Experimental approaches to the study of early hominin technology and cognition using great apes as behavioral models

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To the women of my family

A las mujeres de mi familia

A les dones de la meua família

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Abstract

Humans are a ubiquitous species on the planet and our success in adapting and transforming the environments we inhabit is arguably the result of our ability to successively improve traits across generations to increase our fitness (Henrich, 2017). This process is known as cumulative culture (Boyd & Richerson, 1996; Tomasello, 1999) and involves the modification and transmission of detailed information via the direct observation (e.g. copying) of a model's actions or products. Despite the growing interest in human cumulative culture, its origins are still debated. Some authors have proposed that early stone tools represent the earliest signs of cumulative cultural evolution in our lineage. According to this hypothesis, early hominins could not have learnt how to produce or use early stone tools individually without copying a model. A more parsimonious hypothesis regarding the learning mechanisms underlying the production and use of early stone tools could be derived from great apes (Tennie et al., 2009), who learn most of their tool behaviors individually without the need of copying a model (Chapter 2; Tennie et al., 2009). According to this hypothesis, early hominins acquired early stone tool making and using abilities via individual learning catalyzed by non-copying social learning mechanisms. Given that it is not possible to test early hominins directly in behavioral experiments, I investigated if and how two species of great apes (chimpanzees and orangutans) could acquire early stone tool making and using abilities in a series of baselines and social learning experiments (Chapters 2 to 5). The main finding from these experiments is that not all behaviors involved in the production and use of early stone tools are learnt in the same way by naïve, unenculturated chimpanzees and orangutans. Orangutans, but not chimpanzees, spontaneously perform percussive actions in which an active element is used to strike a hard surface. In one occasion, this behavior led to the detachment of sharp-edged stones from a flint core. In addition, one orangutan spontaneously used a human-made flake as a cutting tool to severe the lid of a baited puzzle box. Finally, after seeing demonstrations performed by a human model of how to make and use flakes, one orangutan and two chimpanzees engaged in percussive actions using an artificial hammer to strike a core. The results from these experiments show that certain behaviors such as the unintentional production of sharp-edged stone tools and the use of readily-made flakes as cutting tools can be individually learnt by orangutans. By phylogenetic proxy, such findings suggest that our last common

ancestor with orangutans might have already presented the cognitive and physical abilities necessary to perform these behaviors 13 Ma. However, some behaviors such as the intentional production of sharp-edged stone tools for their subsequent use as cutting tools, seem beyond the individual and social learning abilities of ecologically-representative (unenculurated) chimpanzees and orangutans. It is therefore possible, that the intentional production of sharp-edged stone tools only emerged in our lineage when certain abilities (such as copying social learning mechanisms) evolved in our lineage. If this were to be the case, the intentional production of sharp-edged stone tools would represent the starting or catalyzing point of cumulative culture in our lineage.

Abstrakt

Der Mensch ist eine allgegenwärtige Spezies auf diesem Planeten und unser Erfolg bei der Anpassung an - und die Umgestaltung der - Umwelt, in der wir leben, ist wohl das Ergebnis unserer Fähigkeit sukzessive über Generationen hinweg Merkmale zu verbessern, um unsere Fitness zu steigern (Henrich, 2017). Dieser Prozess wird als kumulative Kultur bezeichnet (Boyd & Richerson, 1996; Tomasello, 1999) und beinhaltet die Veränderung und Übermittlung detaillierter Informationen durch die direkte Beobachtung (z.B. durch Kopieren) der Handlungen oder Produkte eines Modells. Trotz des wachsenden Interesses an der menschlichen kumulativen Kultur wird über ihre Ursprünge immer noch debattiert. Einige Autoren haben vorgeschlagen, dass die frühen Steinwerkzeuge die frühesten Anzeichen einer kumulativen kulturellen Entwicklung in unserer Abstammungslinie darstellen. Dieser Hypothese zufolge hätten die frühen Homininen nicht gelernt haben können, wie man frühe Steinwerkzeuge einzeln herstellt oder benutzt, ohne ein Modell zu kopieren. Eine konservativere Hypothese bezüglich der Lernmechanismen, die der Herstellung und Verwendung früher Steinwerkzeuge zugrunde liegen, könnte von Menschenaffen abgeleitet werden (Tennie et al., 2009), die die meisten ihrer Werkzeugverhaltensweisen individuell lernen, ohne ein Modell kopieren zu müssen (Kapitel 2; Tennie et al., 2009). Nach dieser Hypothese erwarben die frühen Homininen die Fähigkeiten zur Herstellung und Verwendung von Steinwerkzeugen durch individuelles Lernen, das durch nicht-kopierende soziale Lernmechanismen katalysiert wurde. Da es nicht möglich ist, frühe Hominine direkt in Verhaltensexperimenten zu testen, untersuchte ich, ob und wie zwei Arten von Menschenaffen (Schimpansen und Orang-Utans) in einer Reihe von Basisexperimenten und sozialen Lernexperimenten (Kapitel 2 bis 5) frühe Fähigkeiten zur Herstellung und Verwendung von Steinwerkzeugen erwerben könnten. Die Haupterkenntnis aus diesen Experimenten ist, dass nicht alle Verhaltensweisen, die mit der Herstellung und dem Gebrauch von frühen Steinwerkzeugen zu tun haben, von naiven, unkultivierten Schimpansen und Orang-Utans auf die gleiche Weise erlernt werden. Orang-Utans, nicht aber Schimpansen, führen spontan perkussive Handlungen aus, bei denen ein aktives Element benutzt wird, um auf eine harte Oberfläche zu schlagen. In einem Fall führte dieses Verhalten dazu, dass sich scharfkantige Steine von einem Feuersteinkern lösten. Darüber hinaus benutzte ein

Orang-Utan spontan eine von Menschenhand gefertigte Flocke als Schneidewerkzeug, um den Deckel einer mit Köder versehenen Puzzleschachtel zu zertrümmern. Nachdem ein menschliches Modell demonstriert hatte, wie man Flocken herstellt und verwendet, führten ein Orang-Utan und zwei Schimpansen Schläge mit einem künstlichen Hammer auf einen Kern aus. Die Ergebnisse dieser Experimente zeigen, dass bestimmte Verhaltensweisen, wie die unbeabsichtigte Herstellung von scharfkantigen Steinwerkzeugen und die Verwendung von vorgefertigten Flocken als Schneidewerkzeuge, von Orang-Utans individuell erlernt werden können. In phylogenetischer Hinsicht deuten solche Befunde darauf hin, dass unser letzter gemeinsamer Vorfahre mit Orang-Utans bereits vor 13 Millionen Jahren die kognitiven und körperlichen Fähigkeiten gezeigt haben könnte, die für diese Verhaltensweisen erforderlich sind. Einige Verhaltensweisen, wie die absichtliche Herstellung von scharfkantigen Steinwerkzeugen für ihre spätere Verwendung als Schneidwerkzeuge, scheinen jedoch über die individuellen und sozialen Lernfähigkeiten ökologisch repräsentativer (unkultivierter) Schimpansen und Orang-Utans hinauszugehen. Es ist daher möglich, dass die absichtliche Herstellung von scharfkantigen Steinwerkzeugen in unserer Abstammungslinie erst dann entstand, als bestimmte Fähigkeiten (wie das Kopieren sozialer Lernmechanismen) in unserer Abstammungslinie entwickelt wurden. Wenn dies der Fall wäre, würde die absichtliche Herstellung von scharfkantigen Steinwerkzeugen den Ausgangspunkt oder den katalysierenden Punkt der kumulativen Kultur in unserer Linie darstellen.

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CHAPTER 1

General introduction

1. Learning mechanisms and cultures

Animal behavioural repertoires are the result of the complex interactions between different factors such as genetic predispositions, environmental affordances, rearing background, personality, motivational levels, ontogeny and learning. The latter, is the focus of this thesis.

Learning occurs when a change is produced in an animal due to an experience in a specific time, which can be later detected in the animal's behaviour (Heyes, 1994). Learning can occur in different ways or via different mechanisms depending on the type of information acquired and the source of this information. These mechanisms can be broadly divided into social learning mechanisms and individual learning mechanisms. Whereas, social learning involves the acquisition of information via the interaction with another individual or its products (Galef, 2003; Galef, 1988), individual learning refers to the process of acquiring information without directly interacting with another individual (Heyes, 1994). Examples of individual learning mechanisms include, among others, different forms of conditioning (e.g. operant, inhibitory, excitatory, etc) and trial and error learning (Heyes, 1994). Social learning can be further divided into copying social learning mechanisms (Tennie et al., in press) and non-copying social learning mechanisms. Copying social learning (generally referred in subsequent chapters as copying) takes place via mechanisms that allow for the detailed transmission of behavioural forms between individuals. This transmission can involve the physical actions themselves (imitation: Zentall, 2006) or the resulting artefacts or outcome of the behaviour (emulation: Tomasello, Kruger, et al., 1993). On the other hand, non-copying social learning takes place via mechanisms that can increase the frequency of a certain behavioural form in the population (e.g. they make it more likely to be performed) but do not allow for the transmission of the behavioural form itself (Bandini & Tennie, 2017; Tennie et al., 2009).

In the following sections I will summarize the methodologies and main findings from studies investigating the learning mechanisms underlying behavioural acquisition in primates. Most of these studies will focus on great apes (given the focus of this thesis) but occasionally examples from other taxa will be used for illustrative purposes. Although the list of studies mentioned in the following sections is by no means exhaustive, it was compiled in order to depict the discrepancies and debates present in the field of animal learning as well as the different experimental designs that have been developed in order to investigate how animals learn.

1.1 Imitation

The debate surrounding the presence of imitation in non-human animals (specially great apes) is about a century old (Galef, 1992). This debate arises from the fact that the ability to imitate, understood as copying the physical form of an action (Galef, 1988; Whiten & Ham, 1992), especially of cognitively opaque behaviours (Tomasello et al., 1993; Zentall, 2006), has been deemed crucial for the emergence of human culture (Tomasello, 1999). However, the ability for spontaneous imitation in non-human animals is still a controversial topic. If non-human animals would present imitative abilities similar to those present in humans this would indicate that these species possess at least some of the necessary cognitive abilities to develop human-like culture. Most imitation studies in non-human animals have focused on great apes, as due to their phylogenetic proximity to humans, they represent valuable behavioural and cognitive models to investigate the origins of our imitative abilities (Call et al., 2005; Horner & Whiten, 2005; Tennie et al., 2006; Tennie et al., 2012; Tomasello et al., 1997; Tomasello et al., 1987; Tomasello et al., 1993; Whiten et al., 1996; Whiten & Ham, 1992; Whiten et al., 2004; Whiten et al., 2009). Studies evaluating the imitative abilities in animals can be divided into those that test behaviours that involve object manipulation in order to solve a task and those that focus on pure actions that do not involve object manipulation nor problem solving.

Most of the studies claiming that non-human animals possess imitative abilities employ a paradigm known as two-target tasks (Custance et al., 1999; Dawson & Foss, 1965; Galef et al., 1986; Hopper et al., 2008; Horner & Whiten, 2005; Horner et al., 2006; Whiten et al., 1996; Whiten et al., 2005; Whiten et al., 2007). Two-target tasks involve puzzles boxes baited with food rewards that can be accessed via two alternative solutions (e.g. move a sliding door to the left or move it to the right in order to access a food reward hidden behind the door). Typically, in two-target tasks, two groups of subjects are exposed to two conspecifics (one conspecific per group), which have been trained in each of the two alternative puzzle solutions. These trained individuals then act as demonstrators in their group showing the observing individuals how to open the puzzle box using the action they have been trained to perform (for example, pushing a sliding door to the left). The rationale behind these experiments is that, if imitation takes place, the individuals of each group should learn to open the puzzle box by performing the action that has been demonstrated in their group. However, this methodology presents several limitations (Motes-Rodrigo et al., in press). First, it is often the case that the actions demonstrated in each of the groups are already within the behavioural repertoire of the tested subjects. These actions are generally simple and are spontaneously performed by the subjects during baseline conditions (e.g. Horner et al., 2006). Baseline conditions are experimental phases often included in behavioural experiments in which no social information is provided to the test subjects regarding how to solve the target task. Thus, if the test subjects are already familiar with the action which learning mechanism is under investigation, as it is often the case in two-target tasks, the results and conclusions of the experiment will not be accurate (reviewed by Tennie et al., in press). Second, the two solutions of the two-target tasks often result in different topographies/behavioural outcomes (e.g. the door ends up at the left or the right of the box; the door needs to be lifted so it ends up above its original position or the door needs to be moved sidewise so it ends up to one side of its original position). These different environmental results further confound if the observers are imitating the actions performed by the demonstrator (i.e. move the door to the left) or emulating the end-result (i.e. somehow the door has to be on the left to obtain a reward, see section 1.2 Emulation). A variation of the two-target task – the two-action task – involves two solutions that require the use of two different body parts (pecking or stepping on a target: Akins & Zentall, 1996). This alternative task design controls for the two different resulting topographies that limit the previously mentioned studies.

Studies on pure action imitation (not involving object manipulation) often use a paradigm known as the "Do-as-I-do" task. In this paradigm, subjects are trained during extensive periods of time to imitate demonstrated familiar actions from humans and then their imitative abilities are tested with the same and novel actions. Unfortunately, this task it also presents some caveats. First, Do-as-I-Do tasks have been shown to cause changes in the brain structure of the tested subjects. Chimpanzees (*Pan troglodytes*, N=4) that were trained to reproduce 23 actions using the Do-as-I-Do tasks were reported to have developed enhanced connectivity between fronto-parietal-temporal regions compared to chimpanzees trained in usual husbandry practices (Pope et al., 2018). These results led Pope et al. (2018) to suggest that these particular changes in brain structure may facilitate the development of imitative abilities, perhaps also in our lineage. Second, the results from Do-as-I-Do tasks are highly influenced by the rearing background of the test subjects. Specifically, it has been shown that enculturated great apes outperform unenculturated individuals in these tasks (Tomasello et al., 1993).

Enculturation is a process that often leads to the presence of human-like cognitive abilities in non-human animals due to the extensive human contact and training experienced during early life (Call & Tomasello, 1996). Enculturation has been shown to alter the cognitive abilities of great apes, enhancing for example their tendency to copy actions (Bjorklund et al., 2000; Bjorklund et al., 2002; Furlong et al., 2008; Tomasello & Call, 2004) and perhaps point (Leavens & Hopkins, 1999 but see Miklósi & Soproni, 2006). Therefore, great apes (and probably animals in general) that have been subjected to processes of enculturation are not cognitively representative of their unenculturated conspecifics neither living in captivity or in the wild (Henrich & Tennie, 2017).

Enhanced imitative abilities of novel actions which were not familiar to test subjects prior to testing (as reported by the authors) have been found in enculturated chimpanzees (N=3: Custance et al., 1995; Hribar et al., 2014), one enculturated orangutan (*Pongo pygmaeus*, Call, 2001) and one enculturated gorilla (*Gorilla*

gorilla, Byrne & Tanner, 2006) tested with the Do-as-I-Do task. Contrary to these results, studies testing the imitative abilities of unenculturated apes failed to find positive evidence that apes imitate actions. Three studies have tested unenculturated apes on their ability to imitate actions produced by human demonstrators (Clay & Tennie, 2017; Tennie et al., 2012; Tomasello et al., 1997). Tomasello et al. (1997) separately trained two female chimpanzees (ages 27 and 22 years) from two different groups to perform one and two begging gestures, respectively, in order to obtain food from a human. After reliably performing the trained gestures, the two females were returned to their groups where they performed the trained gestures for a reward while other individuals were present. None of the subjects that observed the two chimpanzee demonstrators reproduced the target gestures, despite the fact that these actions were not entirely novel to the chimpanzees according to the authors (Tomasello et al., 1997). Tennie et al. (2012) expanded and addressed some of the limitations discussed in the study by Tomasello et al. (1997) by training one male chimpanzee to demonstrate in front of conspecifics both familiar and unfamiliar actions across begging and non-begging contexts in order to obtain a reward. Only one male chimpanzee (who might have been enculturated) performed a familiar action demonstrated by the model in a begging context, which was interpreted as evidence of imitation of familiar actions (Tennie et al., 2012). No imitation of unfamiliar (novel) actions took place (Tennie et al., 2012). Finally, Clay and Tennie (2017) demonstrated familiar and unfamiliar actions to 46 bonobos (*Pan paniscus*) of various ages and found that none of the tested bonobos copied any of the demonstrated actions (Clay & Tennie, 2017).

In summary, and perhaps surprisingly, there is no compelling evidence suggesting that unenculturated apes copy novel actions. Tennie et al. (in press) reviewed the studies using two-target tasks to test the abilities of chimpanzees to copy demonstrated actions involving object manipulation. The authors found that in all but one of these studies (Whiten et al., 2007), the target actions were spontaneously performed by the test subjects during baseline conditions, showing that the chimpanzees were already familiar with the target actions beforehand. In addition, in most of these studies (including Whiten et al., 2007), the test subjects sometimes performed the alternative action to solve the puzzle box that had not been demonstrated by the trained conspecific. Both of these observations indicate that the chimpanzees did not rely on imitation to learn the actions necessary to solve the task and that often individual learning was sufficient to acquire the target behavioural forms. Therefore studies that have employed two-target tasks do not provide conclusive evidence that chimpanzees imitate novel actions. Studies that have investigated if great apes can copy actions that do not involve object manipulation using the Do-as-I-Do task have shown that the level of enculturation (i.e. the rearing background of the test subjects) is a crucial factor determining subjects' performance in the task. Studies testing trained, enculturated apes using the Do-as-I-Do task found that they could often imitate familiar and unfamiliar actions demonstrated (generally) by a human model. On the other hand, studies testing the spontaneous imitative abilities of unenculturated great apes found only very limited evidence that such apes copy familiar actions (Tennie et al., 2012) and no evidence that they can copy novel, unfamiliar actions. Thus, as noted by Köhler in 1927 imitation seems to be "a very rare occurrence [in the animal world] even among chimpanzees" (Köhler, 1927 sensu Tomasello, 1994).

1.2 Emulation

Emulation learning occurs when an individual learns about environmental affordances by observing the behaviour of another individual and uses this knowledge to develop its own behavioural strategies (Tomasello, 1996). According to this definition, emulation learning allows acquiring information about the causal structure of behaviours. The term emulation, which was originally coined by Wood (1989), was promoted and applied to great apes by Tomasello and colleagues, who tested chimpanzees' emulative abilities (Tomasello et al., 1987) and later compared these abilities with those of human children (Call et al., 2005; Nagell et al., 1993).

In their first emulation study, Tomasello and colleagues provided two groups of chimpanzees (a "young" and an "old" group) with a T-bar that could be used to rake in food items out of reach (Tomasello et al., 1987). The chimpanzees in each group were randomly divided in experimental subjects, which were exposed to a conspecific using the tool, and control subjects, which were not exposed to a conspecific using the tool. The authors of the study found that all young chimpanzees and one old chimpanzee learnt to use the tool. Within the young group, chimpanzees exposed to a conspecific using the tool learnt much faster to use the tool than those in the control group. However, the chimpanzees that learnt to use the tool in the experimental group did not use the tool in the same fashion as the demonstrator. This was interpreted by the authors as evidence that the tested chimpanzees did not copy the demonstrator but rather acquired information about the causal structure of the task (i.e. the tool could be used to bring food closer, but see Whiten et al., 2004).

