and 30 years old) in a new task: "nut cracking"; Study 2) Tests the efficiency in the same task in pairs of children from a different cultural context (East Africans) of school age (between 4 and 15 years old), under different experimental conditions: 1) Without any role model; 2) With a video model showing 15 sec. of chimpanzee nut-cracking; 3) With a human role model performing the nut-cracking before the test).

The results of the present study show that the individuals select the tools function for the execution of the task based on its morphological features. These results have parallels with field studies in wild chimpanzees. The study also indicates important differences in the performance of nut cracking between human and non-human primates. Similar to what literature shows us about differences between genders in the performance of this task in chimpanzees (where females are more effective than males), the data of the two experimental studies in human primates shows that gender also has preponderance in the performance of the task. However, the results indicate that human males are more effective than females, requiring fewer bouts to be successful. Results demonstrate that when performing a new task, human primates tend to acquire and learn to improve their abilities significantly faster than nonhuman primates, nevertheless, in comparison to what literature indicates about the proficiency of non-human primates in nut cracking, human subjects required on average significantly more bouts to crack open a nut.

Regarding Study 2, results show that the age of the individuals seems to have a preponderant role in the ability for the task execution: younger individuals have more difficulty performing the task than older individuals. Concerning the behavioural patterns demonstrated by individuals, the study shows that there is a tendency for "over-imitation" by older individuals. On the other hand, younger individuals tend to observe their pairs more often, thus, it seems to indicate that acquiring new behaviours via horizontal transmission can be an important mechanism for social learning.

This study also corroborates that the acquisition of new capacities, such as percussive tasks, can share parallels with species of the genus *Pan*, without the need for complex mechanisms for cultural transmission.

Keywords: Social learning; Stone-tool acquisition; Percussive behaviour; human and non-human primates.

Acknowledgements

I want to express my deep gratitude to both my thesis' supervisors: Professor Sofia Wasterlain and Professor Susana Carvalho. Firstly, to Professor Sofia, for the endless patience helping me to analyse the data and to Professor Susana for sharing her data with me and allow me to produce my thesis with it. To both my sincere gratitude for their help and their unconditional support throughout the development of this work. I also want to thank my family and closest friends for their support and for endured my interminable discourses about this topic.

Finally, we want to acknowledge all the subjects that kindly agreed on participating in the experiments: Students of the Koobi Fora Field Schools of the seasons 2010, 2011 and 2012, and the Master and students of the Illeret School in Northern Kenya.

1 – Introduction

1.1 -Tool use in humans and other animals

Human primates are known to be prolific stone tool users and stone tool makers (Leroi-Gourhan, 1964; 1965; 1983; Michael Tomasello and Call, 1997; Valentine Roux and Bril, 2005). Evidences show that these behaviours date back to our Australopithecines ancestors – with *A. afarensis* capable of using tools (McPherron *et al.*, 2010), and *A. garhi and Kenyanthropus platyops* of making tools (Heinzelin *et al.*, 1999; Harmand *et al.*, 2015). Stone tool use and making is still present nowadays where it is ethnographically documented in several human communities (e.g. Stout, 2002).

Defining animal tool-use is at the core of a long-standing debate (van Lawick-Goodall, 1971; St Amant and Horton, 2008; Seed and Byrne, 2010; Bentley-Condit and Smith, 2010). For this study we followed an operational definition: "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 the tool during or prior to use and is responsible for the proper and effective orientation of the tool" (Shumaker *et al.*, 2011: 5).

Several studies carried out in the last decades showed that whether in captivity or in their natural habitat, the capability for tool use seems to be present in all great apes e.g., chimpanzees (*Pan troglodytes*) (van Lawick-Goodall, 1968; Boesch and Boesch, 1990; Humle, 2011), bonobos (*Pan paniscus*) (Schick *et al.*, 1999), gorillas (*Gorilla gorilla*) (Breuer *et al.*, 2005), and orang-utans (*Pongo pygmaeus*) (van Schaik and Knott, 2001). Other primates like the New World monkeys, e.g. capuchin monkeys (*Sapajus. sp*) (Ottoni and Izar, 2008), and Old World monkeys, e.g. long-tailed macaque (*Macaca fascicularis aurea*) (Malaivijitnond *et al.*, 2007; Gumert and Malaivijitnond, 2012), show the same capabilities, using lithic tools for digging ground tuber, cracking nuts and sea molluscs, respectively. Tool use is also not exclusive of primates, and other species have been reported to use tools, some with impressive levels of sophistication, e.g., dolphins (*Tursiops sp.*) (Mann *et al.*, 2005), or New Caledonian crows (*Corvus moneduloides*) (Chappell and Kacelnik, 2002; McGrew, 2013).

However, in the wild, chimpanzees are unique in that they show a variety and complexity of technological behaviours that is only bypassed by human primates (Whiten, 2011). Chimpanzees display a large repertoire of tool-use behaviours (Ohashi, 2006; Humle, 2011; Matsuzawa, 2011), for different functions, such as: 1) Extraction by insertion (e.g. ant-fishing); 2) Probing (e.g. wood-boring); 3) Cleaning, Hygiene 4) Display (e.g. hitting) and finally, 4) Extraction by pounding (e.g., nut-cracking, honey-gathering) (Boesch and Boesch, 1990; Boesch *et al.*, 2009).

1.2 – Stone tool use in wild primates

In the wild, only the chimpanzee, the capuchin monkeys and the long-tailed macaques are known to use stones as tools to crack nuts (Sugiyama and Koman, 1979; Fragaszy *et al.*, 2004; Luncz pers. Comm.), or to break molluscs and crabs (Gumert and Malaivijitnond, 2013). Nevertheless, chimpanzee nut cracking, consisting in placing nuts on the stone anvil once at a time and cracking them with a hammer stone (Hayashi and Inoue-Nakamura, 2011), is still considered one of the most complex forms of tool-use in the wild (Biro *et al.*, 2006).

According to Matsuzawa (2011), nut cracking represents "level 2" of tool use behaviour where three objects must be related to each other in a specific temporal and spatial pattern, where a nut (object 1) must be stably placed on an anvil stone (object 2), and a hammer stone (object 3) must be used to strike the nut leaving the contents (the kernel) relatively unharmed. In fact, chimpanzees can go one-step further and use what is called a "metatool", i.e. they sometimes use an additional stone (a wedge) in order to stabilize the upper surface of the anvil. This task reveals a great cognitive ability (Carvalho *et al.*, 2008; Biro *et al.*, 2010).

Chimpanzee stone tool use also displays complexity regarding the systematics of tool selection, use, reuse and discard (Carvalho *et al.*, 2008; Carvalho *et al.*, 2009; Biro *et al.*, under review). This selection is predictable on the basis of certain tool characteristics, like the width and weight and the type of rock, raw material used. This has been interpreted as an indicator that chimpanzees distinguish objects morphological features, thus attributing them a specific function (Biro *et al.*, 2010), while novel data shows that they also recognize mechanical properties of stones that are invisible to the eye (Carvalho *et al.*, in prep.).

Capuchins monkeys and long-tailed macaques show different stone tool use behavioural variants. These species have been known for their ability to crack open hardshelled fruit and some kind of molluscs species by pounding it against a hard substrate (Izawa and Mizuno, 1977; Malaivijitnond *et al.*, 2007; Tan *et al.*, 2015). As with chimpanzees, studies show that capuchins and long-tailed macaque consistently select hammer stones by size and weight, displaying planning abilities and the rapid employment of visual clues to correctly identify suitable tools (Visalberghi *et al.*, 2009; Gumert and Malaivijitnond, 2013).

1.3 – Percussive behaviour in extant and extinct primates

Percussive technology in the form of stone tool use is the only tool-use behaviour common across the three extant non-human primate genera (*Pan, Cebus, Macaca*), the only extant human genus (*Homo*), and several extinct hominin genus (*Kenyanthropus, Australopithecus* and *Homo*). While its emergence and development may be explained by convergent evolution, some shared primitive traits between stone tool use in chimpanzees and modern humans indicate that the "Pancestor" (i.e. the last common ancestor between *Pan* and *Homo*) was likely to be able to use percussive behaviour.

Percussive tools are present throughout the entire human evolution and the archaeological record documents the appearance of this behaviour around 3.3 Ma (McPherron *et al.*, 2010; Harmand *et al.*, 2015). This is the only tool type that is ubiquitous in the archaeological record, regardless of time and space (Caruana *et al.*, 2014; Benito-Calvo *et al.*, 2015). A representative example may be the recent discovery from Lomekwi 3 in West Turkana, Kenya that shows the earliest known stages of stone tool technology. These findings show that the majority of the assemblage is composed by what are supposed to be by-products of percussive activities and possible use of different knapping techniques: bipolar and passive hammer (Harmand *et al.*, 2015; Lewis *et al.*, 2016). Nevertheless, a recent study (Proffitt *et al.*, 2016), demonstrates that wild bearded capuchin monkeys (*Sapajus libidinosus*) can produce entirely unintentionally conchoidally fractured, sharp-edged flakes and cores that have the characteristics and morphology of intentionally produced hominin tools. These new findings reveal that we urgently need to expand on modern experimental approaches to better understand the behaviours and processes that occur before and during stone tool use.

The Lomekwian and Oldowan records extend to half way back to the time of our common ancestor with chimpanzees (Pozzi *et al.*, 2014; Harmand *et al.*, 2015). This combined with our knowledge of chimpanzee stone tool percussive behaviour to open crack nuts suggests a possible transition from percussive behaviours in our common ancestor to more complex stone tool making achievements (Whiten *et al.*, 2009; Stout *et*

al., 2010; d'Errico and Stringer, 2011). Several studies have drawn parallels between the percussive behaviour in our hominin ancestors and the nut-cracking behaviour of modern chimpanzees (Mercader *et al.*, 2002, 2007; Marchant and McGrew, 2005; Carvalho *et al.*, 2008, 2009; Carvalho and McGrew, 2012). Certainly, one undisputable similarity is that our LCA and our extinct hominin ancestors were, somehow, able to acquire novel tool behaviours and transmit that knowledge across generations (Smyrl, 2014).

1.4 – Social learning in chimpanzees and humans

As mentioned above, chimpanzees possess various tool-use traditions (Whiten et al., 1999). These represent sets of behaviours, knowledge, and values whose occurrence cannot be explained solely by environmental and genetic factors but which are passed on from one generation to the next facilitated by social learning (Whiten, 2000, 2005); Matsuzawa et al., 2001; but see Koops et al., 2015 for a critical addition to the method of exclusion). Albeit humans and chimpanzees possess this feature in common, there is a substantial difference in the complexity and rates of innovation/development of the human tool kits (Tomasello, 2011). While some authors have tried to understand if anatomical differences play a role in these differences, e.g. shape of hand or precision grip (see Ambrose, 2001; Byrne, 2004), others focused on the neuro-correlates of tool use, recording which parts of the brain are processing information during stone tool making (Johnson-Frey, 2004; Iriki, 2006; Stout and Chaminade, 2009). Additionally, one of the main pathways to understand how humans ended up with our modern full dependence on technology and with the ability to transmit an overwhelming amount of information units between individuals is to focus on the processes of social transmission and on the ontogeny of acquiring new tool behaviours, looking at both extant human and nonhuman primates during the performance of shared tool-use behaviours, as it is the case of the anvil-hammer use.

Social learning is the process of learning that is influenced by the interaction with another animal, that means the capability to learn from others (Heyes, 1994). It is believed that nonhuman primates such as chimpanzees may acquire new behavioural skills such as tool use by emulation rather than imitation (Tomasello, 1998; Whiten *et al.*, 2009; Buttelmann *et al.*, 2013). Studies reveal that chimpanzees can produce imitative pattern-behaviours in certain tasks (Whiten, 1998; Myowa-Yamakoshi *et al.*, 2004; Buttelmann *et al.*, 2013). Horner and Whiten (2005) showed that young chimpanzees may be capable of switching from emulation to imitation. In tasks such as nut-cracking, chimpanzees'

infants are capable of performing all the actions of the nut-cracking sequence by the age of 1.5 years, although they never combine the elements in the appropriate order. It takes another 2 years before the infants combine the correct actions to be able to crack the first nut (Biro *et al.*, 2006). Chimpanzees are able to perform nut-cracking successfully by the age of 4 to 5 years old (Matsuzawa, 2006). Moreover, it appears that there is a critical period for learning this skill; individuals who fail to acquire this skill by the end of the period (between age 3 and age 5) were never seen to acquire the skill later in life (Matsuzawa, 2002; Biro *et al.*, 2003).

Chimpanzee process of learning stone tool use has been labelled "education by master-apprenticeship", which is characterized by the attentive observation of the older individuals' behaviour by the young individuals (Matsuzawa, 2011). Primarily the mothers are the main target of observation, as infants spend a significant amount of time with them and mothers have high levels of tolerance toward them (Biro, 2011). Later, when juveniles are already able to use stone tools but are still learning how to become more efficient, the target of observation shifts from kinship to the most skilled individuals in the group, who are equally tolerant allowing the observers (Carvalho *et al.*, in prep.) This tolerance facilitates skill transmission, and emulation may be an additional social learning process involved in the acquisition of this behaviour (Hayashi and Inoue-Nakamura, 2011). Other processes typically studied in humans, like teaching seem to be only anecdotally reported (see Boesch, 1991) or rare (Musgrave *et al.*, 2016) in chimpanzees (and absent in other apes, albeit see Thornton and McAuliffe, 2006 for a compelling case of teaching in non-primates).

Chimpanzee learning process is unidirectional, i.e., younger individuals observe the behaviour of older individuals but not vice versa (S. Carvalho *et al.*, in prep.). Moreover, once the behaviour is learned, chimpanzees can be very conservative towards innovations (Hrubesch *et al.*, 2009). Similar conservative behaviours seem to occur in the New World monkeys that possess stone tool behaviour (Visalberghi and Addessi, 2000). This might represent an obstacle for the "ratchet effect" to develop and complex cumulative culture to emerge in nonhuman primates (Tennie *et al.*, 2009; Perry, 2011).

Human children are equally dependent on social interactions and in engaging in imitating/over-imitation-like behaviours in order to acquire new skills (Horner and Whiten, 2005; Lyons *et al.*, 2007; Behne *et al.*, 2008). Human children's understanding of tool use appears at around 18 months of age (Rat-Fischer *et al.*, 2012) and, during the second year of life (i.e. between 18 and 24 months) children are able to use simple tools

(e.g. using a tool to retrieve an out-of-reach toy), and they copy others closely after observation, showing a behavioural variant that may be unique to humans: over-imitation, high-fidelity copying (Whiten *et al.*, 1996; McGuigan *et al.*, 2007). When making a tool (a hook to retrieve a sticker in a plastic tube) children between 3–5 year-old need to rely on demonstrators and the majority of individuals will not succeed independently without a demonstration of the solution until about 8 years old (Beck *et al.*, 2011). This dependence on the adult demonstration has been suggested to be a mechanism to overcome children's lack of innovation. Such difficulties might relate with cognitive maturation (Chappell *et al.*, 2013). Another explanation links to the "ill-structured problem", that suggests that children have difficulty to recognize and coordinate knowledge in order to solve a task (Cutting *et al.*, 2014).

Along with imitation, active teaching or pedagogy is essential for knowledge acquisition (Csibra and Gergely, 2006; Tehrani and Riede, 2008). Studies in modern hunter-gatherer communities support that knowledge transmission is primarily vertical (knowledge transmitted by the parents), where sometimes parents use direct instruction to show the infants how to use the tools (Hewlett *et al.*, 2011). However, horizontal transmission (knowledge acquired by multi-aged children), and oblique transmission (passed from one generation to another younger generation via non-kin), appear to have important impacts throughout the different stages of the development of knowledge acquisition. Children teach each other and they are likely to observe and imitate older children (Stout, 2002; Horner *et al.*, 2006; Flynn and Whiten, 2008; Hewlett *et al.*, 2011).

Playing might also serve a critical function in the transmission of human technological knowledge for the reason that the engagement in such activities can provide mechanisms for arbitrary ideas to spread between children (Mithen, 2001; Nielsen *et al.*, 2012). Apparently, pedagogy and teaching play a crucial role in the transmission of skills across generations, and perhaps act as a central mechanism to propagate and maintain culture traditions (Tehrani and Riede, 2008; Dean *et al.*, 2012, Dean *et al.*, 2014). These type of human interactions and cross-generational cooperation developed a unique human feature called *cumulative cultural inheritance*, i.e. a generation makes a precise copy of the previously generations' way of doing things. By adding some modification or improvement, the behaviour persists across generations until further changes are made (Tomasello *et al.*, 1993).

To sum, from the analyses of the ontogenetic processes of acquisition and transmission of tool use in nonhuman and human primates we can state that social learning, i.e. the opportunity to learn from conspecifics, is a common denominator allowing novice individuals to acquire both tool making and tool use (e.g. chimpanzees: Biro *et al.*, 2006; humans: Geribàs *et al.*, 2010).

There have been extensive studies on how modern humans learn novel tool-making tasks, usually focused on relatively complex knapping activities (Stout, 2002; Geribàs *et al.*, 2010; Bril *et al.*, 2010; Rein *et al.*, 2013). Recently, a study focusing on the ability to innovate in the absence of cultural knowledge reports that UK and German children spontaneously invent great ape tool use behaviours without the need of previous experience or of a demonstrator (Reindl *et al.*, 2016).

However, previous studies did not account for: 1) Likelihood of different performances influenced by the cultural background of the sampled individuals (e.g. subjects with little to no access to the Western technological kits); 2) Likelihood of different performances if subjects are tested in pairs; 3) What happens to the ability to innovate or learn a novel type of tool use at a later developmental stage in humans? Can modern adult humans, succeed in learning tool-use tasks that are normally described as "rudimentary" or "simple" technologies, if they were never exposed to social contexts in which similar tools were used?

The present study aimed to address these questions and tested individuals performing a new tool-use task to which they were totally naïve. It comprised two different experimental conditions, both focusing on the first stage of learning a novel type of tool use.