After the definition of the term emulation by Tomasello, Whiten and colleagues re-described emulation as an umbrella term including several processes, namely end-state emulation, goal emulation, object movement re-enactment and affordance learning (Whiten et al., 2004). End-state emulation was described as the process where the presence of an end-result motivates an individual to replicate the result without encoding the relationship between the result and the model's goal (sensu Huang & Charman, 2005). Goal emulation refers to a process where an individual identifies the goal of a model and individually develops a strategy to reach that goal (Whiten & Ham, 1992). Object movement re-enactment refers to a process where the observation of a moving object that leads to a salient result motivates an observing subject to learn about the way in which the object or its parts can be manipulated to achieve the desired result (Custance et al., 1999). Finally, affordance learning refers to a process where the observer learns the temporal-spatial causal relationships of objects by observing a model manipulating said object (which matches the original definition of emulation by Tomasello, 1996).

Later studies (Byrne, 2002; Hopper et al., 2008), questioned the original criteria used by Tomasello and colleagues to assign emulative abilities to chimpanzees and employed a different experimental set up in order to assess the presence of emulative processes (Hopper et al., 2008): ghost conditions (Heyes et al., 1994). In ghost conditions there is no visible agent performing the demonstrated actions to observing individuals but instead the actions are remotely controlled (Heyes et al., 1994). For instance, in the study by Hopper et al. (2008) the door of a baited box was remotely moved by the experimenter using fishing line and keeping the experimenters actions out of sight of the observing chimpanzees. The goal of this study was to investigate if chimpanzees and human children would match the direction of movement of the box's sliding door demonstrated to them. As no agent was operating the testing apparatus in this condition, the subjects could not copy physical actions themselves but only the movement of the door (object movement re-enactment) or the end-position of the door (end-state emulation). Hopper and colleagues found that both chimpanzees and human children matched the first direction of the door demonstrated to them in the ghost condition, but only children continued to match it in later trials. Consequently, and as concluded by Hopper et al. (2008), chimpanzees seem to emulate at least in relatively simple tasks such as those involving a sliding door, using a raking tool (Tomasello et al., 1987) or opening a tube (Call et al., 2005).

1.3 Non-copying social learning mechanisms

Contrary to copying social learning mechanisms, non-copying social learning mechanisms do not allow for the direct transmission of behavioural forms (i.e. physical actions and behavioural outcomes or artefacts) between individuals. There is a wide variety of non-copying social learning mechanisms (Hoppitt & Laland, 2013) but local and stimulus enhancement are arguably the two mechanisms to which most experimental studies have been dedicated. Local enhancement occurs when the probability that an individual is drawn to a specific location increases because the salience of the location has been enhanced, generally by the presence of a conspecific or its interaction with an object at the target location (Hoppitt & Laland, 2013; Thorpe, 1963). A classical example of local enhancement is the opening of milk bottles by great tits in the UK (Fisher & Hinde, 1949). In the 50s, great tits were reported to have learnt how to open the top of milk bottles to access the milk all across the country (Fisher & Hinde, 1949), a finding that some authors interpreted as an example of imitation in birds (Marler, 1972). However, later studies showed that such behaviour could also emerge spontaneously in naïve individuals as well as by the mere exposure to opened bottles (Sherry & Galef, 1984). Therefore, a more parsimonious explanation for the great tit observations would be that naïve great tits were attracted to the milk bottles by the presence of conspecifics, which then led the tits to individually learn how to open the bottle tops.

Stimulus enhancement occurs when the attention of an individual is drawn towards a certain type of stimulus (e.g. an object class) because a conspecific was interacting with said stimulus (Hoppitt & Laland, 2013; Spence, 1937). For example, captive task-naïve macaques that observed a demonstrator using a tool to rake in food from outside their enclosure, used the same object class as the demonstrator to perform the behaviour, but the specific actions used did not match those of the demonstrator (Zuberbühler et al., 1996). These findings were interpreted as evidence that the macaques were attracted to the object class (stimulus) but did not imitate the demonstrated actions.

1.4 Culture

Understanding which learning mechanism(s) underlie the acquisition of a behaviour is necessary in order to establish the type of culture that a species possesses. In a broad sense, a species is deemed to possess culture if it presents a pattern of behavioural variation across populations that cannot be solely explained by environmental and/or genetic differences between these populations (see Chapter 2 for an in-depth review of the concept of culture). Cultures can be broadly divided into copying-based and non-copying based cultures (after Galef, 1992). Human cumulative culture is – in most if not all cases – a copying-based culture in which behavioural forms that are modified during and across generations are transmitted via copying social learning mechanisms (such as imitation) to culturally connected individuals (Boyd & Richerson, 1996; Tomasello, 1999). In turn, these connected individuals modify the behavioural forms further by adding innovations (Legare & Nielsen, 2015) or making mistakes during the transmission process (Eerkens & Lipo, 2005).

As a consequence of the successive modifications applied by different individuals through time, behavioural forms that result from cumulative cultural evolution often become causally opaque and/or so complex that no isolated individual can spontaneously learn them on his/her own (Tomasello et al., 1993) and can only learn them via copying social learning mechanisms. Such behavioural forms have become dependent on the knowledge stored in their containing cultures and thus have been named culture-dependent forms (after Reindl et al., 2017).

Many animal species, including great apes, have been argued to posses a different type of culture from that of humans, namely non-copying based cultures (Galef, 1992; Tennie et al., 2009; Tomasello, 2001). Contrary to cumulative culture, non-copying based cultures do not rely on copying social learning mechanisms and therefore, behavioural forms per se are not acquired by copying a model (via imitation or emulation). Instead, individuals of species that possess non-copying based cultures learn the species-specific behavioural forms via individual learning. These individually learnt behavioural forms, which all members of a species can spontaneously learn without the need of directly observing a model or its products, have been named latent solutions and constitute the species latent repertoire (Tennie et al., 2009). Nevertheless, the fact that behavioural forms are individually learnt in non-copying based cultures does not deny a role for social learning. In this type of cultures non-copying social learning mechanisms play an important role in determining how often a certain behavioural form appears in a population (Bandini & Tennie, 2017; Neadle et al., 2017; Tennie et al., 2009). Social learning mechanisms catalyse the individual re-innovations of behavioural forms that are within the species-specific latent solution repertoires, a process that Bandini and Tennie (2017) termed socially-mediated serial re-innovations. This term illustrates that in non-copying based cultures behavioural forms are repeated but not replicated (Tennie et al., in press), meaning that each individual individually learns a given behavioural form but the learning event is prompted or fueled by socially acquired information. For example, finding a partly excavated hole with a stick inside and half-eaten tubers by chimpanzees (as indicated by the presence of feces in the area) might prompt another chimpanzee to individually re-innovate the use of the stick to obtain underground food. In this example, local enhancement and environmental affordances would have catalysed the re-innovation of the behavioural form (tool excavation) in the chimpanzee.

Discussing the learning abilities of great apes, Reindl et al. (2018) proposed that these species do not only possess non-copying based cultures, but that ecologically-representative apes (those that are not enculturated) cannot learn any new behaviour that is not within their latent solutions repertoires (ZLS-only hypothesis: Reindl et al., 2018). That is, great apes cannot learn anything that they would not have learnt individually given the appropriate environmental affordances.

In order to differentiate between these two types of cultures (copying-based and non-copying based) it is necessary to determine if the culture of a given species is composed by culture-dependent forms or by latent solutions. In a non-copying based culture, behavioural forms would be individually learnt and catalysed by non-copying social learning mechanisms (as proposed for great apes, see also Chapter 2) whereas in a copying-based culture, behavioural forms would be acquired by copying experienced models in the population (as it is the case in humans). In other words, to be able to identify human-like culture, it is necessary to unequivocally detect copying social learning mechanisms.

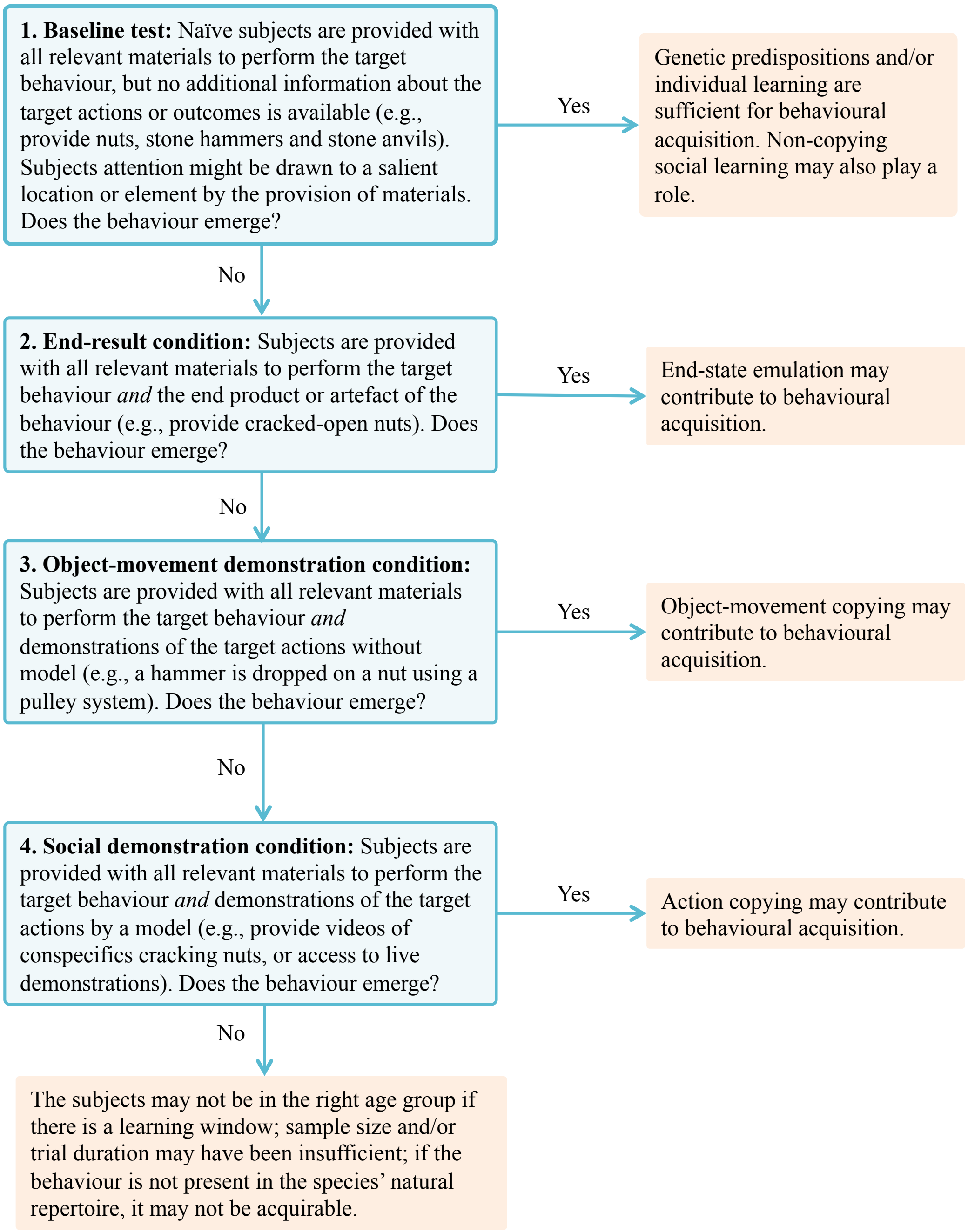
2. The extended baseline methodology

Already in 1986, Galef wrote that "Progress in the study of learning by imitation in animals would obviously be greatly facilitated by identification of an experimental procedure in which imitation could be unambiguously and repeatedly demonstrated" (Galef et al., 1986). One such procedure is the extended baseline methodology. The goal of the extended baseline methodology is to isolate the influence of different learning mechanisms on the acquisition of a novel behaviour (Bandini & Tennie, 2018). Specifically the extended baseline methodology allows to detect whether a behavioural form can be individually learnt when the right environmental conditions are present or if a behavioural form relies on copying social learning mechanisms to be acquired. Thus, the extended baseline methodology directly allows to identify if imitation or emulation are required to learn a behaviour and consequently if a behaviour is a culture-dependent form.

The first step in the extended baseline methodology is the baseline condition, in which the test subject/s has/have access to the necessary materials to perform the behaviour in question but no information regarding the target behavioural form (i.e. the physical actions involved in the behaviour or the outcome) is provided. For example, if the target behavioural form is nut cracking, test subjects are provided with hammers, anvils and nuts. It is important to take into account that no experiment can be conducted in an informational vacuum, and thus, when conducting baseline conditions, some information about the target behaviour is unavoidably provided. For example, the introduction of a novel puzzle box in the environment or enclosure of an animal might attract the animal towards this novel object and thus inadvertently inform it that this object is required to perform the target behavioural form. Crucially, however, as no information about the target behavioural form is provided during baseline conditions, the subjects remain target-naïve.

If the target behavioural form under investigation does not emerge in the baseline condition of the extended baseline methodology, a series of social learning conditions are conducted (Figure 1). The goal of the social learning conditions is to determine the minimum amount/type of social information that the subjects need in order to acquire the behaviour. Examples of these types of information can be the end result of the behavioural form, the movement that needs to be performed in order to accomplish the target behavioural form and finally the target behavioural form itself (Figure 1). Therefore, each social learning condition included in the extended baseline methodology builds on the previous condition by sequentially increasing the amount of social information about the target behavioural form provided until a full action demonstration is performed. A practical example of the information provided in each of these conditions is given in Figure 1.

Determining that the test subjects are naïve to the target behavioural form is a necessary step before the extended baseline methodology can be applied. This naivety assessment is required in order to ensure that the entire learning process is investigated and controlled for: if the subjects already know how to perform a behaviour it is not possible to test if they could individually learn it (see discussion of two-target tasks in section 1.1). The necessary naivety of the individuals to the target behavioural form is much easier to determine in captive settings that in the wild, as records of the behaviour of captive individuals are sometimes available in zoological institutions and the keepers can be asked about the presence of the target behaviour in the population of interest. Theoretically, the extended baseline methodology could also be applied in the wild if long-term observational data is available regarding the behavioural repertoire of the population of interest (see for example Gruber et al., 2011), but it would be logistically more complicated.



1. Baseline test: Naïve subjects are provided with all relevant materials to perform the target behaviour, but no additional information about the target actions or outcomes is available (e.g., provide nuts, stone hammers and stone anvils). Subjects attention might be drawn to a salient location or element by the provision of materials. Does the behaviour emerge?

Genetic predispositions and/or individual learning are sufficient for behavioural acquisition. Non-copying social learning may also play a role.

2. End-result condition: Subjects are provided with all relevant materials to perform the target behaviour *and* the end product or artefact of the behaviour (e.g., provide cracked-open nuts). Does the behaviour emerge?

End-state emulation may contribute to behavioural acquisition.

3. Object-movement demonstration condition: Subjects are provided with all relevant materials to perform the target behaviour *and* demonstrations of the target actions without model (e.g., a hammer is dropped on a nut using a pulley system). Does the behaviour emerge?

Object-movement copying may contribute to behavioural acquisition.

4. Social demonstration condition: Subjects are provided with all relevant materials to perform the target behaviour *and* demonstrations of the target actions by a model (e.g., provide videos of conspecifics cracking nuts, or access to live demonstrations). Does the behaviour emerge?

Action copying may contribute to behavioural acquisition.

The subjects may not be in the right age group if there is a learning window; sample size and/or trial duration may have been insufficient; if the behaviour is not present in the species' natural repertoire, it may not be acquirable.

Figure 1: Decision tree with possible outcomes of baseline and extended social learning conditions. For clarity, practical examples of a hypothetical nut-cracking study are included for each condition. The baseline condition is a test for individual learning abilities assuming a certain (unavoidable) degree of local and/or stimulus enhancement derived from the provision of novel objects. This initial condition tests for individual learning catalysed by non-copying forms of social learning. The end-result condition tests for end-state emulation, the object movement demonstrations

would be the equivalent to a ghost condition testing for object movement re-enactment and the social demonstration condition is a direct test for imitation. Figure adapted from Bandini et al., (in press).

So far most of the experiments that have applied the extended baseline methodology have found that naïve individuals (without previous experience or exposure to the target behaviour) could spontaneously learn the target behavioural form in the baseline condition. Some of these experiments have shown that various tool use behaviours performed by wild great apes can be spontaneously re-innovated by captive, target-naïve conspecifics that did not have previous experience in the task nor had been exposed to models performing the target behavioural forms. These studies found that behaviours such as pounding (Bandini & Tennie, 2019), food cleaning (Fiore et al., 2020; Neadle et al., 2017), food washing (Allritz et al., 2013), algae scooping (Bandini & Tennie, 2017), nettle feeding (Tennie & Hedwig, 2009) and tool-assisted extractive foraging (Lonsdorf et al., 2009) are re-innovated by captive naïve individuals. Therefore, these experiments show that behaviours (including tool behaviours) that were previously thought to rely on copying variants of social learning to be acquired (Whiten et al., 1999; Whiten et al., 2001), are actually latent solutions rather than culture-dependent forms dependent on copying variants of social learning.

Just two studies to date have applied the extended baseline methodology to investigate the sources of primate tool behaviors. One recent study tested if captive task-naïve chimpanzees could learn nut-cracking, a behaviour performed by some populations of wild chimpanzees (Whiten et al., 2001), following the extended baseline methodology (Neadle et al., 2020). Neadle and colleagues found that the captive chimpanzees did not learn to crack nuts using a wooden hammer and anvil even after full demonstrations were provided. The authors hypothesised that the chimpanzees might not have learnt the behavior due to their age, as they we all adults outside the suggested sensitive period for learning nut-cracking (Biro et al., 2006). Bandini and Tennie (2018) tested long-tailed macaques (*Macaca fascicularis fascicularis, Mff*) for their ability to crack nuts using stone hammers and anvils. This subspecies of long-tailed macaque does not perform the target behaviour in the wild but another closely related subspecies (*Macaca fascicularis aurea, Mfa*) often engages in this behaviour. After applying the extended baseline methodology, the authors found that the tested subjects did not perform the target behaviour even when full demonstrations were provided. The authors hypothesized that genetic differences between the two long-tailed macaque subspecies might explain why the behaviour did not emerge in captive *Mff* subjects (Bandini & Tennie, 2018). A later study (Gumert et al., 2019) confirmed the hypothesis that nut-cracking in long-tailed macaques is under strong genetic control. Gumert et al. (2019) reported that wild hybrids from the two macaque subspecies (*Mff* x *Mfa*) that phenotypically resembled the tool-using subspecies (and thus were genetically closer to *Mfa*), engaged in nut-cracking behaviour, whereas hybrids that phenotypically resembled the non-tool-using subspecies (and were genetically closer to the non-tool using subspecies *Mff*), did not perform the behaviour (Gumert et al., 2019).

In addition to testing the sources of non-human animal behaviours, the extended baseline methodology can also be applied to the fields of cognitive and primate archaeology in order to investigate the sources of early hominin tool behaviours. Such investigation can indirectly assess – via phylogenetic proxy – which learning mechanisms likely underlay the acquisition of behavioural forms in our ancestors and, consequently, which type of culture early hominins might have possessed. In turn, this endeavor can help us identify which early hominin behaviours were the result of cumulative cultural processes and thus, represent potential origins of our modern culture.