Study 1 tested adult human subjects (Westerns) in a novel task: The use of a hammer stone and anvil stone to crack open nuts (*Macadamia sp.*). Study 2 tested the same tool-use task, but looking at pairs of school-age human subjects, from a different cultural background (East Africans) and across different ages, across three experimental conditions: 1) Without any role model; 2) With a video model showing 15 sec. of chimpanzee nut-cracking; 3) With a human role model performing the nut-cracking before the test. We compared the results of both studies with the current data on the earliest stages of tool use acquisition in non-human primates (e.g., Sakura and Matsuzawa, 1991; Biro *et al.*, 2006; de Resende *et al.*, 2008; Carvalho *et al.*, 2008, 2009). The study sheds light on the necessary prerequisites for rudimentary tool use and on the role of sociality in developing tool use skills, while also discussing the meaning of tool use complexity, i.e. is nut-cracking a complex task if the individual is devoided of opportunities for social learning? Furthermore, the results of the subjects' behaviour when

tested in pairs provide knowledge about the effects of having role models or social exposure to learning contexts.

2 – Material and Methods

2.1 - Study 1: Nut cracking experiment with human adults

2.1.1 – *Subjects:*

The present study used longitudinal data collected by S. Carvalho in 2010, 2011 and 2012 in the context of the Koobi Fora Field School, in East Lake Turkana, Kenya. Subjects belong to four different groups of participants of the Field School, with ages between 19 and 30 years old. A total of 70 subject (32 males and 38 females) participated in Study 1. From these, 64 subjects (29 males and 35 females) had no previous experience with nut-cracking activities, and 6 subjects (3 males and 3 females) were used as control group, since they had been previously exposed to a similar task. Each adult participant gave verbal consent. The study conducted is under the research permit given to the Koobi Fora Field School and to S. Carvalho by the National Museums of Kenya.

2.1.2 – Apparatus and methods

A matrix of stones was located on the top of a tarp, and the tarp placed in a sandy location (e.g. river bed, see Fig. 1). A set of 32 stones was provided, where stones were labelled with a number (1 to 32), after being measured (width, length, height, weight) and classified according with raw material type (chert, basalt, phonolite, quartzite). Stones varied from 4.3cm to 30.9cm in length and 102.15g to 3649g.



Figure 1: Examples of the location where the matrix of stones was placed.

Three nut were placed on the top of the tarp and the participant given a minimum amount of verbal information, i.e. "your goal is to successfully crack these nuts to eat, you are allowed to use as many stones as you need".

After each trial, the matrix of stones was randomised. Participants were not allowed to see or interact with other participants while the experiment was ongoing. Each experimental trial started when the subject initiated the selection of stones, and finished when the three nuts had been successfully open. For each subject several variables were recorded (Table 1). The same set of stones was used in the three years of data collection. Records were performed taking written notes and using a timer (S. Carvalho plus research assistants), and extensive photo and video record was taken.

The comparisons between measures of continuous variables, between genders or between control group and the rest of the subjects, were made using the student t-test. In order to verify if there were differences in the performance between attempts a pairedsamples *t*-test was used. The relation between tool dimensions (width, weight, length, and height) and tool function was studied by the Pearson correlation (two-tailed) coefficient.

Variables recorded	Description
1) Gender	Male or Female
 2) Time to select hammer and anvil 3) Time to crack three nuts 4) Number of bouts to open each nut 	Time that took each subject to select the tools Time that took each subject to crack the three nuts Number of bouts necessaries to open each nut
5) Changes of tools during the trial	Number of times that each subject selected a different tool during the trial
6) Innovations	An innovative method performed by a subject during the trial

Table 1: Variables recorded for each subject.

2.2 – Study 2: Nut cracking experiment in school-age subjects

2.2.1 – *Subjects:*

Data was collected in 2012 on a local Northern Kenyan school (Ileret Primary School). In total, 78 subjects (44 males and 34 females) participated in the experiment. From this sample, 12 subjects (10 males and 2 females) were excluded due to the lack of consistent data for further analysis. Hence, the study reports on results from a total of 66 subjects (34 males and 32 females) aged between 4 and 15 years old (see Table 2). Verbal consent was given by the Head Master of the Ileret School on behalf of all the parents.

The study conducted is under the research permit given to the Koobi Fora Field School and to S. Carvalho by the National Museums of Kenya.

Age	N	%	Age Groups	N	%
4 y/o	3	4.5			
5 y/o	2	3	Age group I	15	22.7
6 y/o	8	12.1	(4 y/o to 7 y/o)	15	22.1
7 y/o	2	3			
8 y/o	3	4.5			
9 y/o	8	12.1	Age group II	24	36.4
10 y/o	7	10.6	(8 y/o to 11 y/o)	24	50.4
11 y/o	6	9.1			
12 y/o	8	12.1			
13 y/o	12	18.2	Age group III	77	40.9
14 y/o	5	7.6	(12 y/o to 15 y/o)	27 5 y/o)	
15 y/o	2	3			
Total	66	100	Total	66	100

Table 2: Age range and age groups of the Study 2 subjects'.

2.2.2 – Apparatus and method:

Study 2 followed a different experimental setting from Study 1. Due to limitations of space in the School, a smaller stone matrix was used (N = 15 stones). Stones were numbered (1 to 15), after being measured (width, length, height) and classified according with raw material type (chert, basalt, ignimbrite red, ignimbrite grey, quartz). Three nuts were placed on the top of the tarp and the participant given a minimum amount of verbal information, i.e. "your goal is to successfully crack these nuts to eat, you are allowed to use as many stones as you need". After each trial, the matrix of stones was randomised. With the exception of the two-paired subjects tested in each trial, participants were not allowed to see or interact with other participants while the experiment was ongoing. Each experimental trial started when the subject initiated the selection of stones, and finished when the three nuts had been successfully open.

Subjects were tested in pairs, within a range of different ages. Three experimental conditions were tested:

- 1- Without any role model: Participants (n=24 subjects) were asked to perform nut-cracking (n=72 trials) by themselves without help or prior instructions;
- 2- With a video model: Participants (n=22 subjects) watched a 15 sec. video of chimpanzees performing nut cracking (n= 66 trials) and then were asked to perform the nut-cracking;
- 3- With a human role model: Participants (n=20 subjects) watched an adult model selecting a set of stones (an anvil and a hammer) and performing nut cracking. (n=27 trials). In some trials (n=33), the adult uses a wedge without any functionality (i.e. stabilize an anvil that is not unstable). Subjects are asked to perform nut cracking after observing the adult model.

The main goal of this study was similar to Study 1: to record individual efficiency regarding tool selection, efficiency in the task, plus, to record the effects of different models in the performance of the novice(s).

Individual performance was measured by counting the number of bouts to crackopen one nut. As in the previous experiments, the total number of bouts per nut in a total of three attempts was registered. Each stone chosen by the participants to perform nut cracking was recorded and categorized by tool function (i.e. hammer, anvil, wedge).

Efficiency in tool selection and tool use was measured per pair of subjects in each trial, i.e. a trial starts when the first individual selects the first tool and ends when the last subject of the pair finished the task.

Regarding the data analysis, two procedures were adopted: the number of bouts and efficiency to crack each of the three nuts were analysed individually (i.e. per subject, since we have individual data for efficiency and recorded number of bouts for each subject). The remaining variables (time for selection and total time to complete the task) were analysed by pairs of different gender and age groups. The comparisons between measures of continuous variables, between genders and age groups, were made using the student t-test and the one-way ANOVA test, respectively. A Tukey post-hoc test was conducted to verify differences in the number of bouts per attempt between the age groups. A paired-samples t-test was used to verify if there were differences in performance over the attempts. Lastly, the relation between tool dimensions (width, weight, length, and height) and tool function was studied by the Pearson correlation (two-tailed) coefficient.

3 – Results

3.1 - Study 1: Nut cracking experiment in human adults

3.1.1 – Tool-use behaviour: Raw material selection, Tool features and Function.

The stones used in the experience (n = 32) (chert, basalt, phonolite, quartzite) were randomly distributed. Of these stones, two materials were selected the most: chert and basalt. However, there was a significant difference in the choice of these materials, the basalt being the most used material (t = -13.632, df = 136; p = < 0.001).

Of the 32 stones, 29 (91%) were used by the subjects. Of these 29, eleven (38%) were used as both anvil and hammer. The remaining 18 stones (62%) were used with one specific function and we sought to verify whether function related with morphological features. Comparing mean dimensions (width, length, height and weight) of anvils and hammers, there were significant differences between the used tools: anvils were wider (t = 7.000, df = 16; p < 0.001), longer (t = 4.038, df = 6.004; p = 0.007), higher (t = 4.845, df = 16; p = < 0.001), and heavier (t = 5.026, df = 14; p = < 0.001) than hammers. Pearson correlation (two-tailed) indicates a significant correlation between tool dimensions and function (Table 3). Concerning the tool selection (number of tools selected to perform the task), there were no differences between genders in the selection of anvils (t = 0.680, df = 68; p = 0.499) or hammers (t = -0.820, df = 68; p = 0.415).

	Tool width	Tool lenght	Tool height	Tool weight	Function
Tool width (cm)		0,915**	0,882**	0,926**	-0,830**
Tool lenght (cm)			0,745**	0,864**	-0,809**
Tool height (cm)				0,896**	-0,720**
Tool weight (g)					-0,799**
** <i>p</i> <0.01					

Table 3: Pearson correlation (r; two-tailed) between tool measures and function in Study 1, experiments with adult subjects (n = 18).