3. ESTs and the origins of human cumulative culture

Stone tools often represent the main component of archaeological assemblages due to their resilience to taphonomic modification and consequent high preservation in the record. The systematic production and use of stone tools is often highlighted as one of the main milestones in human evolution: stone tools opened new ecological niches such as the exploitation of large prey bodies (Potts & Shipman, 1981), extracting bone marrow (Bunn, 1981) and modifying plant tissues (Keeley & Toth, 1981). It is argued that the production of stone tools had major implication for the evolution of hominin dentition, hand morphology, brain size and cognition (Marzke, 2013; Toth & Schick, 2018; Zink & Lieberman, 2016). Stone tools can be classified as flaked pieces (cores and retouched tools), detached pieces (flakes), pounded items and unmodified stones (Isaac et al., 1997; Leakey, 1971). Flaked pieces are those from which stone fragments have been detached via a process of knapping, in which the morphology of an object is modified by hitting it with a hammer (which can be hard, soft, direct, indirect, etc, de la Torre and Mora, 2010). Detached pieces are stones that often present a sharp edge (sharp-edged stone tool) and/or morphological traits derived from a conchoidal fracture (flake), namely, a bulb of percussion, a striking platform, an impact point and ripples (Debénath & Dibble, 1994). Pounded pieces are artefacts that lack artificial shaping but show some evidence of utilization such as chipping, smashing and battering (sensu de la Torre & Mora, 2010). Unmodified stones (such as anvils) are generally passive elements that do not present morphological modifications and receive the force exerted by another element (Leakey, 1971). In the subsequent chapters, I refer to sharp-edged stone tools as intentionally detached pieces produced with the goal of using them as cutting tools. In turn, sharp-edged stones refer to detached pieces that were not used as tools and therefore, their envisioned used is unclear. The term flake is used to refer to sharp-edged stones that present signs of conchoidal fracture (Debénath & Dibble, 1994). Finally, stone tool is used as an umbrella term to refer to both sharp-edged stones (including flakes) and stones without sharp edges (Isaac et al., 1997; Leakey, 1971).

The oldest stone tools include the artefacts associated to the Lomekwian and Oldowan industrial complexes. The Lomekwian was described by Harmand et al. (2015) as a 3.3 million-years old stone technology based on the findings from the LOM3 site in West Turkana, Kenya. In 2015, this technology was described from artefacts including cores, flakes, anvils and percussors. Experiments conducted in order to replicate the reduction strategies employed at LOM3 suggested that the main knapping techniques used to produce the Lomekwi artefacts were the passive hammer and the bipolar knapping technique (Figure 2). The context of the Lomekwian however, has been contended on the grounds that the *in situ* nature of the findings has not been properly justified (Archer et al., 2020; Dominguez-Rodrigo & Alcalá, 2019; Domínguez-Rodrigo & Alcalá, 2016). According to some authors, based on the available information, it is possible that the LOM3 findings may be the result of the intrusion of slope deposits that have migrated vertically (Dominguez-Rodrigo &

Alcalá, 2019; Domínguez-Rodrigo & Alcalá, 2016). The in situ nature of the findings at LOM3 has also been questioned based on the fact that in some of the figures provided by Harmand and colleagues, *in situ* and *ex situ* deposits appear to be at equivalent vertical depth (Archer et al., 2020; Domínguez-Rodrigo & Alcalá, 2016). Furthermore, Archer et al. (2020) have pointed out that some of the findings reported to be 3.3. million years old appear in some of the pictures provided as surface findings rather in situ. If conclusive evidence of the *in situ* nature of the LOM3 artefacts were to be provided and the context of the Lomekwi was clarified, this technology would push significantly back in time the origin of stone tool technologies. If the dating of the LOM3 artefacts were confirmed, this would allow for the possibility that older species outside of the *Homo* and *Australopithecus* genera, such as *Kenyantrhopus platyops*, were also stone tool-makers. However, more evidence is needed in order to conclusively establish the context of the Lomekwi findings.

The Oldowan industrial complex is the oldest undisputed stone tool technology. The oldest Oldowan site was recently dated to <2.58 Ma in Ledi-Gerau, Ethiopia (Braun et al., 2019) and 2.58 at Gona, Ethiopia (Semaw et al., 1997; Semaw et al., 2003). Although it is generally considered that the mainstream production of Oldowan tools finished 1.4 Ma, Oldowan tools were still produced during subsequent time periods. Even today, Oldowan-like technologies can be found in some modern hunter-gatherers populations (Hayden, 2015). The Oldowan is characterized by the systematic production of flakes with signs of conchoidal fracture (such as bulb and point of percussion and striking platform) and the presence of contiguous flake scars on cores (Debénath & Dibble, 1994). Oldowan assemblages also include battered hammerstones, simple core forms, retouched pieces and débitage (reviewed by Schick & Toth, 2006). Of particular relevance for the purpose of this thesis, are the behavioural forms that were used to produce Oldowan flakes. Diverse knapping techniques have been attributed to Oldowan tool-makers (Schick & Toth, 2006), namely freehand, bipolar and passive hammer percussion (Figure 2). Oldowan tools were produced for more than a million years across East, South and North Africa, the Mediterranean basin and central, southern and eastern Asia (Barsky, 2009). Regarding who where the Oldowan tool-makers and users, there are several candidate hominin species (*Australopithecus africanus*, *A. garhi*, *A. sediba, A. (Parantrhopus) aethiopicus*, *A.* (*Paranthropus*) *robustus, Homo abilis, Homo ergaster/erectus, Homo* *rudolfensis*) that could have produced Oldowan tools based on their presence in Africa between 2.6 and 1.4 Ma (reviewed by Schick & Toth, 2006).

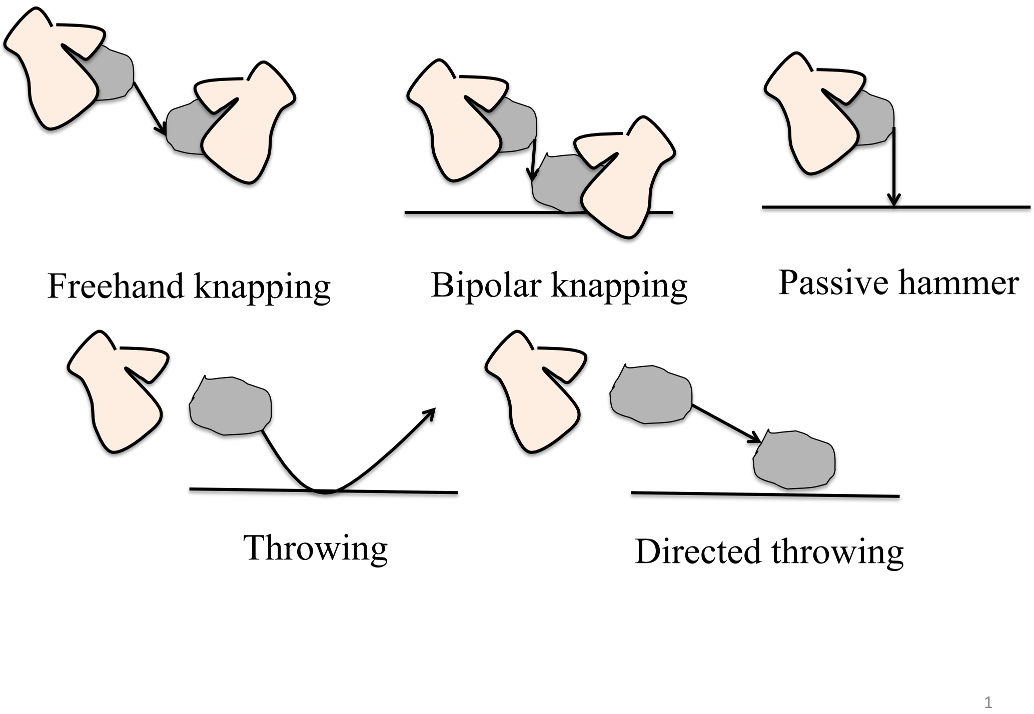


Figure 2: Schematic representation of knapping techniques.

3.1 Great apes as models of early hominin cognition

Stone tools are the oldest remains of hominin behaviour, providing insight on early hominin problem-solving abilities and decision-making (Schick et al., 1999). Given the large time range and broad geographic distribution of stone tools, scientists from different disciplines have turned to the archaeological record in order to investigate the origins of our culture (Davidson & McGrew, 2005). As mentioned above, modern human cumulative culture is composed by culture-dependent forms that can only be learnt from direct observation of a model or its products (via copying social learning mechanisms). In order to assess if early hominins already possessed modern human-like cumulative culture, different research groups have set to investigate if stone tool-related behaviours and stone tools morphologies (particularly early stone tools, Tennie et al., 2016; Tennie et al., 2017) qualify as culture-dependent forms. As it is (unfortunately) not possible to directly test how early hominins learnt to make and use stone tools in cognitive experiments, some researchers have turned to our closest living relatives, the great apes, as behavioural models to test hypotheses on early hominin cognitive abilities (Byrne, 2004; Carvalho & McGrew, 2012; Davidson & McGrew, 2005; Schick et al., 1999; Wright, 1972; Wynn et al., 2011; Wynn & McGrew, 1989).

Two previous projects have tested the abilities of one male juvenile orangutan (Wright, 1972) and one language-trained bonobo (Schick et al., 1999; Toth et al., 1993) to learn to use and produce stone tools after observing a human demonstrator. The orangutan in Wright's study (Abang) was provided with a stabilized and pre-shaped flint core fixed on a wooden platform, a hammerstone and an opaque puzzle box baited with food. The lid of the box was kept closed by a rope, which needed to be cut in order to access the food rewards contained inside. This puzzle box represented an indirect approach in which the action of cutting with a sharp object did not grant immediate access to the food rewards but instead allowed a door to open through which food could be obtained. Before the onset of the experiments, Abang was given several demonstrations of how to produce a sharp-edged stones using freehand percussion (a technique that the orangutan could not perform as the core was fixed) and how to use the sharp-edged stones as cutting tools. During the second testing day and after nine demonstrations, Abang used a human-made flake as a cutting tool to open the baited box (Wright, 1972). During the 10th testing day and after 16 demonstrations, Abang produced his own sharp-edged stones by striking a handheld hammerstone against the fixed core. Abang then proceeded to use a sharp-edged stone as a cutting tool to open the baited box and obtain the food rewards (Wright, 1972).

In the 90s, Schick, Toth and colleagues similarly tested the bonobo Kanzi on his abilities to use and produce stone tools after being exposed to demonstrations by a human model (Toth et al., 1993) as well as investigated the development of these skills over a period of several years (Schick et al., 1999). In the first set of experiments, Kanzi was provided with social demonstrations (before the start of the tests) on how to produce sharp-edged stones using the freehand knapping technique as well as on how to use these sharp-edged stones as cutting tools (Toth et al., 1993). After having been exposed to the demonstrations, Kanzi was given hammerstones and cores of different sizes as well as a puzzle box similar to the one used by Wright baited with food rewards. In addition, Kanzi was also provided with a second drum-like puzzle box, which allowed access to food rewards directly after using a cutting tool. This second box consisted on a cylinder covered by a transparent plastic lid, which needed to be cut in order to access the food placed inside the cylinder. The first day of the experiment, Kanzi started to use human-made flakes as cutting tools to access the baited boxes. To ensure that Kanzi could identify functional flakes, 10 trials were conducted where Kanzi was provided with a series of flakes, only one of which was sharp enough to be used as a cutting tool. Kanzi then had to select the functional flake in each of the trials, which he did consistently in the last five trials (Toth et al., 1993). During the third phase of the study, Kanzi's abilities to produce sharp-edged stone tools were evaluated. After a month of experiments and several unsuccessful attempts at producing sharp-edged stones using the demonstrated freehand knapping technique, Kanzi developed his own technique to initiate stone fracture in which he threw a core against a hard surface. Eventually, Kanzi also effectively developed the demonstrated freehand technique and a third technique, namely the directed throw of a cobble against another stationary cobble. Kanzi continued to use this latter technique together with the technique that involved throwing a cobble against a hard surface during later tests in the following years (Schick et al., 1999). Later on, Kanzi's half-sister Panbanisha was reported to have learnt to use and produce sharp-edged stone tools via freehand percussion by observing a female human demonstrator (Savage-Rumbaugh & Fields, 2006). Similarly, Panbanisha's two sons were also reported to have acquired sharp-edged stone making and using skills via the observation the two more experienced bonobos, although the learning process and their skills were not described in detail (Toth et al., 2006).

Despite being relevant and innovative for their time, the ape stone tool studies described above present a series of methodological issues that limit the applicability of their results to the understanding of early hominin learning abilities. First, all individuals tested in these studies were enculturated, meaning that they were raised in a human cultural environment with extensive human contact and training, invalidating them as representative behavioural models of their wild-counterparts or their last common ancestor with our lineage (Henrich & Tennie, 2017). As an example, Kanzi represents one of the most extreme cases of enculturation and he became a renowned bonobo for his extensive language training and his reported communicative abilities using lexigrams (Savage-Rumbaugh et al., 1986). Second, both Abang and Kanzi were provided with demonstrations on how to use and how to produce sharp-edged stones, meaning that the spontaneous abilities of the apes to perform these behaviours were not tested. Finally, during the course of the experiments conducted by Wright, Abang's keeper molded Abang's behaviour by guiding his hands in order to use the human-made flake as a cutting tool (Wright, 1972). In addition, cobbles were placed on Kanzi's hands to promote stone tool making (Savage-Rumbaugh & Fields, 2006). Therefore, to this date, it remains unknown if wild-representative, unenculturared, stone tool naïve apes possess the necessary cognitive and physical abilities to spontaneously produce and use sharp-edged stone tools.

Experiments using great apes as behavioral and cognitive models of early hominins are a valuable tool to infer the phenotypes of the last common ancestors between each of the great ape species and the *Homo* genus. In turn, this line of research allows us to investigate and test hypothesis about the learning mechanisms employed in the acquisition of technological behaviours throughout the hominoid lineage. Ultimately, assessing if individual or social learning mechanisms underlie the acquisition of novel behavioural forms associated to early hominins, can inform us about which types of culture our ancestors had and how did human cumulative culture emerge.

4. Thesis aims

The overall aim of this thesis was to investigate the learning mechanisms underlying sharp-edged stone tool production and use in early hominins using great apes as phylogenetically relevant models. This thesis contains a general introduction (this chapter) to the theoretical framework behind the experiments and analysis included in later chapters, one literature review (Chapter 2), three experimental chapters (Chapters 3 to 5), and a general discussion (Chapter 6).

The literature review in Chapter 2 consists on a meta-analysis of the distribution patters of great ape behaviours across species and behavioural domains. The main aim of this analysis was to investigate which type of culture (copying or non-copying based) great apes possess using empirical data. If the data would support the null hypothesis that great ape cultures are sustained by non-copying mechanisms this would suggest that great ape cultures are fundamentally different from human cultures. Alternatively, if evidence were found that ape cultures are copying-based, this would equate great ape with human cultures. Support for the null hypothesis would indicate that in the last 6-7 My since the split from the genus *Pan*, specific copying social learning mechanisms must have emerged in the hominin lineage that had not been present before.

Chapters 3 to 5 report a series of experiments in which I applied several conditions of the extended baseline methodology to test if and how chimpanzees and orangutans naïve to the production and use of sharp-edged stone tools, could develop these abilities. These chapters focus on chimpanzees and orangutans because these are the two species of great apes that possess the broadest tool repertoires in the wild (van Schaik et al., 2003; van Schaik et al., 2009; Whiten et al., 2001). In addition, chimpanzees and orangutans provide the opportunity to test which cognitive abilities were presumably present in the last common ancestor (6 Ma) and the oldest common ancestor (13 Ma) of great apes and hominins. In a series of experimental conditions I tested if chimpanzees and orangutans could a) spontaneously develop sharp-edged stone tool production and use (Chapters 3 and 4), b) develop sharp-edged stone production after attributing value to human-made flakes (Chapters 3 and 4) and c) develop sharp-edged stone tool production and use after seeing social demonstrations of how to make and use flakes (Chapter 5).

Finally, Chapter 6 contains an outline of the broader implications that the experiments and analyses included in this thesis have for understanding the emergence and transmission of sharp-edged stone tool making and use as well as what we know so far about early hominin culture and the origins of modern human culture. Limitations of the studies presented here and a research outlook are also discussed.

Chapters 2 to 5 are structured in article format with sections describing background of the chapters' topics, methodologies employed or developed, analyses and results of the experiments and discussions of the results. Each of these chapters is envisioned to become a separate article published in a peer-review journal. The status of each of these four articles and my individual contributions to each of them are described at the beginning of each chapter.

5. Ethics

Ethical approval for all studies on great apes included in this thesis was obtained from the ERC that funded the STONECULT project and the host zoos (Kristiansand Zoo, Twycross Zoo) following EAZA, BIAZA and WAZA protocols on animal research and welfare.

Chapter 2: The method of local restriction: in search of potential great ape culture-dependent forms

This chapter includes the following manuscript under review in Biological Reviews:

Motes-Rodrigo, A. & Tennie, C. (*under review in Biological Reviews*). The Method of Local Restriction: in search of potential great ape culture-dependent forms.

I am the primary author of the manuscript and conducted the literature search presented in this review chapter. The original idea for this meta-analysis was developed in collaboration with Dr. Claudio Tennie. Dr. Claudio Tennie further contributed to authorship by providing feedback and editing the different versions of this manuscript.

CHAPTER 2

The method of local restriction: in search of potential great ape culture-dependent forms

1. Introduction

Social learning in general refers to behaviours that are influenced by the interaction with other individuals or their products (Galef, 1988). A sub-type of social learning, copying, involves recreating the behavioural forms and/or the environmental results produced by a model. Among primates, humans seem to possess a perhaps unique type of culture that is based and maintained by such copying variants of social learning, namely "cumulative culture" (Boyd & Richerson, 1996; Tomasello, Savage-Rumbaugh, & Kruger, 1993). Cumulative culture produces behavioural *forms* (encompassing behavioural actions and artefacts) that are copied by other, culturally connected individuals (Acerbi & Tennie, 2016; Boyd & Richerson, 1996; Caldwell & Millen, 2009; Heyes, 2018; Tennie, Call, & Tomasello, 2009). The new individuals that copy a behavioural form from a model might modify the form by unavoidably making mistakes (copying errors, Eerkens & Lipo, 2005) during the transmission process or by introducing innovations. These modifications may affect the behavioural forms' complexity, efficiency or both. When these modified forms are selectively retained in the population's repertoire, this results in a process known as the ratchet effect (Tennie et al., 2009; Tomasello, 1999). Given sufficient levels of copying fidelity, cumulative culture is open-ended, meaning that forms can theoretically cumulate *infinite* changes over time via the ratchet effect (Lewis & Laland, 2012; Pradhan et al., 2012; Tennie et al., 2018; but see Mesoudi, 2011). Copying not only produces the cumulation of changes in behavioural forms but also the accumulation (increase in number) of behavioural forms per se. Here we will mainly focus on cumulation.

The process of cumulative culture enables the cultural evolution of forms that eventually become "culture-dependent" (Reindl et al., 2017; Tennie et al., 2018).

Culture-dependent forms are cumulated actions and/or products (environmental results) that *cannot* be re-innovated by a single, independent individual without observing (e.g. copying) a model. In humans, examples of culture-dependent forms can be found across behavioural domains. For example, food processing techniques (Boyd et al., 2011; Henrich, 2017), rituals (Legare & Nielsen, 2015; Watson-Jones & Legare, 2016) and languages (LeMaster & Monaghan, 2007) are all culture-dependent as they can only be acquired from a model due to their arbitrariness, complexity and/or causal opacity.

Whether non-human great apes (henceforth apes) possess culture-dependent forms is highly debated. This debate focuses on the issue that in order to develop culture-dependent forms, apes would necessarily have to be able to copy. If we were to find culture-dependent forms also in modern apes, this would have important implications for the point in time when cumulative culture first evolved in the hominoid lineage (Tennie et al., 2017). In the following section we will describe the debate surrounding ape culture.

1.1. Defining ape cultures

Some of the classic definitions of culture exclude forms whose population patterns are not mediated by copying variants of social learning (Galef, 1990, 1992). Galef (1992) stated that non-human animals use social learning mechanisms "different from the behavioural mechanisms that underlie propagation of culture in humans". Based on this view, Galef (1992, 1990) argued that animals do not possess culture, but rather what he labeled “traditions”. He proposed that these traditions were the result of other learning mechanisms, which are still social, but do not produce behavioural copies. Examples of such non-copying social learning mechanisms include local enhancement, stimulus enhancement and social facilitation (for an overview of social learning mechanisms see Whiten, 2000 and Chapter 1). Still, these mechanisms have measurable effects, as they all lead to a *frequency* increase (and subsequent stabilization) of individual re-innovations of behavioural forms.

Although there seems to remain a qualitative difference between human and ape cultures (Galef, 1992; Tomasello, 1999), both are often equated in the literature (e.g.

Ramsey, 2013; Whiten, 2011). Some authors have relabeled *all* social learning mechanisms as variants of copying—even when forms are not actually copied (e.g. Laland, 2017). Others consider a species to have culture not based on its ability to copy, but on the number of traditions it shows. In this case, any species with more than one tradition is said to have culture (Whiten, 2005; Whiten & van Schaik, 2007). Still others focus on factors such as longevity or stability, and grant cultural status to traditions that remain present after several generations (Perry, 2009; Whiten & van Schaik, 2007). Generally speaking, current definitions of animal culture often do not require any actual evidence for copying social learning mechanisms.

Rather than focusing on the definition of culture itself and debating whether non-human species possess culture, we join the call of other cultural evolutionary researchers (e.g. Schuppli & van Schaik, 2019) to adopt a broad definition that allows for the study of culture across the animal kingdom (and potentially even beyond: Baluška & Mancuso, 2007). The broadest possible definition of culture equates any instance of a variant of social learning with culture itself (Neadle, Allritz, & Tennie, 2017). According to this minimal definition of culture, a trait is cultural if "social learning of any [variant] plays any role at all in the form and/or the frequency of the behaviour and/or any produced artifacts […]" (Neadle et al. 2017). Under this minimal definition, culture is widespread, from insects (e.g. Alem et al., 2016) to apes (e.g. Whiten et al., 2001). Such a broad definition includes the widest range of traits and, perhaps most importantly, circumvents the semantic disputes of the past. Yet, this minimal definition is still fully compatible with questions about the learning mechanisms underlying animal cultures. For example, any culture can be tested for the presence of copying variants of social learning and the resulting culture-dependent forms. As mentioned above, culture-dependent forms must be based on copying variants of social learning and therefore are also considered as (indirect) evidence of copying social learning mechanisms. If we could uncover any evidence supporting the presence of culture-dependent forms in apes, we could, in turn, uncover copying variants of social learning present in these species.

Evidence of culture-dependent forms in apes would necessarily have to stem from wild or wild-representative captive apes. Wild-representative captive apes must be unenculturated, mother-reared, lacking extensive human training and human interaction and, ideally, living in conspecific groups under non-deprived conditions (Henrich & Tennie, 2017). These exclusion criteria are well justified, as these types of human interactions are not present in the apes' natural environment. The presence of culture-dependent forms should not be assessed in deprived apes, for several reasons. Firstly, it would be unethical to encourage such husbandry practices by conducting research in an institution that deprives apes from social and ecological stimuli. Secondly, impoverished rearing has been shown to cause long-term cognitive deficits in primates (Davenport et al., 1973; French & Carp, 2016). Lastly, deprived apes are much less likely to show the skills (and behaviours) of unenculturated and untrained apes. However, we should note that, if deprived apes show such behaviours after all, this would show that the development of these behavioural forms is robust against atypical raising conditions.

Although the evidence that wild-representative apes can spontaneously copy actions is weak (Chapter 1), these abilities are commonly assumed in the literature (Whiten et al., 1999). Previous experiments with great apes have pointed to some copying abilities in the physical domain (emulation learning of environmental results; Hopper et al., 2008). However, these abilities are apparently very limited and never go beyond what apes can spontaneously re-innovate in the absence of social information (Köhler, 1925; Tennie et al., 2009). Several studies have directly tested whether apes can copy novel behavioural forms not present in the species-typical behavioural repertoire by having trained demonstrators perform a novel, rewarded behaviour in front of observer apes. Regardless of behavioural domain, all apes tested so far (across three studies) failed to copy these novel, unfamiliar behaviours (Clay & Tennie, 2017; Tennie et al., 2012; Tomasello, 1999). In the only experiment that tested the ability to copy novel tool use behaviour in great apes to date, all four species of apes failed to copy the demonstrated solution (Tennie et al., 2009). Furthermore, other studies have shown that apes often even fail to apply observed behaviours from within their latent repertoires to novel situations (Tennie et al., 2012). To our knowledge there exists a single exception (of one potentially enculturated ape) that might have copied one demonstrated familiar action (Tennie et al. 2012).

Several studies have now shown that wild ape behaviours spontaneously reappear in culturally unconnected populations that have never observed a model demonstrate the behaviour in question (e.g. nettle feeding in gorillas: Tennie et al., 2008; probing in chimpanzees: Londsorf et al., 2009; tool-modification to create probing tools in chimpanzees: Hopper et al., 2014; leaf-swallowing in all four great ape species: Menzel et al., 2013; food cleaning in gorillas: Neadle et al., 2017; algae scooping and pestle pounding in chimpanzees: Bandini & Tennie, 2017, 2019).

Therefore, it is plausible that ape cultures, as other non-human cultures, consist of culture-independent traits (term by C. Schuppli, pers. comm.), whose innovation rate is harmonised and maintained via non-copying variants of social learning ("socially mediated re-innovations" of so-called latent solutions: Bandini & Tennie, 2017). The evidence outlined above suggests that as a field we need to move beyond the assumption that apes systematically rely on copying social learning to acquire novel behavioural forms and instead test if there is any evidence of specific culture-dependent forms in great apes. Such tests can be conducted by analyzing patterns of behavioural variation across populations that provide insights into the underlying learning mechanisms sustaining cultures. In the following section, we describe previous attempts to analyse these patterns, their main conclusions, and potential limitations.

2. Charting differences in trait frequencies: the Method of Exclusion

2.1 Tool use and food processing

Several putative ape cultural behaviours have been identified by applying the Method of Exclusion. The general logic of the Method of Exclusion is that, when an effort is made to exclude genetic and ecological factors, behaviours can be classified as cultural if they are identified in certain populations but absent in others (Whiten et al. 1999). This method was originally used for studying wild chimpanzee behaviour (Whiten et al., 1999; Whiten et al., 2001) and later applied to the other great apes (orangutans: van Schaik et al., 2003; bonobos: Hohmann & Fruth, 2003; gorillas: Robbins et al., 2016). These research efforts mainly focused on tool use behaviours (technological domain) and food processing techniques. Whiten et al. collected and compared data on the frequency of 65 potentially cultural behaviours from seven wild chimpanzee sites. The authors concluded that 39 of these behaviours were cultural as they were present at some sites but not at others despite having equivalent ecological settings. The authors further excluded behaviours that were universal (present in all sites) and those that occurred in very low frequencies ("failed to exhibit habitual or customary status in any community"; Whiten et al., 2001). However, other explanations remained possible, as the observed patterns of behavioural variation could also be the result of subtle genetic and/or environmental differences between populations.

Regarding the possibility that some behavioural patterns were genetically predisposed, the authors merely stated that "[…] many of the behaviour patterns concern tool use, and particularly where this is complex, the evidence that chimpanzees readily and flexibly learn such object use (Byrne, 1995; McGrew, 1989) means that these are poor candidates for merely instinctual variations". In an attempt to exclude behaviours that varied between sites due to ecological differences, Whiten et al. (1999) relied on the site director's judgment to exclude behaviours which variation could be readily explained by (obvious) ecological differences (a limitation that the authors acknowledged). Critics of the method claim that the proposed cultural patterns described by Whiten and colleagues could still have been due to hidden genetic and/or environmental differences between populations (Laland & Janik, 2006; Langergraber et al., 2011; van Schaik et al., 2009). After all, environmental differences can be subtle, and yet have an important effect on behavioural forms (Koops et al., 2013; Koops et al., 2014), as the authors themselves recognized to some degree (Whiten et al. 2001). In addition, given that naïve subjects who have never observed a model performing the target behaviour can individually re-innovate some of the behavioural forms described by Whiten et al. (see section 1.1), genetic predispositions cannot be ruled out as a contributing factor to the expression of these behaviours. For instance, Langergraber et al. (2011) measured the levels of genetic dissimilarity between several chimpanzee communities included in Whiten et al. (1999) and compared them with the patterns of between-group behavioural variation described by Whiten and colleagues. Langergraber et al. (2011) found a significant correlation between genetic and behavioural dissimilarities, although some behavioural differences were also found between genetically similar groups (but see Lycett et al., 2007, 2011).

Finally, the Method of Exclusion may rely too heavily on differences of form frequencies; namely, the potentially powerful effects of non-copying social learning mechanisms on these frequencies were not factored into the Method of Exclusion despite predicting the same variation patterns. It is also possible that a combination of factors (genetic, environmental and non-copying social learning) could underlie the patterns of frequency variation uncovered by the Method of Exclusion. Failing to account for these factors might also have actually led Whiten and colleagues to underestimate the extent of (minimal) culture if, for example, it wrongly excluded cases where environmental factors play some role but only in addition to the role of non-copying social learning (Koops et al., 2014; Laland & Janik, 2006). The exclusion of universal behaviours (behaviours present in all communities studied, i.e. branch shake) from the cultural list in the original chimpanzee study has also been criticised (Byrne, 2007; McElreath et al., 2018), as even culture-dependent forms can reach universal status. It would therefore be possible that some chimpanzee cultural behaviours are hiding in plain sight among behaviours shared by all populations.

Despite these limitations, the study by Whiten et al. (1999) was groundbreaking and their general conclusion that culture (at least minimal) exists in apes profoundly impacted the field of primatology. Furthermore, Langergraber et al. (2011) noted that when the focus of the method is on differences between neighboring, genetically interacting (intermixing) communities, both environmental and genetic differences could indeed be assumed to be negligible. Focusing on these communities, Langergraber et al. (2011) found different behavioural frequencies between the neighboring, intermixing chimpanzees of Bossou, Taï North and Taï South and between the K and M groups at Mahale. The most parsimonious inference that could be made from these differences is that, at such a small spatial scale, behavioural variation (in frequency) is maintained by non-copying variants of social learning (such as stimulus or local enhancement and social facilitation). Examples of traits that differ between neighboring communities of chimpanzees include the average length of termite and ant fishing tools (Koops et al., 2015), the variety of raw materials used to manufacture fishing tools (Pascual-Garrido, 2019), nut cracking efficiency (Luncz et al., 2018), how frequently chimpanzees use stone hammers, and the size of their wooden hammers (Luncz & Boesch, 2014; Luncz et al., 2012). In some of these cases, it remains untested if all observed behavioural forms (e.g. stick lengths) are individually re-innovatable, in which case they would still be within the spontaneous abilities of the species. In other words, social learning may make it more likely that observer B chooses a similar stick length as model A, but it remains untested if observer B could have independently re-innovated this length (among other lengths) on her own.

Overall, the Method of Exclusion is a useful first step towards pinpointing cultural candidates, but it is prone to both false positives and false negatives. It cannot determine whether a cultural signal is caused by mere differences in behavioural form frequencies (as a result of non-copying variants of social learning) or whether it is due to differences in form (i.e. the product of copying variants of social learning). Therefore, one important aspect that the Method of Exclusion does not address is the question of whether any of these cultural behaviours require copying social learning mechanisms for their acquisition—i.e. whether they are culture-dependent. We will return to this question in section 3.4 after presenting a similar approach to the study of great ape communication.

2.2 The gestural domain

Applying the Method of Exclusion, researchers have also explicitly studied the variation in great apes' *gestural repertoires* across populations within and across species (reviewed in Byrne et al., 2017; Call & Tomasello, 2007). However, in contrast to the original Method of Exclusion (Whiten et al. 1999, 2001), this approach typically included data both from the wild and captivity (see Supplementary Table 1).

Researching gestural communication in chimpanzees, Hobaiter and Byrne (2011a) found that nearly 100% of the gestures they described as present in the wild Sonso chimpanzee community in Uganda had already been previously reported in earlier studies across a range of wild and captive chimpanzee populations: 100% of the Sonso gestures overlapped with those found at Gombe (wild, Tanzania), 97% with those at Mahale (wild, Tanzania) and 97% with those at Yerkes National Primate Research Center in Atlanta, Georgia (captive, US). Referring to these findings, Byrne et al. (2017) wrote: "[…] the level of overlap between all chimpanzee studies—captive and wild—was found to be so high that, to a first approximation, the repertoires could be described as the same [...]". In the case of gorillas, Genty et al. (2009) found that 85% of the gestures described for this species were found at more than one of the four sites included in the study (three captive, and one wild site), and 39% occurred across all four sites. Cartmill & Byrne (2010) compared the gesture repertoires of captive orangutans across three sites. Out of the 62 gesture types that they described, only one gesture was present in just a single population, where it was idiosyncratic to a single individual (Cartmill & Byrne, 2010). Liebal et al. (2006) compared the gestural repertoire of two further groups of orangutans (both captive). Out of the 30 gestures described, 23 of them (76%) overlapped between both groups. Knox et al. (2019) compared the repertoires of wild Bornean orangutans and found that, of the 21 gestures described, 20 had been previously reported in captive orangutans. Finally, Pika et al. (2005) compared the gestural repertoires of two captive populations of bonobos and found that out of 20 gestures, 18 (90%) overlapped between both groups.

When the repertoires of the three genera of great apes (*Gorilla, Pan* and *Pongo*) were compared, they also greatly overlapped (Byrne et al., 2017). Pair-wise repertoire comparisons showed that *Pan* repertoires overlapped 60% and 80% with *Gorilla* and *Pongo*, respectively (Hobaiter & Byrne, 2011a). When chimpanzees and bonobo were compared, repertoires overlapped in 88% of their gestures (Graham et al., 2016). Lastly, 89% of the gestures of 1-to 2-year old humans (i.e. pre-linguistic) are shared with chimpanzees (Kersken et al., 2019).

The most parsimonious explanation for these gestural overlaps is individual re-innovations of gestural forms. Byrne and colleagues summarised this as: "The great majority of gestures in the ape repertoire […] are innate, in the sense that the potential to develop a particular gestural form and use it for a particular, restricted range of purposes is part of the species' biological inheritance." (Byrne et al., 2017). Therefore, recent findings in ape gestural communication strongly suggest that *most* gestural forms can independently reappear in—often multiple—unconnected populations of *all* great ape species (including humans). These results suggest that most ape gestures (see Table 1 for potential exceptions) can be individually re-innovated and are part of the spontaneous behavioural repertoire of great apes. Given the large empirical overlap among ape species, the majority of these gestures were also likely present in the gestural repertoire of the last common ancestor of great apes (and can therefore also be assumed to have been present in all hominins).

2.3 The vocal domain

Great ape vocal repertoires have been studied less often than tool use or gesture repertoires, and comparisons across species are rare. Regarding the acoustic structure of great ape vocalisations, these seem to be rather similar across species (and populations) and can be classified broadly into grunts, hoots, screams and barks (Marler, 1969 sensu Salmi et al., 2013). Evidence for vocal learning in great apes (and primates) is scarce (Crockford et al., 2004), and it is widely agreed that the vocal repertoire of great ape species is more or less genetically determined, with some plasticity due to arousal and valence (Fedurek & Slocombe, 2011). In particular, great apes seem to be largely unable to acquire novel vocalisations that significantly differ from their species-specific repertoire (Fischer et al., 2015; Janik & Slater, 2000 but see Lameira, 2017). Nevertheless, claims about the acquisition (or honing) of novel acoustic signals (non-voiced sounds) by captive great apes exist in the literature: "Raspberry" and "extended grunt" in captive chimpanzees (Hopkins et al., 2007) and "whistling" in a captive orangutan (Wich et al., 2009) have been reported as examples of novel acoustic signal acquisition by great apes.

Furthermore, some evidence suggests that great apes can modify (to a certain degree) the acoustic structure of vocalisations that are already within their vocal repertoire. For example, different populations of orangutans use calls with varying frequency, and these calls also differ in their detailed acoustic properties (Wich et al., 2012). Acoustic modifications (e.g. in mean frequency of the first formant and peak frequency) could have also led to the convergence in structure of food grunts after group integration in the study by Watson et al. (2015). Call structure convergence as a result of call modification was also shown in two male chimpanzee dyads at Mahale (Mitani & Gros-Louis, 1998). There are also reports of significant differences in the structure of pant hoots (e.g. pitch, number of introduction elements, duration of climax scream) between wild neighboring chimpanzee communities in the Taï forest (Crockford et al., 2004) which might help individuals recognize each other. Overall, there is evidence that apes present some degree of plasticity in the production of vocalisations (e.g. changes in the mean acoustic frequencies of calls), but so far, there is no evidence that they can copy new vocalisations (Fischer & Hammerschmidt, 2019).

Similar to the efforts made for charting geographical variation in other behavioural domains explored above, several studies have attempted to map patterns of presence and absence of great ape vocalisations across populations and species. De Waal (1988) compiled the vocal repertoire of captive bonobos from one institution and compared it with wild chimpanzee vocalisations. de Waal identified 12 vocalisation types in bonobos, all of which had a comparable correlate in wild chimpanzees. Similarly, Hardus et al. (2009) compared orangutan calls across seven wild populations, one captive population and one population of rehabilitant orangutans. Out of the 32 calls that they identified, 25 appeared in more than one population. However, it is important to note that several of these calls were differentiated not based on their acoustic structure, but on the context of use. For example, one of the calls that was present in only one population appeared in other contexts in other populations but seemingly in the same form ("squeak"/"fear squeak"), and two calls were performed exclusively and idiosyncratically by a single individual in captivity ("whine" and "fear whine"). Wich et al. (2012) compared nesting calls and mother-infant calls in five wild orangutan populations and calculated the genetic distances between the populations studied. The authors found that nest and mother-infant calls were present in some populations but absent in others and that the type of calls in these two contexts also differed between some of the populations. Three of the calls ("nest smack", "harmonic uuh", and "throat scrape") were considered group-specific (but see section 4) and call variation was found to be independent of genetic variation The fourth call type ("raspberries") was found in more than one orangutan population. Based on their results, Wich et al. suggested "[…] that these sounds were invented in each population and subsequently spread through social learning […]". Salmi et al. (2013) compiled the vocal repertoire of two groups of western lowland gorillas and described 17 different vocalisations. When compared with the vocal repertoire of mountain gorillas, 16 of the 17 vocalisations were found to overlap between these two species. "Sex-whinny", which was found in western—but not mountain—gorillas seemed to be a context-specific version of "whinny", which was found in both species (Salmi et al., 2013).

In summary, the few studies that have applied the Method of Exclusion to great ape vocalisations suggest that these are not copied from other individuals as they appear in unconnected populations. However, there is evidence that non-copying variants of social learning play a role, as vocalizations can be modified in response to external stimuli (reviewed by Fischer and Hammerschmidt, 2019).