3.1.2 – Time to select tools and time to complete task

There were no significant differences between males and females regarding the time used to select tools (t = 0.077, df = 68; p = 0.344) or between the control group (with some previous experience) and the Study 1 subjects (t = 0.186, df = 68; p = 0.853). Similarly, there were no differences between males and females when analysing the total time necessary to execute the task of cracking three nuts (t = -1.232, df = 68; p = 0.222),

and no differences between the control group and the study subjects (t = -0.644, df = 68; p = 0.936). Besides, no differences were found between genders within the control group (t = -0.983, df = 68; p = 0.381).

3.1.3 – Nut cracking efficiency: Number of bouts to crack nut #1, #2 and #3

The subjects had a set of three nuts to perform the experiment, of which the number of bouts to complete the task was counted. The paired-samples t-test, conducted to compare the first attempt (M = 9.87, SD= 21.945) to the second one (M = 6.94, SD = 12.813) revealed no differences in the performances (t = 1.228, df = 69; p = 0.224). The same result was obtained when the second attempt (M = 6.94, SD = 12.813) was compared to the third (M = 6.29, SD = 12.437) (t = 0.510, df = 69; p = 0.611). However, there were significant differences in the first attempt (Fig. 2) between males (M = 3.59, SD = 4.339) and females (M = 15.16, SD = 28.628) (t = -2.601, df = 35.127; p = 0.014). For the remaining attempts (numbers 2 and 3) no differences were found between the two genders (second attempt: t = -1.847, df = 38.690; p = 0.072; third attempt: t = -1.211, df = 62; p = 0.230).

There were no observable differences between the subjects and the control group over the attempts: first attempt (t = -0.546, df = 68; p = 0.587), second attempt (t = -0.519, df = 68; p = 0.605) and third attempt (t = 0.223, df = 68; p = 0.824).

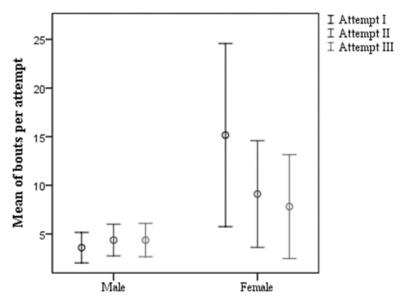


Figure 2: Error bar for the adult experiment with the mean of bouts per attempt by gender.

3.1.4 – Subjects' behaviour

Regarding the proficiency of the subjects it is important to mention that 21% of the subjects (n = 15) failed to open at least one nut without smashing the kernel. Concerning the use of the tools – specifically the hammer – some individuals (n = 6, 9%) used the hammer not for pounding but instead to press the nuts. Moreover, it is necessary to refer that some individuals used a stone wedge (n = 4, 6%). Others, instead of a stone, used sand to stabilise the anvil (n = 2 individuals, 3%). One subject used an innovative technique: he used an anvil, a wedge to stabilise the anvil, and next to the anvil he placed a stone to make a kind of "wall" to prevent the nuts from falling.

3.2 – Study 2: Nut cracking experiment in school-age subjects

3.2.1 – Tool-use behaviour: Raw material selection, Tool features and Function

For this experiment a different set of stones (chert, basalt, ignimbrite red, ignimbrite grey, quartz) was presented to the subjects (n = 15). Like in the previous experiment, there were also two stone materials that were preferred: basalt and ignimbrite. Of these two, ignimbrite was the most selected material (t = 2.445, df = 41,303; p = 0,019).

All stones were used by the subjects. Of the 15 stones, six (40%) were used as both hammer and anvil. Thus, we sought to verify if the other 9 stones (60%) were used due to their morphological features as well. Results showed significant differences between anvil and hammers in width (t = 3.705, df = 15.687; p = 0.002), length (t = 3.755, df = 14.273; p = 0.002), and height (t = 2.984, df = 15.695; p = 0.009). Anvils were wider, longer and taller than hammers. Pearson correlation (two-tailed) indicated a significant correlation between tool dimensions and function (Table 4). On the use of tools, it is important to note that seven subjects (11%), instead of using an anvil, preferred to perform the task on the ground. Most of the occurrences (n=6) happened when performing the task without any previous model. Only one subject did not use an anvil after watching the chimpanzee video demonstration.

Table 4: Pearson correlation (r; two-tailed) between tool measures and function in Study 2, school-age human experiments (n = 9).

	Tool width	Tool lenght	Tool height	Function
Tool width (cm)		0,956**	0,952**	-0,843**
Tool lenght (cm)			0,954**	-0,794*
Tool height (cm)				-0,847**
* <i>p</i> < 0.05				

**p < 0.01

3.2.2 – *Time to select tools and time to complete task*

We analysed the time taken to select tools in male and female pairs, and the results show a significant difference between genders (t = -4.054, df = 37; p = <0.001): males took less time to select tools than females. Regarding the time of tool selection according to the three experimental conditions, the one-way ANOVA test showed no differences between the groups [F (3, 35) = 1.870, p = 0.153]. Moreover, the one-way ANOVA was also conducted to analyse differences between the total times to complete the task regarding the experiment conditions. No differences were found between the groups [F (3, 35) = 0.221, p = 0.881]. The same result was observed for the total time to complete the task according to gender (t = -1.588, df = 15.896; p = 0.132).

3.2.3 – Nut cracking efficiency: Number of bouts to crack nut #1, #2 and #3

Similarly to the experiments with adults, three nuts were presented to each subject and he/she had three attempts to complete the task. Hence, a paired-samples t-test was conducted to compare if there were differences over the three attempts. Results show no differences between the first attempt (M = 14.61, SD= 47.333) and the second one (M= 8.67, SD= 28.221) (t =1.913, df = 63; p = 0.60), or between the second attempt (M = 8.67, SD = 28,221) and the third (M = 11.38, SD= 22.447) (t = -0.676, df = 65; p = 0.501). No differences were found between genders in the first two attempts of nut cracking: first attempt (t = -1.948, df = 31.860; p = 0.060), second attempt (t = -1.468, df = 31.759; p= 0.152). However, there were significant differences in the third attempt (t = -2.533, df =33.239; p = 0.016), with males needing less bouts to succeed than females.

To see if there were differences in the number of bouts per attempt regarding the different age groups (Fig. 3), an one-way ANOVA test was conducted, that showed differences for the first attempt [F (2, 64) = 7.510, p = 0.001). The Tukey post-hoc test showed that the children from the age group I needed more bouts than children from age group II (p = 0.002), and the children from age group III (p = 0.003). There were no significant differences between the age groups II and III (p = 0.988). For the second attempt, Tukey test showed no differences between age group I and age group II (p = 0.063), and between age group I and age group III (p = 0.068), the same occurred between age group II and age group III (p = 0.850). Regarding the third attempt, Tukey test showed that children from age group I needed more bouts than the children from the other age groups: age group I and age group II (p = 0.003) and age group II (p = 0.003).

0.027), results show no significant differences between children from age group II and children from age group III (p = 0.601).

Furthermore, in order to understand if the experimental conditions influenced the amount of bouts over the attempts, an one-way ANOVA test was conducted, not revealing significant differences: first attempt [F (2, 64) = 1.010, p = 0.370], second attempt [F (2, 63) = 1.318, p = 0.275] and finally the third attempt [F (2, 63) = 0.841, p = 0.436].

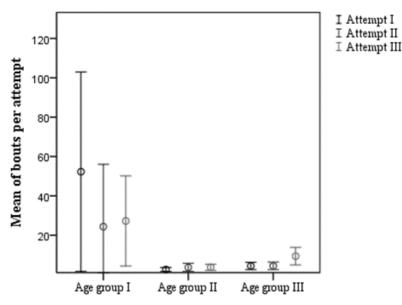


Figure 3: Error bar for the school age subjects experiment with the mean of bouts per attempt by age group.

3.2.4 – Subjects' behaviour

The analysis of the subjects' behaviour according to the different experimental conditions revealed different patterns according to the three age groups. The two conditions – nut cracking performed with no human role model and a video model – could be analysed together since the same behavioural pattern was observed (Fig. 4).

Concerning the subjects from age group I (n = 10), six subjects (60%) observed their partner performing the task, contrasting with four subjects (40%) who performed the task without watching their partner. The opposite occurred for the other age groups: in the age group II (n = 20), four subjects (20%) observed the partner and 14 subjects (70%) did not watch the partner. It is important to mention that two subjects (10%), innovated by using a wedge stone when performing the condition with the video model. For the age group III (n = 16), two subjects (12.5%) watched their partner and 13 (81.3%) did not watch their partner. In this case an innovation was also observed by using a wedge stone performed by one subject (6.3%) when performing the condition with the video model.

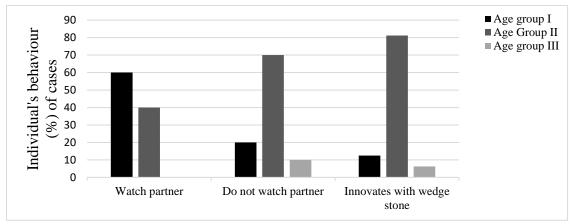


Figure 4: Behavioural patterns in school-age subjects with no human role model and video model by age group.

Regarding condition 3, using a human role model (a demonstration with/without a wedge stone), several behavioural patterns were observed (Fig 5): in subjects from age group I (n = 5) three (60%) did not copy the adult demonstrator, one subject (20%) used the same anvil as the demonstrator and one (20%) used the same hammer as the adult in the demonstration, while none of the subjects followed the wedge example. For the age group II (n = 4), three subjects (75%) did not copy the adult demonstrator, one subject (25%) used the same tools as the adult, and none of the subjects followed the wedge example. Finally, a different behavioural pattern emerged for the children from the age group III (n = 11), where four subjects (36.4%) did not copy the model, one subject (9.1%) used the same anvil, two subjects (18.1%) used the same tools as the adult, and four subjects (36.4%) followed the (non-functional) wedge example.