2.4 What can the Method of Exclusion tell us about culture-dependent forms?

The Method of Exclusion provides indirect information regarding the underlying social learning mechanisms that may sustain ape cultures. This is because the data collected using this method allows for the likely identification of independent and individual re-innovations whenever a behavioural form reappears in several culturally-unconnected populations. Whenever independent re-innovations occur, the most parsimonious explanation for the pattern of frequency variation across populations is that the behavioural form is a latent solution (Tennie et al., 2009). Latent solutions are culture-independent forms that can be individually re-innovated without the need of exposure to social demonstrations (Tennie et al., 2009). As a null hypothesis, we should consider that all wild behaviours can be produced in this way, obviating any need to assume copying to play any role in wild ape cultures (because apes do not seem to copy, see above). Only those behaviours that have not been re-innovated elsewhere should remain candidate cases for copying social learning. Introducing and following this line of logic, Byrne (2007) re-evaluated the list of cultural behaviours compiled using the Method of Exclusion in chimpanzees (Whiten et al., 2001) and concluded that most behaviours that were originally considered to be culture-dependent "are not difficult for chimpanzees to invent, and that invention has occurred independently at many sites" (Byrne, 2007). For example, all five behaviours that differ between groups K and M at Mahale, Tanzania (Langergraber et al., 2011) also appear in the same form in other, culturally unconnected populations (Whiten et al., 2001): "termite fishing using a leaf midrib" and "termite fishing using non-leaf materials" are present at Assirik (Senegal) and Bossou (Guinea); "pull stems noisily" is present at Bossou and Kibale (Uganda); "throw objects" is present at Gombe (Tanzania), Bossou and Taï (Côte d'Ivoire); "squash stems underfoot" is also present at Bossou. This pattern is therefore best explained by a scenario where the acquisition of the behavioural forms studied by Whiten et al. do not rely on copying social learning. Instead, at least one individual in each of these unconnected populations has likely independently re-innovated the behavioural form (because these unconnected populations could not have observed one another). Consequently, the Method of Exclusion allows for the evaluation of behavioural forms in terms of their likely dependence on culture. Here, we apply this approach to all behavioural domains within all species of great apes.

3. Locally restricted forms

To test whether great ape cultures are composed of latent solutions, culture-dependent forms, or both, we looked for indirect signs of copying in wild ape behaviour. Instead of merely focusing on the overlap between behavioural repertoires from different populations (as the Method of Exclusion does), we took the complementary approach of looking for *locally restricted forms*. As mentioned before, if copying underlies trait acquisition, copying error would have led to forms that are path-dependent and population-specific. Consequently, finding locally restricted forms in apes would provide (albeit indirectly) evidence for copying in the affected ape species. We have defined locally restricted forms as behaviours and/or artefacts expressed by at least two individuals of a single population or population cluster of one species. Locally restricted forms must have been observed in at least two individuals in order to exclude idiosyncratic behaviours (Call & Tomasello, 2007; Tomasello et al., 1994). Locally restricted forms are also not necessarily restricted to a particular species. Locally restricted forms of species A can be also present in additional populations of species B, but if they only appear in one population of species A, they are locally restricted in that species (A). We named the latter *locally unique forms*.

Locally unique forms are a sub-type of locally restricted forms that are not found in any other unconnected population of any other primate species. Unlike locally restricted forms, locally unique forms are exclusively present in one population (or population cluster) of only one great ape species. Locally restricted forms—and especially locally unique forms—represent the most likely cases for culture-dependent forms and copying in apes (though, in and of themselves, they cannot prove either, see section 5).

In the following section we will present all locally restricted and locally unique forms that we were able to identify across all great ape populations. We include all species of apes and all behavioural domains for which there is enough data to apply the Method of Local Restriction (see below): this list includes tool use, food processing, gestures and vocalisations/sounds (though note that we never excluded any behavioural form from any domain).

4. The Method of Local Restriction: in search of potential great ape culture-dependent forms

In order to determine which behaviours are locally restricted, we first analysed the studies that had reported detailed behavioural repertoires across behavioural domains of wild and captive chimpanzees (Call & Tomasello, 2007; Hobaiter & Byrne, 2011a; Liebal, Call, & Tomasello, 2004; Nishida et al., 2010; Roberts, Roberts, & Vick, 2014; Tomasello et al., 1994; Tomasello et al., 1997; Tomasello et al., 1985; Tomasello, Gust, & Frost, 1989; Whiten et al., 1999; Whiten et al., 2001), bonobos (De Waal, 1988; Graham et al., 2016; Hohmann & Fruth, 2003; Pika et al., 2005), gorillas (Genty et al., 2009; Pika, 2007; Pika, Liebal, & Tomasello, 2003; Robbins et al., 2016; Salmi et al., 2013) and orangutans (Cartmill & Byrne, 2010; Hardus et al., 2009; Liebal et al., 2006; van Schaik et al., 2009; Wich et al., 2012). To identify potential locally restricted behaviours, we followed a series of steps:

1. From the studies cited above, we selected those behaviours that were present in a single population or population cluster and whose form was unlikely to be the product of environmental factors (according to the authors of the studies). We did not include forms that were present in more than one site, if the sites were not connected by migrating individuals as reported in the literature (or visual contact in captive settings). If no migration data between sites were available, we considered as unconnected populations those that were more than 50 km apart (Herbinger, Boesch, & Rothe, 2001) or separated by geographic barriers such as rivers more than 8 m wide (Bender & Bender, 2013). If the study only included one population, we considered

all described behaviours as possibly restricted to that population unless we could confirm that the behaviour was present elsewhere.

2. We conducted an additional literature search on Google Scholar for reports of potential locally restricted behaviours that were not included in the studies cited above. To conduct this new search (carried out by AMR between March 2018 and September 2019), we used the terms "restricted behaviour", "new behaviour", "local behaviour", "local tradition", and "new tradition" in combination with specific great ape species names and the terms "population" and "group". As before, we only included forms that had been originally observed in at least two individuals to avoid selecting idiosyncratic behaviours. However, it was not always possible to determine the number of individuals that performed the behaviour. In such cases, we still included the behaviour in our list but labeled it accordingly (number of individuals observed: "unknown").

3. We conducted an additional search for reports of potential candidate locally restricted forms using the names of the behaviours obtained from the two previous steps. We searched for reports of these behaviours in additional populations from the ones where the behaviour was reported as restricted. In addition, we looked for these behaviours in the same and other great ape species.

4. We invited 15 ape experts to contribute to the creation of our list by adding locally restricted behaviours that were not included in our literature search, and/or by providing data on additional populations (of any great ape species) where our candidate locally restricted behaviours had been observed. These collaborations are indicated as personal communications in Supplementary Table 2 (though we offered anonymised contributions too).

5. Additionally, we have created a collaborative webpage including our current list of locally restricted behaviours (https://sites.google.com/view/group-specific-ape-behaviours/home). The main reason for the creation of this online resource is that identifying locally restricted behaviours is necessarily an ongoing project that should be updated with future observations. Moreover, it was not feasible to personally contact all known great ape researchers individually in step 4. This website provides

an online platform to establish a large-scale and enduring collaboration to help identify both new locally restricted behaviours or new populations where locally restricted behaviours have been observed. Scientists and field researchers are herewith invited to visit the webpage and contact the authors regarding these types of observations.

4.1 Results of the Method of Local Restriction

The initial list of reports of locally restricted behaviours derived from steps 1 and 2 included 78 entries across all four great ape species based on the classification by the authors of the studies (see Supplementary Table 2). Following the search in the published literature on additional unconnected populations where these reported locally restricted behaviours were present (step 3) and after consulting with great ape experts (step 4), this list was reduced to 27 behaviours at the time of submission (Supplementary Table 2). Of these 27 locally restricted forms, 20 were present in additional primate species (Table 1). We identified seven locally unique forms (Table 2), which are currently only known to appear in a single population, or population cluster, of a single ape species.

Initially, we only considered behaviours from four domains: tool use, food processing, gestures and vocalisations/sounds. However, we found that some locally restricted behaviours could not be adequately classified within these categories. Following Robbins et al. (2016) we classified as environment-related those behaviours that involved a physical component of the environment and not another individual, but were not related to foraging (Robbins et al. 2016). In addition, when we compiled our list, there were some behaviours (n=7) that we could not easily classify within any defined domain, since the goals of the behaviours were not clear from their descriptions. However, as we were interested in locally restricted forms regardless of domain, we did not exclude them.

Table 1: Locally restricted vs. locally unique behaviours in great apes by behavioural domain.

Species / Domain	**Tool use**		**Food processing**		**Gestures**		**Vocalisations/ Sounds**		**Environment-related**		**Other**	
	Locally unique	Locally restricted	Locally unique	Locally restricted	Locally unique	Locally restricted	Locally unique	Locally restricted	Locally unique	Locally restricted	Locally unique	Locally restricted
Chimpanzees	1 ("liana scratch")	2 ("branch-hook", "nasal probe")	0	0	0	3 ("nipple stimulate", "rub", "tap object")	0	0	1 ("nest tying")	0	0	0
Orangutans	0	0	0	0	0	2 ("tandem walk", "tongue out")	2 ("harmonic uuh", "grinding")	0	0	0	0	0
Gorillas	0	2 ("lap cover", "shaking leaves")	0	1 ("dug hole drinking")	0	0	0	0	0	0	2 ("mouth washing", "tooth brushing")	0
Bonobos	0	3 ("fly whisk", "vegetation seat", "leaf sponge")	1 ("fruit detachment with feet")	0	0	6 ("chest beat", "groom slap", "leaf clip", "lower head", "move hand and arm across body", "teeth chatter")	0	0	0	1 ("branch slap")	0	0

Table 2: Candidate locally unique behaviours in great apes. The names of the behaviours and descriptions are those used by the original references. When the number of individuals in which the behaviour was observed in the original publication was not indicated, we labeled it unk=unknown. T= tool use behaviour; O= other; ER= environment related behaviour; V= vocalisation/sound; FP= food processing; W=western lowland (*Gorilla gorilla gorilla*); S=Sumatran (*Pongo abelii*).

Nr (arbitrary number 1-n)	**Behaviour**	**Definition**	**Domain**	**Species**	**N**	**Original reference**	**Original population**
1	Liana scratch	Grasping a growing liana, pulling it downwards or sideways in order to hold the flexible stem taut, and then rubbing his body back-and-forth against the taut liana	T	Chimpanzees	>1	Hobaiter and Byrne (2010)	Sonso (Uganda)
2	Nest tying	Tie nest into trunk when no strong weight-bearing structures support the nests	ER	Chimpanzees	unk	McLennan (2018)	Bulindi (Uganda)
3	Harmonic uuh	Call type made by mothers to call infants	V	S Orangutans	>1	Wich et al., (2012)	Ketambe (Sumatra)
4	Grinding	Loud grinding of the teeth	V	S Orangutans	>1	Hardus et al., (2009)	Ketambe rehabilitants (Sumatra)
5	Mouth washing	Taking water into mouth, then moving it back and forth within mouth before swallowing	O	W Gorillas	unk	Robbins et al., (2016)	Bai Hokou (CAR)
6	Tooth brushing	Rubbing fingers against teeth	O	W Gorillas	unk	Robbins et al., (2016)	Bai Hokou (CAR)
7	Fruit detachment with feet	Holding fast to a branch, she stepped on the fruit and pushed with her feet until the fruit became detached and dropped	FP	Bonobos	4	Hohmann & Frutz (2003)	Lomako (DRC)

We found an extensive overlap of behavioural forms across great apes species (and occasionally other primates) and domains (Supplementary Table 2). This overlap suggests that different ape species share, to a large degree, a common behavioural repertoire of latent forms.

In the tool use domain, our results suggest that given similar or equivalent environmental conditions, all great apes seem to use tools in a comparable way. Indeed, we only identified a single locally unique tool behaviour across all ape species ("liana scratch" in chimpanzees: Hobaiter & Byrne, 2010). Although it could be argued that the tool was not detached and therefore it should be considered proto-tool use, we followed the description and terminology used by the authors themselves. We also identified several locally restricted tool behaviours, which were locally restricted in one species but were also found in other primate species (Table 1 and Supplementary Table 2). It is not surprising that gorillas originally showed the lowest number of tool behaviours, as gorilla tool use frequency in the wild is known to be low compared to the other two non-human great ape genera, *Pongo* and *Pan* (Breuer et al., 2005). However, the fact that we could not find any locally unique (nor locally restricted) tool behaviour in orangutans, who are proficient tool users in the wild, suggests that our method compensates for differences in natural frequencies of tool use between species. We only found one food processing behaviour that was locally unique ("fruit detachment with feet" - in bonobos) and one that was locally restricted ("dug hole drinking" - in gorillas).

In the gestural domain, we did not find any locally unique gestures in any great ape species. Locally restricted gestures were found in all ape species except gorillas. Numerically, bonobos had the highest number of locally restricted gestures compared to the other species (Table 1). Variation in the number of locally restricted behaviours (including gestures) reflects, most likely, differences between great ape species in the number of populations studied and the duration of these studies. Chimpanzees were the first species for which a gestural repertoire was compiled in the wild (Hobaiter & Byrne, 2011), and more studies in captivity have been dedicated to the study of chimpanzee gestures than to any other ape species. Consequently, chimpanzee gestures are available from a wider sample of populations, which allows for a broader and more exhaustive comparison. The relatively small number of gestural repertoires recorded from other populations of great ape species could have affected our list in two ways: firstly, it could have led to an underestimation of locally restricted gestures because these have not yet been described, or, secondly, to an overestimation of locally restricted behaviours due to a lack of comparative data from additional populations. With more gestural data being published every year, we will hopefully be able to adjust our conclusions.

In the vocalisation/sound domain, one locally unique vocalisation and one locally unique sound were found among Sumatran orangutans ("harmonic uuh" and "grinding"). The "harmonic uuh" is a call performed by all mothers in the Ketambe population (Sumatra) to call their infants just before retrieving them. "Grinding" was found only in rehabilitant orangutans (Rijksen, 1978) and was interpreted as a fear sign when individuals finished quarantine and were reintroduced to a group. Subjects recently caught from the wild also usually performed this behaviour. No further locally unique or locally restricted vocalisations/sounds were found in any great ape species.

In the environment-related category, we found one locally unique form ("nest tying") in the chimpanzees of Bulindi (Uganda) and one locally restricted form in bonobos ("branch slap", DRC), which may result from yet undescribed unique environmental conditions occurring in those populations. Alternatively, the lack of additional bonobo populations where "branch slap" occurs could be the result of the low number of bonobo behavioural repertoires published. Given that other unconnected great ape populations of two species also perform this behaviour (Supplementary Table 2), it seems plausible that when more data is available, this behaviour will also appear in other unconnected bonobo populations.

We found two locally unique forms in gorillas ("mouth washing" and "tooth brushing") that we classified as belonging to the "other" domain, although these forms could potentially be hygiene-related. No additional locally unique or locally restricted forms in the “other” domain were found.

5. Are locally restricted behaviours culture-dependent forms?

The Method of Local Restriction allows us to identify potential culture-dependent forms in animals based on the premise that behaviours only found in one population of a single species are less likely to be individually re-innovated elsewhere. These forms could therefore be dependent on copying social learning to be locally acquired.

Although we believe that the Method of Local Restriction provides a useful (and necessary) step towards identifying culture-dependent traits in great apes, copying social learning cannot be unambiguously identified using this method. Instead, copying can only be indirectly inferred from the data in the sense that these behavioural patterns are at least compatible with a role of copying in their acquisition. Additional evidence for copying underlying any specific locally restricted behaviours (and especially locally unique behaviours) can also come from baseline experiments investigating the cultural-dependence of a target behaviour.

Testing if the locally restricted and unique behaviours that we identified are re-innovated during an asocial baseline experiments (Bandini & Tennie, 2017, 2019), can conclusively reveal if these behaviours are actually independent from copying social learning. During baseline experiments, individuals naïve to the target behaviour are provided with the raw materials necessary to perform the behaviour in question. If naïve individuals perform the behavioural form in the absence of a model, this logically shows that copying social learning is not strictly required for the acquisition of the behavioral form. Any form appearing in a baseline experiment cannot be a culture-dependent form (by definition). However, negative data from these tests are also informative, as they are indirect evidence that the target behaviour may require copying. Yet, the best evidence supporting a culture-dependence argument would require not only that the target behaviour resist spontaneous re-innovation in a baseline experiment, but, also, that the target behaviour appears once demonstrators have modeled the behaviour to observers (extended baseline methdology described in Chapter 1). Baseline experiments have yet to be undertaken for any of the 20 locally restricted and 7 locally unique behavioural forms that we identified (Table 1 and

Supplementary Table 2) and we urge researchers to join our efforts to test these as target forms with the extended baseline methodology (Chapter 1).

A more direct way to rule out culture-dependence (and with it, copying social learning) in locally restricted behaviours would be via observations of these forms in additional, culturally unconnected populations (both in the wild or in captivity). These observations would, in essence, represent outcomes of natural baseline experiments.

6. Discussion

The results we obtained using the Method of Local Restriction show that the vast majority of great ape behavioural forms across behavioural domains (tool use, food processing, gestures, vocalisations/sounds and environment-related behaviours) are not culture-dependent forms, but culture-independent latent solutions. These forms are individually re-innovatable and appear to be shared (to a large degree) between ape species. To date, the most complete behavioural repertoire of any one great ape species has been compiled for chimpanzees (Nishida et al., 2010), and included 891 behaviours. If we take this value as even a *minimal* approximation of the great ape behavioural repertoire size, we found that less than 1% of behaviours are locally restricted. However, this value is just an estimate, as the total number of great ape behaviours has not yet been calculated (although we would expect it to be below 5000). According to our results, the vast majority of ape behavioural forms can be best explained as follows: individual learning underlies the acquisitions of these forms, while non-copying social learning influences—and even stabilizes—the frequency of the forms in the affected populations (Bandini & Tennie, 2019; Tennie et al., 2009). The existence of such latent solutions is not only the most parsimonious hypothesis to date for ape behavioural repertoires, as it does not assume the need for copying variants of social learning, but also the largest encompassing hypothesis for great ape culture and behaviour in a broader sense. This scenario is also in agreement with the outcome of natural experiments (re-innovation across populations and ape species) and with baseline experiments carried out so far where, in the majority of cases, the target forms were re-innovated by naïve subjects (Bandini & Tennie, 2017, 2019; Lonsdorf et al., 2009; Neadle et al., 2017; Tennie & Hedwig, 2009).

However, despite our best efforts, we acknowledge that there are certain methodological limitations that could have affected our results. These limitations can be classified into those that affected our input data, data analysis and data output.

6.1 Limitations in data input

First, we encountered the difficulty that authors often use different terminology to describe the same behavioural form. When details were provided, we could circumvent this problem by comparing the descriptions of the behaviours directly. Moreover, great ape experts also helpfully provided additional examples of equivalent behaviours named differently in the literature. Projects such as the Great Ape Dictionary were a valuable resource for comparative research as they provided graphical examples of great ape gestures. The ethogram of the Mahale chimpanzees compiled by Nishida et al. (2010) was also a useful resource for determining and comparing behavioural forms. It would be a welcome development if more sites and research groups would create behavioural libraries—including video footage—from different behavioural domains and species.

Second, given the difficulties described above, it is certainly possible that we overlooked potential locally restricted behaviours, as well as additional descriptions of behaviours in the literature—likely due to unpublished results and the amount of data to be analysed. It was precisely for these two reasons that we consulted with experts in the field of great ape behaviour (step 4) prior to the completion of this manuscript. These were also the reasons why we created an online resource for researchers to continuously update the locations where the listed behaviours are observed, as well as add additional candidate locally restricted behaviours. As more data is entered in the website, and more repertoires are published from across different locations, we will be able to refine which behaviours are truly locally restricted. Large-scale projects, such as the ongoing Pan African Project: the Cultured Chimpanzee (PanAf), will be of particular help to reveal the full scope of the overlap and specificity of behavioural forms across wild great ape populations.

Third, the initial numbers of behaviours that we compiled for each species could have been influenced by discrepancies in research intensity. Differences in the number of populations studied and general observation time per species could have influenced the amount of initial locally restricted candidates that we considered. Chimpanzees, for instance, have been systematically studied for a longer time than all the other great ape species (Lameira & Call, 2020). Furthermore, the number of chimpanzee sites under continuous observation surpasses that of any other great ape species (Vaidyanathan, 2011). However, following the Method of Local Restriction, understudied species or domains would be *more* likely to exhibit even more locally restricted behaviours than species studied more intensely, as less comparative data from additional populations is available (see examples from bonobos in section 5.1).

Fourth, differences in population size are likely to cause differences in innovation rates (Kline & Boyd, 2010; Shennan, 2001), and different innovation rates will influence the number of locally restricted behaviours in a population, regardless of whether copying social learning is present/required or not. Smaller populations are more likely to have smaller behavioural repertoires because innovations are less likely to occur with smaller population sizes. On the other hand, larger, more gregarious populations present more possibilities for various forms of social learning because more between-individual encounters take place (Whiten & van Schaik, 2007). Given that wild apes are declining in numbers, and that reducing population sizes can reduce repertoire size (Kühl et al., 2019) we may be losing the opportunity to compile a fully comprehensive list of behaviours present across ape populations over time.

6.2 Limitations in data analysis

In our method, data analysis was limited by the fact that different projects have often used slightly different reference repertoires when coding behaviours—especially gestures—depending on the level of detail included in the gesture category (Pika & Fröhlich, 2019). We could correct for some of these instances when consulting with experts on primate gestural communication, who informed us about changes in the degree of grouping on gestural forms since the publication of their papers. Nevertheless, it is possible that we did not account for all these instances. In addition, new lines of research in which gestural forms are being classified according to the meanings assigned by the species in question rather than by the human observers

(Graham et al., 2018; Hobaiter & Byrne, 2014) might change in future the classification of gestural forms.

In the present study, it was not always possible to effectively search for certain candidate locally restricted behaviours in additional publications due to the somewhat ambiguous descriptions given for certain behaviours. As an example, one of the candidate locally restricted behaviours was defined as "move hand and arm across body" (Savage and Bakeman 1978 sensu Pika et al., 2005). This definition is ambiguous since the action described could be part of several gestural forms, such as "loud scratching" or "wiping hair". The lack of detail in this definition makes it impossible to compare with the published repertoires. If more precise definitions were made available, we suspect that this behaviour would be found in additional populations, lowering the number of locally restricted behaviours. The website of our project will allow for constant revisions of the behaviours' descriptions, which will account for some of the limitations we have encountered during data analysis.

6.3 Limitations in data output

The first issue with data output is that it remains to be determined if locally restricted behaviours (especially locally unique behaviours) can be individually re-innovated by naïve individuals when the adequate environmental conditions exist. Future studies should investigate if the locally restricted behaviours that we found could be elicited when following the extended baseline methodology (see Chapter 1).

Second, we cannot rule out the possibility that we underestimated the number of locally restricted behaviours due to potential false negatives in our sample. Five of the 78 candidate locally restricted behaviours that we initially identified in the literature were additionally found in populations of rehabilitant orangutans. Most of these individuals were captured during infancy, and might have experienced some level of deprivation, possibly delaying the appearance of latent solutions (Russon et al., 2009). The rehabilitant orangutans, however, provided a unique opportunity to study the influence of individual learning in the development of behavioural repertoires. These rehabilitatant individuals were re-introduced to different forests from their native ones, which did not have a local population that provided social learning opportunities of any kind (Russon et al., 2009). Consequently, these populations are culturally unconnected from wild populations and represented a large-scale baseline experiment for the individual re-innovation of wild orangutan behaviours. Nevertheless, it was not possible to determine the degree of human enculturation these individuals might have experienced. In our literature search, we did not include enculturated individuals because these are not wild-representative apes (Henrich & Tennie, 2017). If we underestimated the level of enculturation of the individuals studied by Russon et al., and they were in fact enculturated, this population of rehabilitant orangutans would not be wild-representative. If that were the case, the additional observations of potential locally restricted behaviours that were conducted in this population ought to be excluded, and thus, there would be a larger number a locally restricted behaviours in orangutans.

Third, there remains the theoretical possibility that culture-dependent forms across culturally unconnected populations are sometimes sustained via copying. In this case, our method would not have detected local restriction and consequently would have missed such behaviours. Inherently, this scenario should be more likely in recently-innovated forms, where copying error has not yet caused divergent behavioural forms. But overall, and as we argued above, this scenario is unlikely due to unavoidable copying error during transmission. In addition, apes do not seem to spontaneously copy what they could not already do on their own and many wild ape behaviours have already been shown not to depend on copying (Tennie et al., 2009). Alternatively, local genetic predispositions and/or environmental channeling could have also produce similar forms across different populations (Galef, 1992; Tomasello, 1999). But note that in these latter cases, copying would not actually need to contribute to the acquisition and maintenance of the form in the population.

6.4 The role of social learning in behavioural form acquisition

According to our results, the vast majority of ape behavioural forms are not locally restricted and therefore their acquisition is more likely mediated by individual learning rather than by copying social learning. Nevertheless, neither our paradigm nor our results, deny the possibility that social learning processes influence the frequency of these individual re-innovations at different ontogenetic stages. To the contrary, data conclusively shows that non-copying social learning mechanisms increase and maintain the frequency of behavioural forms within a culturally connected group, producing the observed wild great ape cultural patterns (e.g. Allritz, Tennie, & Call, 2013; Bandini & Tennie, 2017, 2019; Menzel et al., 2013; Neadle et al., 2017; Reindl et al., 2016; Tennie et al., 2009; Tennie et al., 2008). These differences in frequencies can be detected by the Method of Exclusion mentioned above, as they can lead to the differential accumulation of behavioural forms between populations.

Several authors and working groups have also been very prolific in the debate on the learning mechanisms behind gestural acquisition and usage. Some of this work has focused in describing potential social learning mechanisms that shape gestural repertoires, influencing gesture frequency and use. Hobaiter and Byrne (2011b) suggested that juvenile chimpanzees produce gestures in rapid sequences because they are unsure of which is the appropriate—or most effective—gesture for achieving a particular outcome. This early phase would be equivalent to the trial and error phase described for nut-cracking (Inoue-Nakamura & Matsuzawa, 1997). As they grow, chimpanzees only use the most effective gestures from the species' repertoire (Hobaiter & Byrne, 2011b). The final repertoire of an adult is shaped and modulated by social interactions, and adult repertoires are smaller than those of younger individuals (Fröhlich & Hobaiter, 2018; Hobaiter & Byrne, 2011b). Final adult repertoires will vary slightly between individuals, even of the same community, as each individual adult would have had different experiences that modulated their repertoire and gesture use (Hobaiter & Byrne, 2011b, Fröhlich & Hobaiter, 2018). Future studies could investigate whether gesture usage and meaning varies systematically across populations within-and between-species. The presence of locally restricted gesture usages and meanings would suggest that these variables are socially acquired and perhaps even culture-dependent – even if their forms are not.

6.5 Implications of the Method of Local Restriction for conservation

Although it is clear that social interactions contribute to the patterns of expressed behavioural repertoires in great apes, the literature search of potential culture-dependent forms we undertook demonstrates that latent solutions are the rule rather than the exception: most behavioural forms across domains are not locally restricted and can therefore likely be individually re-innovated by naïve individuals (captive and wild) in unconnected populations. The fact that we found several locally unique behaviours leaves open the possibility for copying social learning to play a role especially in the acquisition of these forms. This geographic isolation, as well as their possible dependence on copying social learning, implies that these behaviours are the most likely forms susceptible to disappearing – perhaps forever – if the populations in which they are present are decimated or completely destroyed. A recent study has suggested that populations with the highest behavioural diversity should be protected as "cultural heritage sites" (Kühl et al., 2019). Although we definitely support Kühl and colleagues in their efforts to increase the protection of great ape populations, we believe that behavioural diversity in and of itself should not automatically prioritise the protection of one ape population above another. It is possible that even very diverse behaviours can entirely re-appear in other populations. Instead, we argue that the focus of conservation efforts directed towards protecting ape cultures should rest on locally restricted behaviours and especially locally unique behaviours. It is these forms that are the most likely to be potentially dependent on copying social learning (Table 2)—and thus unlikely to be individually re-innovated in other populations. As such, they are the most susceptible behaviours to disappear due to human impact. In our view, the presence of the largest number of such behaviours in a population should be the main criterion towards prioritising the protection of their containing ape population. This is especially true if, during future baseline experiments, these behaviours fail to be re-innovated and evidence is found of their reliance on copying.

7. Conclusion

Our results suggest that there exists a common framework to explain how ape cultural repertoires come about and are maintained. Most ape behavioural forms are latent solutions that can be individually learnt as they appear in culturally unconnected populations (sometimes even in various species of great apes). Using the Method of Local Restriction, we present a list of locally restricted and locally unique behaviours in great apes that stand as the most likely candidates for culture-dependent forms across domains and species. These forms represent, to date, the most likely behavioural forms that might depend on copying social learning. To determine whether any of these candidate forms are truly culture-dependent, they need to be subjected to dedicated observation efforts in culturally unconnected populations, as well as tested for their reliance on copying social learning. Finally, the Method of Local Restriction could also be applied to other animal species and to the archaeological record (for instance to stone tool assemblages) allowing us to identify potential cases of culture-dependent forms in our lineage.

Data availability

All code and raw data used in this chapter can be found in the Open Science Framework project named "The Method of Local Restriction":
https://osf.io/7xny8/?view_only=c4e733fe902b4c609dd685f438f6664f

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Chapter 3: Testing the spontaneous abilities of chimpanzees to make and use sharp-edged stone tools

This chapter includes text and analyses that are part of a manuscript that is currently under review in Science Advances.

Bandini, E., Motes-Rodrigo, A., Archer, W., Minchin, T., Axelsen, H., Hernandez-Aguilar, R. A., McPherron, S. P. & Tennie, C. *(under review in Science Advances*) Naïve unenculturated chimpanzees fail to make and use flaked stone tools.

In addition, this chapter includes the results from a second experiment that was not included in the abovementioned manuscript. Consequently, the Methods, Results and Discussion have been modified in this Chapter to accomodate the additional experiment. I am shared first author of the manuscript submitted to Science Advances together with Dr. Elisa Bandini, as we both conducted experiments that are included in the manuscript. The original idea for this study was developed in collaboration with Dr. Claudio Tennie, Dr. McPherron and Dr. Bandini.

Regarding the data presented in this chapter, I was the main experimenter and conducted all data collection. I analysed the data both presented here and in the abovementioned submitted manuscript.

CHAPTER 3

Testing the spontaneous abilities of chimpanzees to make and use sharp-edged stone tools

1. Introduction

The systematic production and use of sharp-edged stone tools played a key role in human evolution by allowing the exploitation of new ecological niches (e.g. Laland et al., 2000). The two oldest lithic industries containing flakes (sharp-edged stone tools with traits derived from conchoidal fracture: Debénath & Dibble, 1994) described to date are the Lomekwian (Harmand et al., 2015; although see Domínguez-Rodrigo & Alcalá, 2016 and Archer et al., 2020 for a critique on the in situ context of the findings) and the Oldowan (Braun et al., 2019; Toth & Schick, 2006). The artefacts present in these two technologies have been previously referred to as 'Early Stone Tools' (EST: Tennie et al., 2017). Previous studies have hypothesized that the ability to manufacture flakes was acquired via special mechanisms of cultural transmission, namely copying variants of social learning (McNabb et al., 2004). However, this hypothesis is not universally accepted (Boyd & Richerson, 2005; Foley, 1987), and still under debate (Corbey et al., 2016; Tennie et al., 2016; Tennie et al., 2017). Due to the impossibility of directly testing the learning mechanisms underlying flake production and use in early hominins, researchers have to resort to indirect methods in order to study early hominin cognition. Non-human great apes are the taxa most closely related to us phylogenetically and so can be used as models to examine how behaviours were likely acquired by our ancestors (Arroyo et al., 2016; Panger et al., 2002; Wynn et al., 2011). So far, only three apes – one orangutan (*Pongo pymaeus*; 'Abang'; Wright, 1972) and two bonobos (*Pan paniscus*; 'Kanzi' and 'Panbanisha'; Toth et al., 1993; Schick et al., 1999) – have been tested for their ability to learn how to make and use flakes. In the first study, a male orangutan (Abang) was provided with a fixed stone core, a loose hammerstone and a puzzle box that could only be opened with a sharp tool. During testing, Abang was shown how to flake stone by a human demonstrator (Wright), and was physically 'molded' to do so (i.e., Abang's keeper held his hands and guided his movements to use a flake as a cutting tool; Wright, 1972). Subsequently, Toth and colleagues provided a similar array of materials and social demonstrations to the bonobos Kanzi and Panbanisha, except that the bonobos were given loose cobbles to be used as cores and hammerstones instead of a fixed one (Toth et al., 1993). Reportedly, the bonobos became proficient in manufacturing and using sharp-edges stone tools (Schick et al., 1999) and Kanzi even innovated his own techniques to produce sharp-edged stones, namely throwing a cobble onto the hard floor and throwing a cobble against another cobble (Toth et al., 1993).

Although these early ape studies were clearly innovative in their methods, there are several factors that limit the conclusions that can be drawn from them. Firstly, all of the tested apes were enculturated. Enculturated apes are those that have experienced extensive human training or contact (Henrich & Tennie, 2017). This is an important limitation, as it is now known that the process of enculturation affects ape cognition (Damerius et al., 2017; Hecht et al., 2013). In particular, enculturation allows apes to acquire abilities not normally observed in wild and/or unenculturated conspecifics (Buttelmann et al., 2007; Tomasello et al., 1993; Call, 2001). Secondly, all previous ape subjects were given human demonstrations before testing and Abang was even molded to produce and use sharp-edged stone tools (Wright, 1972). Therefore the spontaneous abilities of apes to perform these behaviours have never been investigated. Lastly, although chimpanzees are one of our two closest living relatives (alongside bonobos) and possess the most extensive tool-use repertoires of all great apes (including some stone tool behaviours such as nut-cracking using stone hammers and anvils; Boesch & Boesch, 1984), their spontaneous abilities to produce sharp-edged stone tools have never been tested.

Investigating the spontaneous production and use of sharp-edged stone tools in naïve, unenculturated chimpanzees can provide insight on whether the production and use of sharp-edged stones are within the cognitive reach of apes. If chimpanzees can spontaneously produce or use sharp-edged stone tools, this would indicate that these abilities were also likely within the cognitive reach of our last common ancestor with the genus *Pan*. Consequently, the aims of this study are to investigate the spontaneous individual abilities of task-naïve, mother reared (unenculturated) chimpanzees to

1) make and use sharp-edged stone tools to access a reward (Experiment 1; Baseline conditions I and II); 2) use human-made flakes to access a reward (Experiment 1; Flake condition); and 3) make sharp-edged stone after repeatedly exchanging human-made flakes for food rewards (Experiment 2). Our study addresses one of the outstanding questions in the field of cognitive archaeology, namely whether individual learning mechanisms are sufficient for the acquisition of sharp-edged stone tool making abilities. Thus, this study provides insight into the evolution of lithic technology in both human and non-human primates.

2. Methods

2.1 Subjects and housing

Subjects included in this study were housed at the Kristiansand Zoo in Kristiansand, Norway (Table 1). Seven chimpanzees (M_{age}=23.7; age range: 7-41; 5F & 3M) were tested individually (except the mother and infant pair, who were tested together). The chimpanzees could not see each other while being in the indoor rooms as there were opaque walls between the rooms. All subjects included in the experiments were naïve to the target behaviours of "sharp-edged stone making" and "sharp-edged stone tool use". This prior naivety was necessary to discriminate between the roles of individual and social learning in the acquisition of the target behaviours.

Tests took place in the sleeping quarters during the morning cleaning routines between 7:30 and 8:30am and in the afternoon between 1pm and 3pm.

Table 1: Demographic data of the chimpanzees tested.

Subject	Birth year	Sex	Raising conditions
Dixie	1977	F	Mother reared
Jane/Yr	1999/2011	F/F	Mother reared
Josefine	1983	F	Mother reared
Junior	2003	M	Mother reared
Knerten	2000	M	Mother reared
Tobias	1994	M	Mother reared

The chimpanzees at Kristiansand zoo have access to two enclosures (one indoors and one outdoors), as well as to a separate indoor sleeping area. Both enclosures are equipped with climbing ropes, feeders and ad libitum water as well as several enrichment devices: tree trunks with holes of different depths filled with honey that the chimpanzees obtained by using both their fingers and tools; automatic dispensers that released nuts into a maze, which the chimpanzees could obtain by guiding the nuts with tools inserted through different holes; an artificial termite mount baited with honey for "fishing" with tools; and PVC tubes and hose fragments approximately 20cm long with honey smeared inside, which the chimpanzees obtained using tools and their fingers. The chimpanzees were also provided with long fresh branches (more than 1m long) in the indoor enclosure. These branches retained side branches, leaves, and bark when they were given to the chimpanzees. The outdoor enclosure was an island of approximately 1840 m^2 surrounded by a water-filled moat, with natural soil, rocks and vegetation.

The chimpanzees participated voluntarily in the experiments as they took place during usual cleaning routines of the indoor enclosure. There were no changes made in their feeding routines during the course of the experiments, as the food rewards used were part of their regular diet. The chimpanzees had previously participated in other two behavioural experiments, but these involved the use of sticks to extract buried food and never stones. After consulting with the keepers and personnel of the zoo and taking into account the nature of the previous experiments, we were confident that the chimpanzees were naïve to the task presented both in terms of sharp-edged stone tool production and use.

2.2 Testing materials Experiment 1

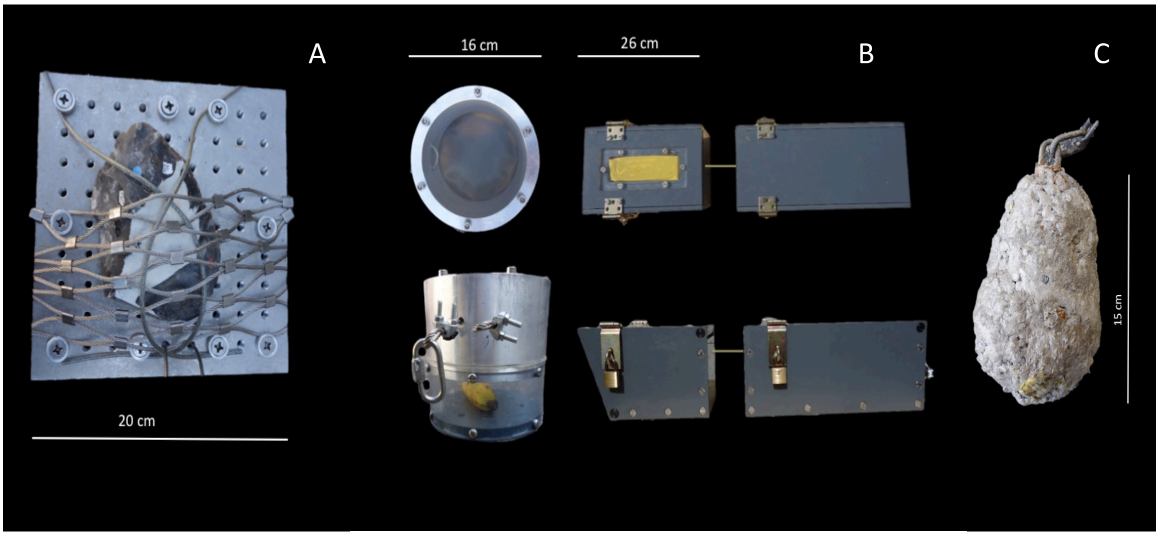

Figure 1: Testing materials used during the experiments. Object A depicts the core used during the experiments and the platform where it was fixed. Object B depicts both the hide box (left) and the tendon box (right) used during the experiments. Object C depicts the artificial hammer made of concrete that was used during the experiments.