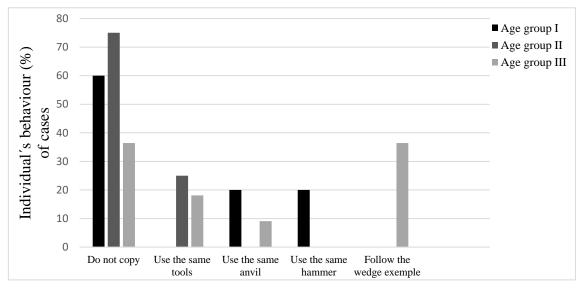


Figure 5: Behavioural pattern in school age subjects with a human role model by age group.

4 – Discussion and conclusions

This study shows similar results for both experiments regarding the tool use behaviour. Despite the variety of raw materials available in both experiments, adults and school-age humans selected one type of material more often: basalt and ignimbrite, respectively. Thus, it appears that both groups had a preference for a certain type of material. Results also show that tools selected for a specific function – anvil or hammer – are differentiated by the subjects based on their morphological features such as width, length, height and weight. This suggest that subjects select tools based on particular raw materials features as well as they distinguish the morphological traits of the stones and give them a specific function. The results show close similarities with those obtained by studies on wild chimpanzees, where tools were reported to be selected based on raw material type and similar morphological traits (Sakura and Matsuzawa, 1991; Carvalho *et al.*, 2008; Carvalho *et al.*, 2009).

Regarding the time to select tools and time to complete task, in Study 1 the results show that there were no significant differences between genders. The same was observable between the control group and the subjects, as well as between the genders within the control group. In relation to Study 2, the results show that the three experimental conditions appear to have no effect on the time spent selecting tools. On the other hand, an analysis by gender indicated that males needed less time to select a tool than females. With regard to the total time for task completion, the results showed that the different conditions of the experiment did not influence the total time to complete the task. The same could be observed for the different genders.

Concerning efficiency during the task itself, i.e. the number of attempts necessary to crack one nut, similar patterns were observed in Studies 1 and 2. No significant differences were observed in the performance over the three attempts by the global group of participants. However, analysing the mean of bouts over the three attempts (Fig. 2 and 3), results appear to illustrate how humans are capable to improve extremely fast when learning a new task, as humans needed significant less bouts in the second and third attempts. This seems to contrast with the data available for chimpanzees: in the wild, chimpanzees need a relatively long period of time to learn how to be proficient in nut cracking (Hayashi and Inoue-Nakamura, 2011). Nevertheless, it is important to mention that the mean of bouts that a human needed to crack open a nut is significantly higher when compared with wild chimpanzees in the same task. Field studies show that chimpanzees proficient in nut cracking need on average more than two bouts to crack open a nut (Biro *et al.*, 2003; 2006), and in this study some subjects needed more than 80 bouts to be successful. Moreover, in both experiments, subjects (n = 32) failed to crack-open at least one nut without smashing the kernel or had some problems dealing with the hammer. Therefore, it appears that when humans are exposed to a novel task the learning curve may very fast undergo an exponential increase when compared to our closest living relatives. However, "fast" does not equal "good": chimpanzees may take about 3.5 years to become proficient nutcrackers, albeit once they reach that stage they are highly efficient in the task – in this study the subjects quickly improve their time to accomplish the task, but their efficiency (both in number of bouts of crack one nut and success in cracking the nut without smashing) is still low, in both human groups tested and regardless of the experimental condition.

These results call for a discussion about our anthropocentric views of what is, supposedly, a "simple" or "rudimentary" technology: a task considered as basic as the use of two stones to crack one nut might be challenging for a modern human (*Homo sapiens*) if there was no previous exposure to the behaviour, In this sense, this study reinforces that, at least for primates, social contexts must have played a key role in the processes of learning and acquiring new technological behaviours throughout our evolution – and mastering what we label as "complex tools" may be more dependent on opportunities for social exposure and observation than necessarily on complex cognition.

When analysed by gender, in the Study 1 females needed more bouts (M = 15.16, SD = 28.628) to complete the task over the attempts than males (M = 3.59, SD = 4.339); in the Study 2 males needed less bouts in the last attempt (M = 4.68, SD = 5.943) than females (M = 18.50, SD = 30,334). These results appear to contrast with studies carried out in wild chimpanzees, in the Taï forest, where adult females were more efficient when cracking open nuts with stone tools than males (Boesch and Boesch, 1981, 1884). Study 2 also showed that the three experimental conditions did not influence the number of bouts necessary to complete the overall task. However, the opposite occurred in relation to age groups: the individual's age seemed to affect the nut-cracking performance, i.e., the younger the individual the harder was for him/her to solve the task.

Regarding the behavioural pattern of the subjects in the Study 1, the experiments with human adults, an "innovative" method of nut cracking could be observed, where the subject rearranged the tools in order to perform the task. This human tendency for behavioural innovation appears to contrast with the chimpanzees' conservative behaviour (Hrubesch *et al.*, 2009; Whiten *et al.*, 2009; Whiten, 2011), and may represent a pivotal difference between human and nonhuman cultural behaviour. Concerning the Study 2, both role models, either a video or an adult, seemed to have influenced the subjects' behaviour. The study shows that watching a video, even though performed by a nonhuman animal, can influence the way children execute their task. Also, older individuals tended to over-imitate the adult demonstrator. These results appear to pinpoint that over-imitation is affected by the age of the individual (Whiten *et al.*, 2009; Nielsen and Tomaselli, 2010).

A behavioural pattern was also observed in subjects that executed the task without any role model. In the school-age subjects organized by pairs, younger subjects tended to observe more their partner's actions performing the task than older children (Fig. 5). This seems to point that the ability of copying or mimic the actions of others or the capacity to imitate the body movements of others (Massen and Prinz, 2009), and to be able of acquiring knowledge via horizontal transmission (Horner *et al.*, 2006; Flynn and Whiten, 2008; Stout, 2014; Hewlett *et al.*, 2011) might represent a key pathway for human social transmission of knowledge. Nevertheless, is important to point that older individuals (age group III) stopped watching their partner (Fig. 4) and copied more the adult model (changing the pathway for transmission from horizontal to vertical). This is different from chimpanzees, as they will observe mostly their kin (mothers) until they reach subadulthood and then will observe their most skilled conspecifics (adults).

The present study appears to support the results of Reindl *et al.* (2016), reporting that naïve individuals in a task, such as nut cracking, are capable of executing it without the need of prior instructions or demonstrations albeit in this study we show that subjects have low levels of efficiency when executing the task; individual's age appears to be preponderate to solve it: older individuals were more likely to solve the task than younger individuals; and also percussive behaviour is likely to have been in the realm of the capabilities of *Homo* and *Pan* last common ancestor (LCA) - to acquire this behaviour it would not be necessary complex cultural transmission mechanisms.

The findings presented here have also some implications regarding the interpretation of early hominin lithic behaviour. Studies suggest similarities between *Pan* nut cracking and early hominin stone tool use behaviour, where evidence indicates an existence of percussion using hammer and anvil tools either for accessing to food or stone-on-stone percussive flacking (Toth and Schick, 2009; Whiten *et al.*, 2009).

Literature shows that percussive flaking is within the capacity of *Pan*. Schick *et al.* (1999) have shown that a bonobo is capable of stone tool making and will spontaneously learn the essence of the skill through observation of others. In this sense we can infer that a pre-Oldowan culture involving basic percussive flaking is actually within the capacity of *Pan* and our common ancestor (Whiten *et al.*, 2009). Furthermore, the transmission of such skills would have parallels between the *Pan* and early Oldowan hominins (Toth and Schick, 2009), and would not require complex cultural transmission mechanisms.

The current work consisted in an experimental study where naive human primates, both adults and school-age subjects, performed a nut-cracking task present in the behavioural spectrum of several extant primates, including the closest relative of the human linage. Through this study we highlight the role of sociality in the development of tool use skills as well as the role of models for learning a new task. Further investigations in this topic with more exhaustive experimental approaches would be important to better comprehend the influence of social learning in the acquisition of novel tasks in human and nonhuman primate and to give further insights into the lives of our hominins ancestors.