Tendon box

For testing flake use, we used a baited box ("tendon box", Figure 1B) modeled on an earlier version described by Wright (1972) and Toth et al. (1993). The tendon box was used to simulate a scenario in which, faced with an animal carcass, a subject must cut through taut tendons (a rope in our experiment) in order to dismember a body.

The tendon box consisted of two opaque boxes secured to a wooden board [box one (reward box): 26cm x 17.3cm x 17.3cm; box two (non-rewarded): 36cm x 15cm x 17.2cm]. The tendon box had a clear Plexiglas window (5cm x 16cm) at the top that allowed for the reward inside being visible to the chimpanzees. The door of the box was pulled shut by a rope that ran through the inside and exited through a hole in the opposite end. The rope then ran between the two boxes for approximately 5cm and entered the second (non-rewarded) box. The rope was secured in the non-rewarded box to a clamp that could be tightened to ensure that the rope was taut. Thus, the rope was only accessible in the area between the two boxes, and had to be cut there to allow the door of box one to open. The rope was a brown twisted hemp rope, approx. 2mm thick. This type of rope was selected as it was found to be (after pilot testing) strong enough to withstand most attempts at removal without a tool, but could be cut using a knife or flake. Collectively, the box weighed approximately 21kg (including the supporting board). Given that cutting the rope itself did not lead directly to the obtention of the reward (but to the opening of the door), the tendon box represented and indirect puzzle box.

Hide box

We used an additional box shaped as a drum ("hide box", thus named due to the material's resemblance to an animal hide. Left of Figure 1B). This box was designed based on the descriptions provided by Westergaard & Suomi (1994a) in their stone tool experiments with tufted capuchin monkeys (*Sapajus apella*). The hide box was used to simulate a scenario in which, faced with an animal carcass, a subject must cut through taut skin/hide (a silicone membrane in our experiment) in order to access the inside of a body. The hide box consisted of a transparent Plexiglass cylinder (16cm wide x 15.5cm high) with a metallic rim. A silicone membrane 2mm thick was screwed in between the cylinder and the rim, blocking the access to the reward placed inside the cylinder. The hide box was then secured vertically to the bars of the sleeping rooms where the experiments took place. Contrary to the tendon box, the hide box represented a direct puzzle box in which cutting an object (the membrane) allowed to directly access the food reward contained inside.

The rewards placed inside the boxes included half a piece of fruit or a yogurt. The rewards were chosen based on the preferred foods of the apes.

Hammers

Due to safety regulations, it was not possible to provide loose hammerstones to the chimpanzees housed at Kristiansand Zoo. Instead, one concrete rounded hammer (ca. 15cm long x 10cm wide, weight 2.2kg) was provided during each trial (Figure 1C). The hammer was built around a metallic scaffold linked to a chain that allowed fixing the hammer to the bars of the sleeping rooms so the chimpanzees could not carry the hammers into the indoor enclosure. The concrete used to build the hammer included particles of up to 1cm in diameter. The hammer was covered with non-toxic transparent epoxy resin to prevent the hammer surface from disintegrating upon hammering.

Cores

Retouched Norfolk Chert cores were provided to the subjects alongside the hammers. The cores were retouched to display angle variability between ~90 degrees and ~40 degrees. During the reduction process the aim was to produce either i) three separate surfaces - with varying angles - from which flakes could potentially be struck off or ii) a continuous edge around the perimeter of the core with continuously varying angles within the above mentioned range. The cores weighed between 0.8 and 1.5Kg. Subjects received one core per trial. If the core was not modified, the core was used in further trials. Due to safety regulations, the core had to be fixed on a metallic platform (Figure 1A, 20cm x 20cm x 2cm) to prevent the chimpanzees from carrying the core into the indoor enclosure. The core was attached to the platform using a metallic wired mesh with holes 50mm wide and 3mm thick wire from XTEND (Carl Stahl ARC GmbH, Architectural Cables and Mesh Systems).

Flakes

A flake was provided to the chimpanzees in the Flake condition that followed the baseline conditions (see below for details on the experimental conditions). The flake was made out of sight of the apes by the experimenter (AMR) using the freehand knapping technique. The flake measured 7.6cm x 5cm x 1.7cm. The flake was placed unfixed (loosely on the floor) next to the hammer, core and puzzle box(es) before the subjects were allowed into the testing area.

2.3 Testing procedure Experiment 1

Experiment 1 was divided into two experimental conditions: Baseline condition and Flake condition. During the Baseline condition the subjects were provided with the testing materials but no additional information (demonstrations, guidance, or artefacts) was provided. A baseline was included in order to test for the spontaneous individual sharp-edged stone tool making abilities of the chimpanzees. The Baseline condition was split into two subconditions (Baseline condition I and Baseline condition II). During the Baseline condition I, seven chimpanzees (Table 1) had access to the tendon box, the hide box, an artificial hammer and the fixed core. All chimpanzees were tested individually (except the mother and infant pair) in three trials each during this condition (condition duration range per individual 01:05:40 to 03:00:49). Trials in all conditions started when the subjects entered the testing room and ended after the cleaning routines were completed.

We included a second baseline condition to focus the attention of the individuals on solving a single task by only providing them with one box. During the Baseline condition II, only the four most engaged chimpanzees (two males and two females; Fragaszy et al., 2011) of the seven that participated in the Baseline condition I were tested. Two chimpanzees (Knerten and Dixie) received the hide box and two chimpanzees (Tobias and Josefine) received the tendon box. The four chimpanzees were tested in three trials each during this condition (condition duration range per individual 01:18:50 to 03:31:12). The same individuals tested in the Baseline condition II were further tested in the Flake condition with the same set up as the Baseline condition II except for the provision of a readily made flake. This condition was included in order to test for the spontaneous tool using abilities of the chimpanzees and each individual was tested in three trials (condition duration range per individual 01:46:23 to 02:38:32). As before, the duration of the trials varied according to the cleaning routines, as this was the time where tests were conducted.

2.4 Testing procedure Experiment 2

The four chimpanzees that participated in the Flake condition also participated Experiment 2, which included a Familiarization phase and a Test condition. The goal of the Familiarization phase was for the chimpanzees to get used to the exchange of flakes for food rewards in order for them to attribute value to flakes. Ten flakes were produced before the start of this condition by the experimenter out of sight of the chimpanzees, using the freehand knapping technique. These flakes were all placed inside the testing room before the chimpanzee was allowed inside. Once the chimpanzee was inside the room, she/he was asked to exchange each flake for a grape. The experimenter asked for the flakes by showing the hand palm up, verbally encouraging the chimpanzee and occasionally pointing at the flakes. If the chimpanzee pushed a flake out of the room through the bars, the experimenter gave her/him a grape. In order to consider the Familiarization phase successful, the apes had to exchange at least eight flakes in ten minutes.

After completing the Familiarization phase, the chimpanzees were further tested in the Test condition. The aim of this condition was to assess if once the chimpanzees have associated flakes with high value rewards (grapes), they would make more sharp-edged stones in order to obtain more rewards. In this condition, a fixed core and two hammers (equivalent to the ones used in Experiment 1), as well as six loose human-made flakes, were placed inside the testing room. The core provided to the chimpanzees in the Test condition of Experiment 2 had two refitted flakes (see Figure 2), which were detached by the experimenter out of sight of the apes using freehand percussion. One of the flakes was weakly refitted to the core using a sugar-based glue (usually used for decorating cakes). The other flake was strongly glued to the core with clear epoxy adhesive glue. Both glues where transparent and non-toxic. These two flakes were refitted to the core in order to increase the chances of flake detachment if a subject hit the core with the hammer. We predicted that if a flake would detach easily and they could obtain a reward, the chimpanzees would keep trying to make more. The loose flakes (N=6) were placed around the core structure to reinforce the association that sharp-edged stones could be detached from the core (see Figure 2). When the subject entered the room in the Test condition, she/he was once more asked to exchange the human-made flakes, following the method used in the Familiarization phase. The chimpanzees were tested in three trials during the Test condition (condition duration range per individual 01:13:28 to 00:25:10).

Figure 2: Design of the core presented to the chimpanzees in the Test condition of Experiment 2. The blue and red areas represent the two flakes refitted into the core, one with soft glue and one with hard glue. The green flakes were loosely attached/placed around the core. The aim of these loose flakes was to motivate the chimpanzees to obtain more sharp-edged stones themselves as well as to try to convey the information that the sharp-edged stones come from the core.

All testing materials (testing box/es, one hammer and the core fixed on the platform) were placed inside the testing area and secured to the bars of the enclosure. Two Sony HDR-CX330E Handycams were set-up half a meter from these bars, and recorded once the subject entered the testing area. Potential tools were cleared from the testing areas before the tests started. However, the chimpanzees often brought tools with them into the testing areas at the start of the tests.

2.5 Coding

From each video-recorded trial the following variables were coded i) the number of interactions (times the chimpanzees touched a testing material); ii) the duration of these interactions (time spent in physical contact with the testing materials, from when the subject started contact until it paused for more than 3s or changed activity);

iii) which testing material the chimpanzees interacted with and iv) if the interaction was manual or using a tool.

3. Results

3.1 Experiment 1

None of the chimpanzees tested in this study spontaneously made sharp-edged stone tools in the Baseline or Flake conditions and no chimpanzee used the flake provided to them during the Flake condition to access the food reward. Although the chimpanzees did not make or use sharp-edged stone tools, all individuals interacted with the apparatuses and objects provided (see Table 2, Figure 3). As no significant correlation was found between the trial length and the number of interactions (Figure 4), the results are presented as sums of interactions rather than sums of interactions divided by trial length. Across all trials, the chimpanzees interacted with the testing materials 710 times.

Table 2: Frequencies and mean durations in seconds ± SD (between brackets) of the interactions with the different testing elements by each individual chimpanzee. Superindexes indicate the individual's sex.

	Tendon box	Core	Hide box	Flake	Hammer	Total
Dixie^F	0	1(1)	115(7.90±9.76)	0	7(3±2.89)	123
Jane^F/Yr^F	2(14±5.66)	2(4.5±2.12)	29(9.10±9.31)	0	5(4.2±3.11)	38
Josefine^F	40(10.3±10)	2(38±50.9)	48(18.4±26)	1(3)	25(14.8±17.1)	116
Junior^M	12(9.9±6.5)	1(1)	29(6.7±7.4)	0	1(1)	43
Knerten^M	7(10.3±8.7)	3(4.3±4.2)	264(12.3±15.0)	1(5)	33(8.7±8)	308
Tobias^M	21(6.9±5.8)	2(3.5±3.5)	35(6.5±5.9)	0	24(9±8.5)	82

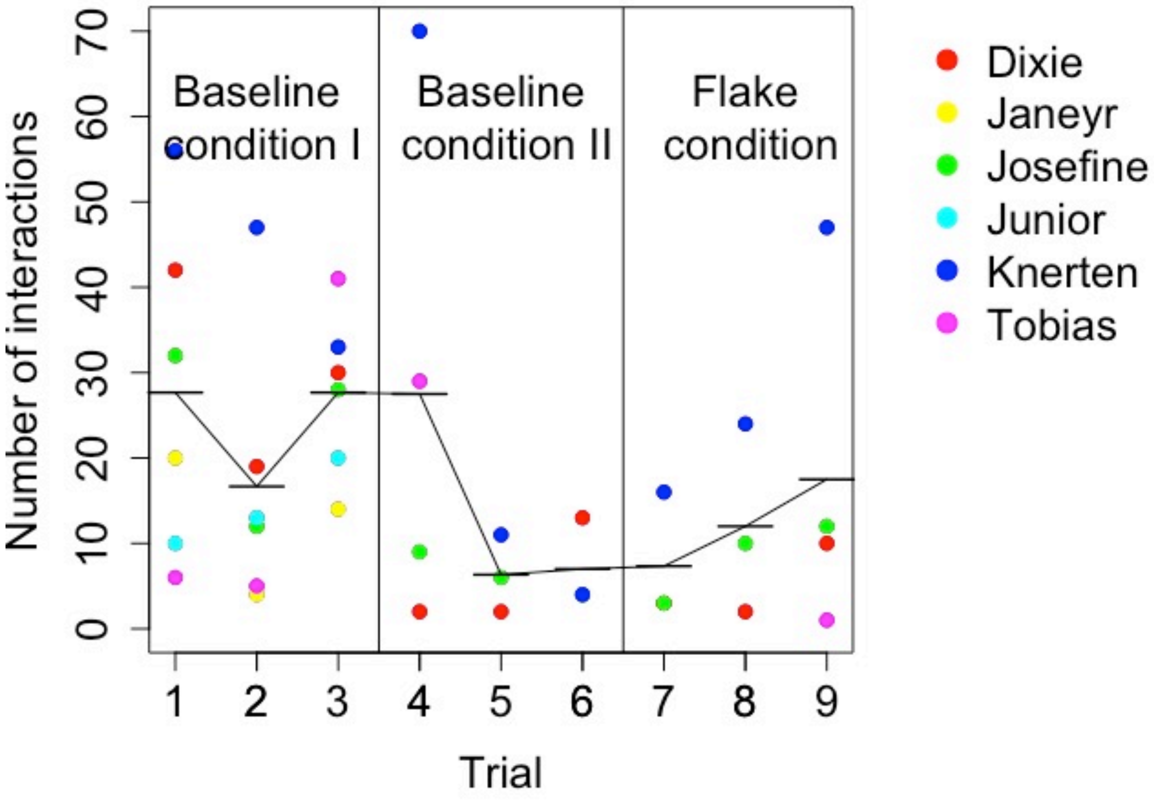

Figure 3: Number of interactions performed by each individual in each trial of the three experimental conditions. Horizontal lines represent mean number of events across individuals per trial. Note that in the Baseline condition II and the Flake condition, only four individuals were tested (Dixie, Josefine, Knerten and Tobias)

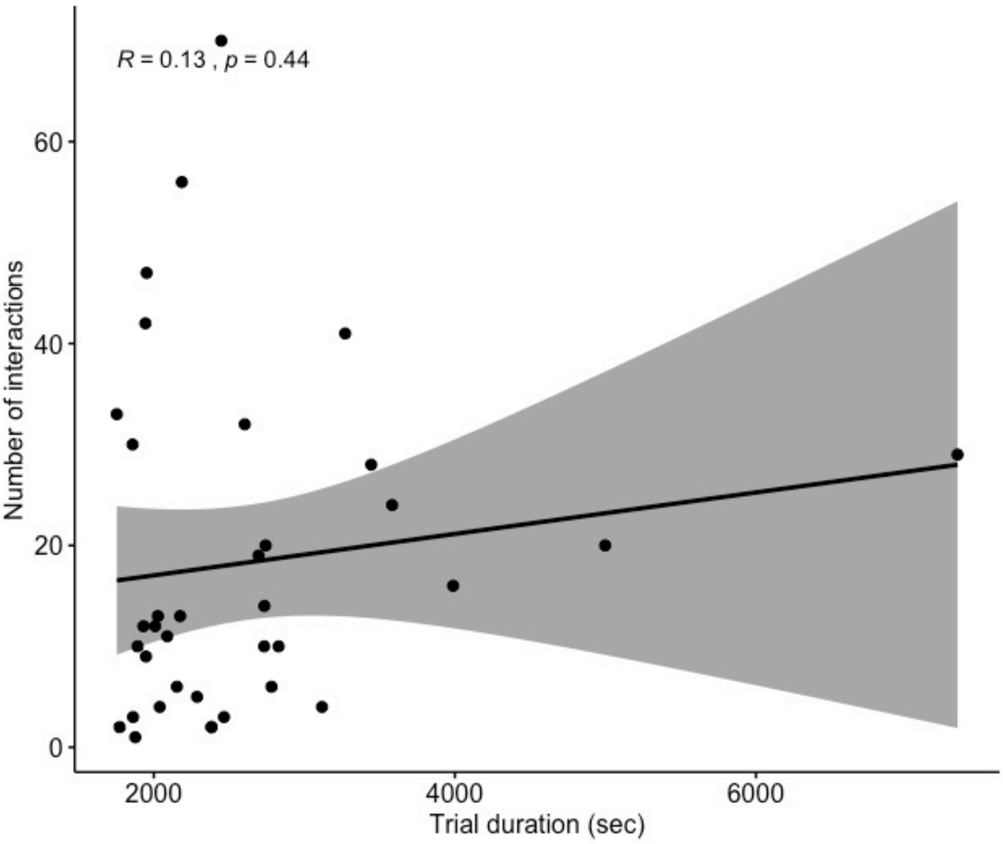

Figure 4: Pearson correlation between the number of interactions performed by the chimpanzees and the trial length.

In all experimental conditions, the chimpanzees interacted the most with the hide box (Figure 5), while the number of interactions with the tendon box was much lower in all conditions. It is possible that in the Baseline condition II (where only one box was provided) and the Flake condition, the chimpanzees that received the hide box were more motivated to interact with their box than those chimpanzees that received the tendon box. The hide box might have been perceived as more interesting because it made noise every time the membrane was hit (like a drum), which might have caused higher interaction frequencies with the hide box than with the tendon box. The chimpanzees also interacted with the hammer in all experimental conditions but the interest in it decreased with each condition.

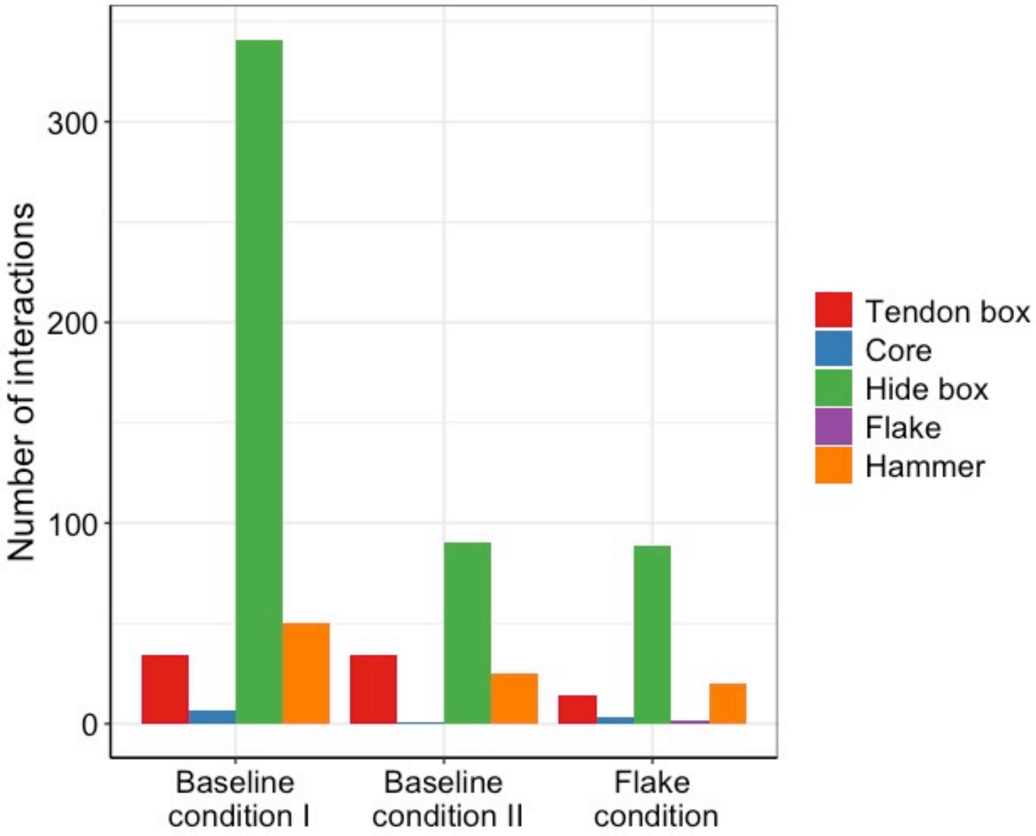

Figure 5: Number of interactions towards the different testing materials in each experimental condition.