5 – References

- Ambrose, S. (2001). Paleolithic technology and human evolution. *Science*, 291(5509), 1748–1753.
- Beck, S. R., Apperly, I., Chappell, J., Guthrie, C., and Cutting, N. (2011). Making tools isn't child's play. *Cognition*, 119(2), 301–306. http://doi.org/10.1016/j.cognition.2011.01.003
- Behne, T., Carpenter, M., Gräfenhain, M., Liebal, K., Liszkowski, U., Moll, H., RaKoczy, H., Tomasello, M., Warneken, F Wyman, E. (2008). Cultural learning and cultural creation. In U. Müller, J. I. M. Carpendale, N. Budwig, and B. Sokol (Eds.), *Social life and social knowledge: Toward a process account of development* (pp. 65–101). L. Erlbaum Associates.
- Benito-Calvo, A., Carvalho, S., Arroyo, A., Matsuzawa, T., and de la Torre, I. (2015). First GIS Analysis of Modern Stone Tools Used by Wild Chimpanzees (*Pan troglodytes verus*) in Bossou, Guinea, West Africa. *PLoS ONE*, 10(3), e0121613. http://doi.org/10.1371/journal.pone.0121613

- Bentley-Condit, V., and Smith, E. O. (2010). Animal tool use: current definitions and an updated comprehensive catalog. *Behaviour*, 147(2), 185–32A. http://doi.org/10.1163/000579509X12512865686555
- Biro, D. (2011). Clues to Culture? The Coula- and Panda-Nut Experiments. In T. Matsuzawa, T. Humle, and Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba*. (pp. 165–173). Tokyo: Springer.
- Biro, D., Carvalho, S., Gwyther, A., and Matsuzawa, T. (n.d.). Tool inheritance: Stonetool "recycling" increases efficiency in wild juvenile chimpanzees. *Submitted to Current Biology*.
- Biro, D., Carvalho, S., and Matsuzawa, T. (2010). Tools, traditions, and technologies: interdisciplinary approaches to chimpanzee nut-cracking. In E. V. Lonsdorf, R. R. Stephen, and T. Matsuzawa (Eds.), *The Mind of the Chimpanzee: Ecological and Experimental Perspectives*. (pp. 141–155). University Of Chicago Press.
- Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., and Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition*, 6(4), 213–223. http://doi.org/10.1007/s10071-003-0183-x
- Biro, D., Sousa, C., and Matsuzawa, T. (2006). Ontogeny and cultural propagation of tool use by wild chimpanzees at Bossou, Guinea: case studies in nut-cracking and leaf folding. In T. Matsuzawa, M. Tomonaga, and M. Tanaka (Eds.), *T. Matsuzawa, Masaki Tomonaga, and M. Tanaka (Eds.) Cognitive Development in Chimpanzees* (pp. 476–522). Springer Japan.
- Boesch, C. (1991). Teaching among wild chimpanzees. Animal Behaviour.
- Boesch, C., and Boesch, H. (1884). Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *Journal of Human Evolution*, 13(5), 415–440. http://doi.org/10.1016/S0047-2484(84)80055-X
- Boesch, C., and Boesch, H. (1981). Sex differences in the use of natural hammers by wild chimpanzees: A preliminary report. *Journal of Human Evolution*, 10(7), 585–593. http://doi.org/10.1016/S0047-2484(81)80049-8
- Boesch, C., and Boesch, H. (1990). Tool use and tool making in wild chimpanzees. *Folia Primatologica; International Journal of Primatology*, 54(1–2), 86–99.

- Boesch, C., Head, J., and Robbins, M. M. (2009). Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution*, 56(6), 560–569.
- Breuer, T., Ndoundou-Hockemba, M., and Fishlock, V. (2005). First observation of tool use in wild gorillas. *PLoS Biology*, 3(11), 2041–2043.
- Bril, B., Rein, R., Nonaka, T., Wenban-Smith, F., and Dietrich, G. (2010). The role of expertise in tool use: skill differences in functional action adaptations to task constraints. *Journal of Experimental Psychology. Human Perception and Performance*, 36(4), 825–39. http://doi.org/10.1037/a0018171
- Buttelmann, D., Carpenter, M., Call, J., and Tomasello, M. (2013a). Chimpanzees, Pan troglodytes, recognize successful actions, but fail to imitate them. *Animal Behaviour*, 86(4), 755–761.
- Buttelmann, D., Carpenter, M., Call, J., and Tomasello, M. (2013b). Chimpanzees , Pan troglodytes, recognize successful actions, but fail to imitate them. *Animal Behaviour*, 86(4), 755–761.
- Byrne, R. (2004). The manual skills and cognition that lie behind hominid tool use. In A.E. Russon and D. R. Begun (Eds.), *Evolutionary Origins of Great Ape Intelligence* (pp. 31-44). Cambridge University Press.
- Carvalho, S., Biro, D., McGrew, W. C., and Matsuzawa, T. (2009). Tool-composite reuse in wild chimpanzees (*Pan troglodytes*): archaeologically invisible steps in the technological evolution of early hominins? *Animal Cognition*, 12(1), 103–114.
- Carvalho, S., Braun, D. R., Kaplan, R., Biro, D., Plummer, T., and Matsuzawa, T. (n.d.).Chimpanzee tool use involves an understanding of mechanical properties of stones:A comparison with the Oldowan archaeological record. *Manuscript in Preparation*.
- Carvalho, S., Cunha, E., Sousa, C., and Matsuzawa, T. (2008). Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal of Human Evolution*, 55(1), 148–63. http://doi.org/10.1016/j.jhevol.2008.02.005
- Carvalho, S., Gama Mota, P., Bobe, R., Marques, R., Biro, D., Braun, D. R., and Matsuzawa, T. (n.d.). Skilled individuals consolidate stone tool use behaviour in wild chimpanzees. *Manuscript in Preparation*.

- Chappell, J., Cutting, N., Apperly, I. A., and Beck, S. R. (2013). The development of tool manufacture in humans: what helps young children make innovative tools? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 368(1630), 20120409.
- Chappell, J., and Kacelnik, A. (2002). Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). Animal Cognition, 5(2), 71–78. http://doi.org/10.1007/s10071-002-0130-2
- Csibra, G., and Gergely, G. (2006). Social learning and social cognition : The case for pedagogy. In Y. Munakata and M. Johnson (Eds.), *Processes of change in brain and cognitive development*. *Attention and performance XXI*. (pp. 249–274). Oxford, UK: Oxford University Press. http://doi.org/10.1.1.103.4994
- Cutting, N., Apperly, I. a, Chappell, J., and Beck, S. R. (2014). The puzzling difficulty of tool innovation: why can't children piece their knowledge together? *Journal of Experimental Child Psychology*, 125, 110–117. http://doi.org/10.1016/j.jecp.2013.11.010
- d'Errico, F., and Stringer, C. B. (2011). Evolution, revolution or saltation scenario for the emergence of modern cultures? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *366*(1567), 1060–1069.
- Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., and Laland, K. L. (2012).
 Identification of the Social and Cognitive Processes Underlying Human Cumulative
 Culture. Science, 335(6072), 1114–1118.
 http://doi.org/http://doi.org/10.1126/science.1213969
- Dean, L., Vale, G. L., Laland, K. N., Flynn, F. G., and Kendal, R. L. (2014). Human cumulative culture: a comparative perspective. *Biological Reviews*, 89(2), 284–301. http://doi.org/http://dx.doi.org/10.1111/brv.12053
- de Resende, B. D., Ottoni, E. B., and Fragaszy, D. M. (2008). Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): a perception-action perspective. *Developmental Science*, 11(6), 828–840. http://doi.org/10.1111/j.1467-7687.2008.00731.x
- Flynn, E., and Whiten, A. (2008). Cultural Transmission of Tool Use in Young Children:A Diffusion Chain Study. *Social Development*, 17(3), 699–718.

http://doi.org/10.1111/j.1467-9507.2007.00453.x

- Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. B., and De Oliveira, M. G. (2004). Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, 64(4), 359–366. http://doi.org/10.1002/ajp.20085
- Geribàs, N., Mosquera, M., and Vergès, J. M. (2010). What novice knappers have to learn to become expert stone toolmakers. *Journal of Archaeological Science*, 37(11), 2857–2870. http://doi.org/10.1016/j.jas.2010.06.026
- Gumert, M. D., and Malaivijitnond, S. (2012). Marine prey processed with stone tools by burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. *American Journal of Physical Anthropology*, 149(3), 447–457. http://doi.org/10.1002/ajpa.22143
- Gumert, M. D., and Malaivijitnond, S. (2013). Long-tailed macaques select mass of stone tools according to food type. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 368(1630), 20120413. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/24101623
- Gumert, M., and Malaivijitnond, S. (2013). Long-tailed macaques select mass of stone tools according to food type. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1630), 20120413. Retrieved from http://rstb.royalsocietypublishing.org/content/368/1630/20120413.short
- Harmand, S., Lewis, J. E., Feibel, C. S., Lepre, C. J., Prat, S., Lenoble, A., Boës, X., Quinn, R. L., Brenet, M., Arroyo, A., Taylor, N., Clément, S., Daver, G., Brugal, J., Leaky, L., Mortlock, R. A., Wright, J. D., Lokorodi, S., Kirwa, C., Kent, D. N., Roche, H. (2015). 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature*, *521*(7552), 310–315. Retrieved from http://www.nature.com/doifinder/10.1038/nature14464
- Hayashi, M., and Inoue-Nakamura, N. (2011). From Handling Stones and Nuts to Tool-Use. In Matsuzawa, T., Humle, T.; Sugiyama, Y. (eds). The chimpanzees of Bossou and Nimba. Tokyo: Springer (pp. 175–182).
- Heinzelin, J. d., Clark, J. D., White, T., Hart, W., and Renne, P. (1999). Environment and Behavior of 2.5-Million-Year-Old Bouri Hominids. *Science*, 284(5414), 625–629. http://doi.org/10.1126/science.284.5414.625

- Hewlett, B. S., Fouts, H. N., Boyette, A. H., and Hewlett, B. L. (2011). Social learning among Congo Basin hunter-gatherers. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 366(1567), 1168–78. http://doi.org/10.1098/rstb.2010.0373
- Heyes, C. (1994). Social learning in animals: categories and mechanisms. *Biological Reviews*. Retrieved from http://onlinelibrary.wiley.com/doi/10.1111/j.1469-185X.1994.tb01506.x/full
- Horner, V., and Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition*, 8(3), 164–181. http://doi.org/10.1007/s10071-004-0239-6
- Horner, V., Whiten, A., Flynn, E., and de Waal, F. B. M. (2006). Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proceedings of the National Academy of Sciences of the United States of America*, 103(37), 13878–13883.
- Hrubesch, C., Preuschoft, S., and van Schaik, C. (2009). Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*). Animal Cognition, 12(2), 209–216. http://doi.org/10.1007/s10071-008-0183-y
- Humle, T. (2011). The Tool Repertoire of Bossou Chimpanzees. In Matsuzawa, T., Humle, T., Sugiyama, Y. (eds). The chimpanzees of Bossou and Nimba. Tokyo: Springer (pp. 61–71).
- Iriki, A. (2006). The neural origins and implications of imitation, mirror neurons and tool use. *Current Opinion in Neurobiology*, 16(6), 660–7. http://doi.org/10.1016/j.conb.2006.10.008
- Izawa, K., and Mizuno, A. (1977). Palm-fruit cracking behavior of wild black-capped capuchin (*Cebus apella*). *Primates*, 18(4), 773–792. http://doi.org/10.1007/BF02382930
- Johnson-Frey, S. H. (2004). The neural bases of complex tool use in humans. *Trends in Cognitive Sciences*, 8(2), 71–8. http://doi.org/10.1016/j.tics.2003.12.002
- Koops, K., Furuichi, T., and Hashimoto, C. (2015). Chimpanzees and bonobos differ in intrinsic motivation for tool use. *Scientific Reports*, 5, 11356. Retrieved from http://www.nature.com/doifinder/10.1038/srep11356%5Cnhttps://www.sciencedail

y.com/releases/2015/06/150616072318.htm

- Leroi-Gourhan, A. (1964). Le Geste et la Parole I: Technique et Language. Paris: A. Michel.
- Leroi-Gourhan, A. (1965). Le Geste et la Parole II: La mémoire et les rhythmes. Paris: A. Michel.
- Leroi-Gourhan, A. (1983). Les chasseurs de la préhistoire. Paris: Editions A.-M. Métailié.
- Lewis, J. E., Harmand, S., Harmand, S., Leakey, L., Tobias, P., Napier, J., Harris, J., Quinn, R. L., Lepre, C. J., Feibel, C. S., Wright, J. D., Mortlock, R. A., Brugal, J-P., Roche, H., Bobe, R., Behrensmeyer, A. K., Chapman, R. E., Potts, R., Wynn, J. G., Stanley, S. M., Leakey, M. D., Tiercelin, J-J., Semaw, S., Renne, P. R., Bernor, R. L., Fesseha, N., Mowbray, K., Prat, S., Kimbel, W. H., Antón, S. C., Aiello, L. C., Panger, M. A., Brooks, AS., Richmond, B. G., Wood, B., Kivell, T. L., Kibii, J. M., Churchill, S. E., Schmid, P., Berger, L. R., Susman, R. L., Skinner, M. M., Stephens, N. B., Tsegai, Z. J., Foote, A. C., Nguyen, N. H., Gross, T., Pahr, D. H., Hublin, J-J., McPherron, S. P., Alemseged, Z., Marean, C. W., Reed, D., Geraads, D., Béarat, H., Campisano, C. J., Torre, I., Delagnes, A., Feibel, C., Kibunjia, M., Mourre, V., Texier, P. J., Stout, D., Rogers, M. J., Cauche, D., Goldman-Neuman, T., Hovers, E., Beaune, S,A., Domínguez-Rodrigo, M., Mora, R., Diez-Martín, F., Sánchez, P., Mabulla, A., Barba, R., Blumenschine, R. J., Selvaggio, M. M., Villmoare, B., Seyoum, C., Dimaggio, E., Rowan, J., Braun, D. R., Arrowsmith, J. R., Reed, K. E., Bril, B., Smaers, J., Steele, J., Rein, R., Nonaka, T., Dietrich, G., Biryukova, E., Hirata, S., Roux, V., Diez-Martin, F., Yustos, P., Mabulla, A. Z., Bunn, H. T., Ashley, G. M., Baquedano, E., Spoor, F., Gunz, P., Neubauer, S., Stelzer, S., Scott, N., Kwekason, A., Dean, M. C., Haile-Selassie, Y., Gibert, L., Melillo, S. M., Ryan, T. M., Alene, M., Deino, A., Levin, N. E., Scott, G., Saylor, B. Z., Ward, C. V., Hammond, A. S., Leakey, L. N., Moffett, E. A., Plavcan, J. M., Leakey, M. G., Dirks, P. H., Almécija, S., Wallace, I. J., Judex, S., Alba, D. M., Moyà-Solà, S., Carvalho, S., Cunha, E., Sousa, C., Matsuzawa, T., Delezene, L. K., Brown, F. H., Gathogo, P. N., Kiarie, C., McDougall, I., Smaers, J. B., Case, C. R., Cowper, A., Amunts, K., Zilles, K., Schoenemann, P. T., Chaminade, T., Dunbar, R. I., Shultz, S., Uylings, H. B., Jacobsen, A. M., Johnson-Frey, S. H., Jäncke, L., Mohlberg, H., Steinmetz, H., Asplund, C. L., Todd, J. J., Snyder, A. P., Marois, R.,

Parry, R., Brown, B., Walker, A., Cavallo, J. A., Pobiner, B. L., Haslam, M., Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R., Boesch, C., Visalberghi, E., Spagnoletti, N., Fragaszy, D. (2016). An earlier origin for stone tool making: implications for cognitive evolution and the transition to Homo. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 371(1698), 310–315. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/27298464

- Lyons, D., Young, A., and Keil, F. (2007). The hidden structure of overimitation. Proceedings of the National Academy of Sciences of the United States of America, 104(50), 19751-6. Retrieved from http://www.pnas.org/content/104/50/19751.short
- Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., and Hamada, Y. (2007). Stone-Tool Usage by Thai Long-Tailed Macaques (*Macaca fascicularis*). American Journal of Primatology, 69(2), 227–233. http://doi.org/10.1002/ajp
- Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., and Hamada, Y. (2007). Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). American Journal of Primatology, 69(2), 227–233.
- Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L., and Sherwin, W. B. (2005). Cultural transmission of tool use in bottlenose dolphins, *102*(25), 8939–8943.
- Marchant, L. F., and McGrew, W. C. (2005). Percussive technology: chimpanzee baobab smashing and the evolutionary modeling of hominin knapping. In V. Roux and B. Bril (Eds.), *Stone knapping: the necessary conditions for a uniquely hominin behaviour*. (pp. 341–350). Cambridge: McDonald Institute for Archaeological Research.
- Massen, C., and Prinz, W. (2009). Movements, actions and tool-use actions: an ideomotor approach to imitation. *Philosophical Transactions of the Royal Society of London*. *Series B, Biological Sciences*, *364*(1528), 2349–2358.
- Matsuzawa, T. (2002). Chimpanzee Ai and her son Ayumu: An episode of education by master-apprenticeship. In M. Bekoff, C. Allen, and G. M. Burghardt (Eds.), *The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition* (pp. 189–196). MIT Press.

Matsuzawa, T. (2006). Sociocognitive development in chimpanzees: A synthesis of

laboratory work and fieldwork. In T. Matsuzawa, Masaki Tomonaga, and M. Tanaka (Eds.), *Cognitive development in chimpanzees* (pp. 3–33). Springer-Verlag.

- Matsuzawa, T. (2011). Stone Tools for Nut-Cracking. In Matsuzawa, T., Humle, T.; Sugiyama, Y. (eds). The chimpanzees of Bossou and Nimba. Tokyo: Springer (pp. 73–83).
- Matsuzawa, T., Biro, D., Humle, T., Inoue-Nakamura, N., Tonooka, R., and Yamakoshi, G. (2001). Emergence of culture in wild chimpanzees: education by masterapprenticeship. In T. Matsuzawa (Ed.), *Primate origins of human cognition and behavior*. (pp. 557–574). Tokyo: Springer.
- McGrew, W. C. (2013). Is primate tool use special? Chimpanzee and New Caledonian crow compared. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1630), 20120422. http://doi.org/10.1098/rstb.2012.0422
- McPherron, S. P., Alemseged, Z., Marean, C. W., Wynn, J. G., Reed, D., Geraads, D., Bobe, R., Béarat, H. A. (2010). Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature*, 466(7308), 857–860.
- Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R., and Boesch, C. (2007). 4,300-Year-old chimpanzee sites and the origins of percussive stone technology. *Proceedings of the National Academy of Sciences of the United States* of America, 104(9), 3043–3048.
- Mercader, J., Panger, M. A., and Boesch, C. (2002). Excavation of a chimpanzee stone tool site in the African rainforest. *Science*, 296(5572), 1452–1455. doi/10.1126/science.1070268
- Mithen, S. (2001). The evolution of imagination: An archaeological perspective. *SubStance*, 30(1), 28–54.
- Musgrave, S., Morgan, D., Lonsdorf, E., Mundry, R., and Sanz, C. (2016). Tool transfers are a form of teaching among chimpanzees. *Scientific Reports*, 6(34783). http://doi.org/10.1038/srep34783
- Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., and Matsuzawa, T. (2004). Imitation in neonatal chimpanzees (*Pan troglodytes*). *Developmental Science*, 7(4), 437–442.

- Nielsen, M., and Tomaselli, K. (2010). Overimitation in Kalahari Bushman children and the origins of human cultural cognition. *Psychological Science : A Journal of the American Psychological Society / APS*, 21(5), 729–36.
- Ohashi, G. (2006). Behavioral Repertoire of Tool Use in the Wild Chimpanzees at Bossou. In T. Matsuzawa, M. Tomonaga, and M. Tanaka (Eds.), *Cognitive Development in Chimpanzees* (Vol. 1987, pp. 439–451). Springer. Retrieved from http://www.springerlink.com/index/10.1007/4-431-30248-4
- Ottoni, E. B., and Izar, P. (2008). Capuchin monkey tool use: Overview and implications. *Evolutionary Anthropology: Issues, News, and Reviews, 17*(4), 171–178. http://doi.org/10.1002/evan.20185
- Perry, S. (2011). Social traditions and social learning in capuchin monkeys (*Cebus*). *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 366(1567), 988–996. http://doi.org/10.1098/rstb.2010.0317
- Pozzi, L., Hodgson, J. A., Burrell, A. S., Sterner, K. N., Raaum, R. L., and Disotell, T. R. (2014). Primate phylogenetic relationships and divergence dates inferred from complete mitochondrial genomes. *Molecular Phylogenetics and Evolution*, 75(1), 165–183.
- Proffitt, T., Luncz, L. V., Falótico, T., Ottoni, E. B., de la Torre, I., and Haslam, M. (2016). Wild monkeys flake stone tools. *Nature*, 539(7627), 85–88. Retrieved from http://www.nature.com/doifinder/10.1038/nature20112
- Rat-Fischer, L., O'Regan, J. K., and Fagard, J. (2012). The emergence of tool use during the second year of life. *Journal of Experimental Child Psychology*, *113*(3), 440–446.
- Rein, R., Bril, B., and Nonaka, T. (2013). Coordination strategies used in stone knapping. *American Journal of Physical Anthropology*, 150(4), 539–550.
- Reindl, E., Beck, S. R., Apperly, I. A., and Tennie, C. (2016). Young children spontaneously invent wild great apes' tool-use behaviours. *Proceedings of the Royal Society B: Biological Sciences*, 283(1825), 20152402. Retrieved from http://rspb.royalsocietypublishing.org/content/283/1825/20152402
- Roux, V., and Bril, B. (2005). Stone knapping: the necessary conditions for a uniquely hominin behaviour. (V. Roux and B. Bril, Eds.). Cambridge: McDonald Institute for Archaeological Research.

- Sakura, O., and Matsuzawa, T. (1991). Flexibility of Wild Chimpanzee Nut-cracking Behavior Using Stone Hammers and Anvils: an Experimental Analysis. *Ethology*, 87, 237–248.
- Schick, K. D., Toth, N., Garufi, G., Savage-Rumbaugh, E. S., Rumbaugh, D., and Sevcik,
 R. (1999). Continuing Investigations into the Stone Tool-making and Tool-using
 Capabilities of a Bonobo (*Pan paniscus*). Journal of Archaeological Science, 26(7),
 821–832. Retrieved from
 http://linkinghub.elsevier.com/retrieve/pii/S0305440398903508
- Seed, A., and Byrne, R. (2010). Animal Tool-use. *Current Biology*, 20(23), 1032–1039. http://doi.org/10.1016/j.cub.2010.09.042
- Shumaker, R. W., Walkup, K. R., and Beck, B. B. (2011). *Animal tool behavior : the use and manufacture of tools by animals*. Baltimore, MD : Johns Hopkins University Press.
- Smyrl, A. (2014). Seen and not heard? Evaluating the prevalence imitation versus guided learning as methods of acquiring skill in the Paleolithic. Undergraduate Honors Theses. Paper199. Retrieved from http://scholar.colorado.edu/honr_theses/199
- St Amant, R., and Horton, T. E. (2008). Revisiting the definition of animal tool use. *Animal Behaviour*, 75(4), 1199–1208. http://doi.org/10.1016/j.anbehav.2007.09.028
- Stout, D. (2002). Skill and cognition in stone tool production: An ethnographic case study from Irian Jaya. *Current Anthropology*, 43(5), 693–723. Retrieved from http://www.jstor.org/stable/10.1086/342638
- Stout, D. (2014). Skill and Cognition in Stone Tool Production. *Current Anthropology*, *43*(5), 693–722.
- Stout, D., and Chaminade, T. (2009). Making tools and making sense: complex, intentional behaviour in human evolution. *Cambridge Archaeological Journal*, 19(1), 85–96.
- Stout, D., Semaw, S., Rogers, M. J., and Cauche, D. (2010). Technological variation in the earliest Oldowan from Gona, Afar, Ethiopia. *Journal of Human Evolution*, 58(6), 474–91. http://doi.org/10.1016/j.jhevol.2010.02.005
- Sugiyama, Y., and Koman, J. (1979). Tool-Using and -Making Behavior in Wild Chimpanzees at Bossou, Guinea. *Primates*, 20(4), 513–524.

- Tan, A., Tan, S. H., Vyas, D., Malaivijitnond, S., and Gumert, M. D. (2015). There is more than one way to crack an oyster: Identifying variation in burmese long-tailed macaque (*Macaca fascicularis aurea*) stone-tool use. *PLoS ONE*, 10(5).
- Tehrani, J. J., and Riede, F. (2008). Towards an archaeology of pedagogy: learning, teaching and the generation of material culture traditions. *World Archaeology*, 40(3), 316–331. http://doi.org/10.1080/00438240802261267
- Tennie, C., Call, J., and Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society of London*. *Series B, Biological Sciences, 364*(1528), 2405–2415. http://doi.org/10.1098/rstb.2009.0052
- Thornton, A., and McAuliffe, K. (2006). Teaching in wild meerkats. *Science*, *313*(5784), 227–9. http://doi.org/10.1126/science.1128727
- Tomasello, M. (1998). Emulation learning and cultural learning. *Behavioral and Brain Sciences*, 21(5), 703–704.
- Tomasello, M. (2011). Human culture in evolutionary perspective. In M. Gelfand, C. Chiu, and Y. Hong (Eds.), *Advances in culture and psychology*. (Volume 1, pp. 5–52). Oxford University Press.
- Tomasello, M., and Call, J. (1997). *Primate cognition*. New York: Oxford University Press.
- Tomasello, M., Kruger, A. C., and Ratner, H. H. (1993). Cultural learning. *Behavioral* and Brain Sciences, 16(3), 495–511. http://doi.org/10.1017/S0140525X0003123X
- Toth, N., and Schick, K. (2009). The Oldowan: The Tool Making of Early Hominins and Chimpanzees Compared. Annual Review of Anthropology, 38(1), 289–305. http://doi.org/10.1146/annurev-anthro-091908-164521
- Van Lawick-Goodall, J. (1968). The Behaviour of Free-living Chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, *1*, 161–IN12.
- Van Lawick-Goodall, J. (1971). Tool-Using in Primates and Other Vertebrates. Advances in the Study of Behavior, 3, 195–249. http://doi.org/10.1016/S0065-3454(08)60157-6

Van Schaik, C. P., and Knott, C. D. (2001). Geographic variation in tool use on Neesia

fruits in orangutans. American Journal of Physical Anthropology, 114(4), 331-342.

- Visalberghi, E., and Addessi, E. (2000). Seeing group members eating a familiar food enhances the acceptance of novel foods in Capuchin Monkeys. *Animal Behaviour*, 60(1), 69–76.
- Visalberghi, E., Addessi, E., Truppa, V., Spagnoletti, N., Ottoni, E., Izar, P., and Fragaszy, D. (2009). Selection of effective stone tools by wild bearded capuchin monkeys. *Current Biology: CB*, 19(3), 213–7. http://doi.org/10.1016/j.cub.2008.11.064
- Whiten, A. (1998). Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *112*(3), 270–281.
- Whiten, A. (2000). Primate culture and social learning. *Cognitive Science*, 24(3), 477–508.
- Whiten, A. (2005). The second inheritance system of chimpanzees and humans. *Nature*, *437*(7055), 52–55.
- Whiten, A. (2011). The scope of culture in chimpanzees, humans and ancestral apes. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 366(1567), 997–1007. http://doi.org/10.1098/rstb.2010.0334
- Whiten, A., Custance, D. M., Gomez, J. C., Teixidor, P., and Bard, K. A. (1996). Imitative learning of artificial fruit processing in children (Homo sapiens) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 110(1), 3–14.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C., Wrangham, R., Boesch, C. (1999). Cultures in chimpanzees. *Nature*, 399(6737), 682–685. Retrieved from http://dx.doi.org/ 10.1038/21415
- Whiten, A., McGuigan, N., Marshall-Pescini, S., and Hopper, L. M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), 2417–2428.

Whiten, A., Schick, K., and Toth, N. (2009). The evolution and cultural transmission of percussive technology: integrating evidence from palaeoanthropology and primatology. *Journal of Human Evolution*, 57(4), 420–435.