Interactions were made both by hand and using tools (Table 3). The chimpanzees used straw, plastic hose fragments, plastic cups, sticks and plastic pieces as tools. However, the chimpanzees were never successful in opening the boxes using these tools.

Table 3: Frequency and total time of the interactions with different testing materials using the hands or tools.

Testing material	Interact via	N	Total time (sec)
Touch tendon box	hand	77	717
Touch tendon box	tool	5	56
Touch core	hand	11	107
Touch hide box	hand	515	5690
Touch hide box	tool	5	28
Touch flake	hand	2	8
Touch hammer	hand	95	915

Although we did not code for specific types of hand touches, we did observe that chimpanzees knocked (touched repeatedly and in quick succession an object with the knuckles), slapped (touched in a fast movement an object with the palm of the hand) and hit (touched fast and using considerable force an object with any part of hand other than the palm) the testing materials provided. However, no percussive actions took place in any of the trials using any tool.

3.2 Experiment 2

During the Familiarization phase all four subjects exchanged the ten flakes provided within the set time limit of ten minutes and therefore all four chimpanzees participated in the test condition. During the test trials, the chimpanzees had the possibility to further exchange loose flakes placed around the fixed core for rewards, which potentially increased the attribution of value to the ten flakes. During the test trials, the chimpanzees interacted with the materials a total of 40 times (Figure 6), 26 times with the fixed core (mean duration ± SD=7 ± 6) and 14 with the hammer (mean duration ± SD=9 ± 12). No percussive activities took place during Experiment 2.

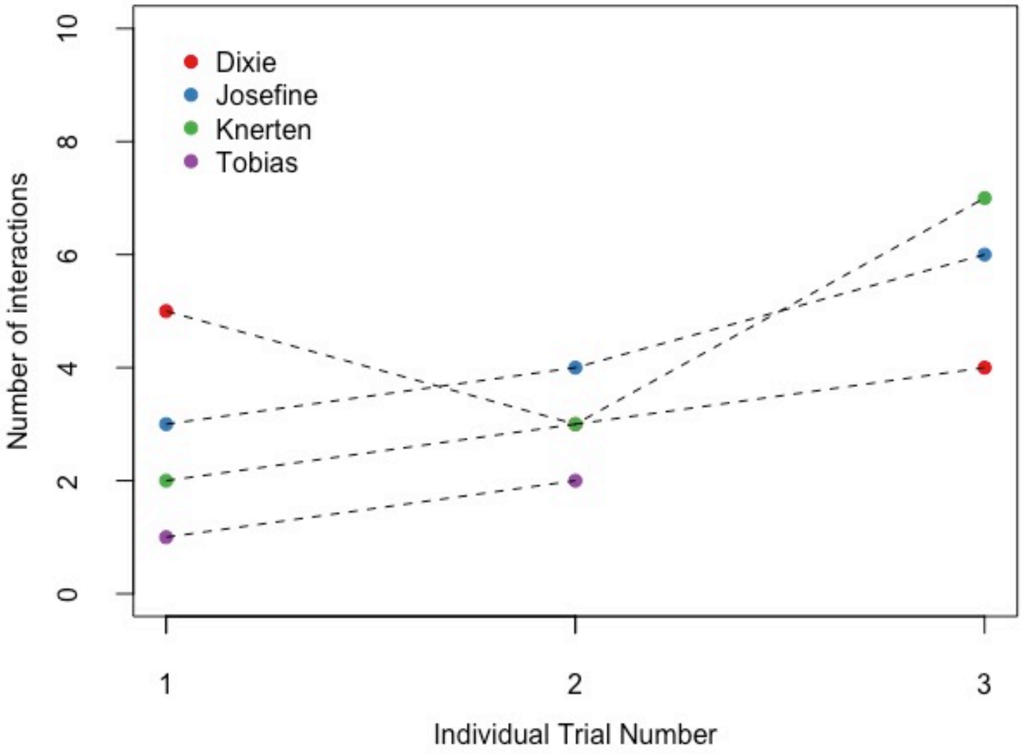

Figure 6: Individual number of interactions during the Test condition of Experiment 2.

4. Discussion

In contrast to the two earlier studies investigating sharp-edged stone tool production and use in great apes, and despite the fact that the chimpanzees were motivated to manipulate the testing materials provided, none of the individuals included in this study made or used a sharp-edged stone either spontaneously (Baselines) or after being given a human-made flake (Flake condition). It is unlikely that the absence of sharp-edged stone production in our study compared to previous ape studies is due to inter-species differences in cognitive and/or physical abilities. Cognitively, chimpanzees are likely to be at least on par in physical skills with orangutans and bonobos and in addition, chimpanzees have the most extensive tool-use repertoires of wild apes, which includes the use of stone hammers and anvils for nut-cracking (Boesch & Boesch, 1983). That chimpanzees are physically able to produce sharp-edged stones is further supported by the fact that wild chimpanzees occasionally produce flakes unintentionally while engaging in nut-cracking (Mercader et al., 2007; Mercader et al., 2002).

A more likely explanation for the discrepancy between the results of our study and those of previous ape studies is the different rearing background of the subjects and/or the provision of information prior to testing. In contrast to previous studies, the chimpanzees in our study were neither enculturated nor provided with any demonstrations of flake production or use before testing. Indeed, previous studies have demonstrated that enculturation (e.g., through imitation training paradigms such as the 'Do-as-I-Do' task) fundamentally changes the brain structures of non-human primates (Pope et al., 2018), allowing them to attend to, and even in some cases copy actions (Tomasello et al., 1993; Call, 2001; Buttelmann et al., 2007). Consequently, our results strongly suggest that the orangutan and bonobos previously tested in sharp-edged stone production experiments were able to make and use sharp-edged stones due to their high degree of human enculturation and/or the social demonstrations provided to them before testing.

Therefore, outside the sphere of human influence, the individual, spontaneous abilities of chimpanzees do not seem to suffice to make or use sharp-edged stones. In the light of these findings, there exist two possible evolutionary explanations for the distribution of sharp-edged stone tool making abilities in the hominin lineage. The first possible scenario is that the last common ancestor of chimpanzees and humans did have the ability to intentionally produce and use sharp-edged stones but that this ability was subsequently lost in the chimpanzee lineage (and maintained in the hominin lineage). However, this explanation does not fully account for the lack of sharp-edged stone tools in the archaeological record for millions of years after the split between hominins and the genus *Pan* 7 Ma. This absence of artefacts could alternatively be due to the low frequency in which they were produced or to their physical characteristics, which make them almost impossible to identify in situ. If stone tools were produced using percussive actions similar to how modern chimpanzees crack nuts (assuming that these assemblages could be found), it would be extremely challenging to systematically identify these artefacts as intentionally produced sharp-edged stone tools rather than by-products of percussive actions in other foraging contexts.

The second evolutionary scenario is that the last common ancestor of hominins and *Pan* did not have the cognitive abilities to spontaneously make or use sharp-edged stones intentionally. According to this second scenario, the ability to intentionally make and use sharp-edged stones would have evolved later in the hominin lineage, resulting in hominins (but not other apes) eventually crossing the cognitive Rubicon for intentional sharp-edged stone tool production via cultural and/or biological evolution (Boyd & Richerson, 1996).

In such a scenario, the question remains of how did sharp-edged stone tool making and using abilities evolved in our lineage, via biological or cultural evolution? Although a biological explanation may seem unusual and therefore unlikely at first, biological evolution has already proven to be the most parsimonious explanation for a phylogenetically independent case of sharp-edged stone tool production and use in capuchin monkeys. Previous studies tested the spontaneous sharp-edged stone tool making abilities of naïve, unenculturated tufted capuchin monkeys (*Sapajus apella*; Westergaard & Suomi, 1994a, 1995b; the naivety of the capuchins to the task was confirmed by G. Westergaard, pers. comm.). In contrast to naïve, unenculturated chimpanzees, unenculturated capuchins spontaneously made and used sharp-edged stone tools (Westergaard & Suomi, 1994a, 1995b). As the capuchins were not shown how to make or use sharp-edged stone tools, these studies show tufted capuchins do not necessarily rely on copying or enculturation to make and use sharp-edged stone tools. Given that cultural evolution of sharp-edged stone tools would have required cultural transmission skills (i.e. copying: Boyd & Richerson, 1996; Galef, 1992; Tomasello, 1999), which proved unnecessary in the case of capuchins, cultural evolution is a less likely driver than biological evolution of the emergence of sharp-edged stone tool production in the hominin lineage.

The studies with naïve capuchins, alongside the archaeological record that dates the oldest evidence of sharp-edged stone tool making much more recently (between 3.3 and 2.58 Ma) than our split from chimpanzees (approximately 6-7 Ma), supports the biological evolution of sharp-edged stone tool abilities: the cognitive skills necessary to make and use sharp-edged stone tools evolved independently, and at least twice during primate evolution (in capuchins and hominins). This scenario would also explain the large time gap (spanning several million years) between the split of hominins and *Pan* and the time when the first flaked stone tools appear in the archaeological record.

Data availability

All code and raw data used in this chapter can be found in the Open Science Framework project named "Chimpanzee stone tool project (Chapter 3)": https://osf.io/yv4nx/?view_only=faade030c40444218fef27e1d2577aa2

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Chapter 4: Orangutans can spontaneously produce and use sharp-edged stones: implications for the evolution of lithic technology

This chapter corresponds to the following manuscript:

Motes-Rodrigo, A., McPherron, S. P., Archer, W., Hernandez-Aguilar, R. A., & Tennie, C. (in prep) Orangutans can spontaneously produce and use sharp-edged stones: Implications for the evolution of lithic technology.

I am the first author of the manuscript corresponding to this chapter. I was the main experimenter and I conducted all data collection and analyses presented in this chapter. The original idea for this study was developed in collaboration with Dr. Claudio Tennie and Dr. McPherron. I was the main writer of the manuscript in collaboration with Dr. Tennie. All coauthors provided feedback on the manuscript.

CHAPTER 4

Orangutans can spontaneously produce and use sharp-edged stones: implications for the evolution of lithic technology

1. Introduction

Scientists across multiple disciplines have long debated which factors allowed humans to spread across land, water and even space. The strongest candidate accounting for this successful expansion is cumulative culture (Boyd & Richerson, 1996; Galef, 1988; Henrich, 2017; Tomasello et al., 1993). Cumulative culture consists of cultural forms that are modified before and/or during their transmission and subsequently copied by other individuals. During this process, naïve individuals acquire previously modified behavioural forms from models by observing their actions and/or the products of their behaviour (e.g. artefact forms). Once the modified forms have been acquired, they might keep cumulating modifications, further increasing their complexity and/or efficiency. This process (known as the ratchet effect: Tennie et al., 2009; Tomasello, 1999) drives cumulative culture and eventually results in the formation of culture-dependent forms (compare Reindl et al., 2017; Tennie et al., 2018). Culture-dependent forms have become so complex or opaque due to the ratchet effect, that individuals can no longer re-innovate them on their own. Instead, culture dependent forms must be copied from knowledgeable models that had access to the specific lines of cultural evolution maintaining these forms in the population (Boyd et al., 2011).

Human cumulative culture is currently present across all behavioural domains (Price et al., 2009). For example, human languages are culture-dependent because word forms (lexicon) need to be acquired from a model. Many human dances are also culture-dependent as they as the sequence of steps cannot be individually learnt but need to be copied (Legare, 2017). Similarly, most modern human technological forms also depend on access to their containing culture and must be copied in order to be learnt (Caldwell & Millen, 2008, 2010; Reindl et al., 2018; Tomasello, 1999).

Despite the advances made in the field of cultural evolution, we still do not know when or how this particular type of culture – i.e. cumulative culture leading to culture-dependent forms – developed in our lineage. As behaviour itself does not fossilize, the earliest human forms preserved to date in the archaeological record are artefact forms, namely early stone tools (ESTs: Tennie et al., 2016). Although hardly complete as a record, ESTs provide an opportunity to study geographical and temporal variation in the technological domain. ESTs include, among others, the products of the so-called Lomekwian (3.3 Ma, Harmand et al., 2015) and the Oldowan industries (2.58 Ma, Braun et al., 2019). The Lomekwian is characterised by large cores, flakes (sharp-edged stones that present evidence of conchoidal fracture, Debénath & Dibble, 1994), anvils, hammerstones, and worked and split cobbles (Harmand et al., 2015). According to experimental replications, Lomekwian flakes were produced by the passive hammer technique and/or the bipolar knapping technique. The passive hammer technique involves taking a core in hand and striking it vertically against a fixed (passive) rock. Therefore, the core acts as an active element and the hammer as a passive. The bipolar knapping technique involves placing the core on a rock anvil (passive element) and then striking it from above with a hammerstone (Harmand et al., 2015), somehow similar to how some wild chimpanzee populations crack nuts (Biro et al., 2003). The Oldowan is broadly composed of flakes, hammerstones, various core forms, rock anvils and flaking debris (Roche, 2000). The main techniques used to produce Oldowan artefacts have been inferred to be bipolar knapping (see above) and free-hand percussion, where a flake is detached from a body-stabilised (usually hand-held) core by striking it with a hand-held hammerstone (reviewed by Plummer, 2004). The production of sharp-edged stone tools has been proposed as the main goal of Oldowan reduction sequences (Toth, 1987), and likely fostered the development of new foraging practices – such as the butchery of large vertebrates (Potts & Shipman, 1981).

Despite the importance of ESTs, and especially sharp-edged stone tools, for the development of our species, it remains debated how the production techniques (behavioural forms) of these artifacts were learned. Understanding the learning mechanisms behind the acquisition of sharp-edged stone tool production techniques in early hominins is necessary in order to determine if EST production and use were culture-dependent forms. If it would be found that EST production techniques and EST use could only be acquired via copying, this would indicate that ESTs might represent the first culture-dependent forms that emerged in our lineage. In turn, such findings would also be indicative of hominin cumulative cultural processes (as it is these that produce culture-dependent forms). Current hypotheses about how EST production techniques were learnt by early hominins range from the view that some of these techniques were genetically mediated adaptations (Corbey et al., 2016, referring to the late Acheulean) to the view that they were acquired via extant human transmission mechanisms – i.e. via copying social learning mechanisms (Shipton, 2010; Stout et al., 2019) and/or specific variants of teaching (Morgan et al., 2015).

The hypothesis that the acquisition of ESTs was mediated by variants of copying (such as imitation: Stout et al., 2019) has been criticized on the grounds that it fails to account for an unavoidable consequence of copying: cumulating copying error (Schillinger et al., 2014; Tennie et al., 2017). Cumulated copying error has been simulated and experimentally demonstrated to introduce variation in material cultures (Eerkens & Lipo, 2005; Hamilton & Buchanan, 2009; Kempe et al., 2012), including artefact shape (Schillinger et al., 2014). Given that copying mechanisms (imitation, emulation and/or specific variants of teaching such as imitation-based teaching) are mechanisms that transmit forms themselves, the unavoidable variation caused by copying error should have inevitably led to path-dependent patterns of these forms in short time frames and across different populations, species and geographical regions (Richerson & Boyd, 2005; Tennie et al., 2016; Tennie et al., 2017). Looking at artefact form, this kind of patterning is however absent from Oldowan sites (and perhaps Acheulean sites, Gowlett, 2015; Tennie et al., 2017). Instead, Oldowan forms are characterized by long-lasting and widespread morphological stasis (around a mean: Charbonneau, 2015; Tennie et al., 2017). Although it might be suspected that the Lomekwian showed stasis too, this cannot yet be ascertained given that the Lomekwian is currently known from a single site which context remains debated (Dominguez-Rodrigo & Alcalá, 2019).

Within the two extremes of genetically determined versus copied EST forms, an alternative view equates the mechanisms underlying the production of sharp-edged stone tools with those mechanisms argued to underlie modern great ape behavioural variation, namely socially mediated re-innovations (Bandini & Tennie, 2017; Tennie et al., 2016; Tennie et al., 2017). Socially mediated re-innovations consist on repeated, independent cases of innovation in which individuals naïve to a species-specific behavioural form, spontaneously learn said form. Although re-innovations can be influenced by genetic predispositions, the prototypical case is one where biologically evolved cognitive skills interact with the environment and lead to the emergence of the final behavioural form(s). Forms that can be re-innovated by naïve subjects who had never seen these behaviours before are considered latent solutions (Tennie et al., 2009; Tennie et al., in press). Latent solutions do not rely on any social learning mechanisms (including copying) to be expressed by an individual but can be catalysed and stabilized by non-copying variants of social learning widespread in the animal kingdom (Tennie et al., in press). In order to investigate if a form is a latent solution, baseline experiments are applied. During baseline experiments, naïve subjects are provided with all relevant materials to produce the target behaviour or artefact form without being exposed to direct information about these forms (Bandini & Tennie, 2017; Neadle et al., 2017; Tennie et al., 2009). If naïve individuals can spontaneously re-innovate the target forms during a baseline experiment, then it logically follows that these forms are latent solutions because they do not rely on copying a model to be learnt. Importantly, when target forms are sufficiently complex, a single instance of re-innovation in a single naïve individual suffices to classify a form as a latent solution (Bandini & Tennie, 2017, 2018).

Although the latent solution approach also includes genetic adaptations (Corbey et al., 2016), it focuses primarily on individual learning of form and on the role that non-copying social learning mechanisms have in mediating how *frequently* a form is re-innovated in a population (Tennie et al., 2009; Tennie et al., in press). By influencing both re-innovation frequency and stability of the forms, non-copying social learning mechanisms play a large role in explaining population patterns of cultures constituted by latent solutions. However, as these mechanisms cannot and do not transmit the behavioural forms themselves, they do not lead to cumulative culture or culture-dependent forms. Instead, this process produces a stasis (or "variable sameness" Gowlett, 2015; Jelinek, 1977) of forms over extended periods of time.

Given the arguable stasis in EST forms over time, it could be argued that they constitute latent solutions and that their distribution pattern is the result of socially mediated re-innovations rather than copying. If copying had underlain the acquisition and maintenance of EST forms, they would instead show clear patterns of path-dependency and fast change over time (Tennie et al., 2016; Tennie et al., 2017). Further evidence supporting the latent solution scenario for ESTs comes from non-human great ape cultures, which are mainly constituted by latent solutions whose form remains stable over time and space (Chapter 2, Tennie et al., 2009; Tennie et al., in press). Accordingly, apes show evidence of spontaneous non-copying social learning (Tennie et al., 2010), but not of copying variants of social learning (Clay & Tennie, 2017; Tennie et al., 2012; Tomasello et al., 1997). Given the evidence presented above, it is therefore not parsimonious to assume that early hominins systematically copied behavioural forms since the split from the genus *Pan* 7 Ma (Tennie et al., 2017).

The hypothesis that ESTs are latent solutions predicts that naïve hominins of the species producing the sharp-edged stone tools of their time (given their respective individual learning capabilities and biases) would have been able to produce these stone tool forms spontaneously without copying a model. Given that early hominins cannot be directly tested in cognitive experiments, we will focus on one of our closest living relatives, orangutans, as relevant models of early hominin cognition. Orangutans are particularly interesting because despite being proficient tool users and having varied technologies (van Schaik et al., 2009), they do not use stone tools in the wild (unlike chimpanzees, Biro et al., 2003; Boesch & Boesch, 1984). Furthermore, orangutans are the ape species most distantly related to humans, allowing us to indirectly shed light on the potential cognitive abilities of the LCA between humans and orangutans (approximately 13 Ma: Glazco & Nei, 2003).

Tests using apes as behavioural models, such as the ones reported here, are much more feasible to conduct in captivity than in the wild. In captivity, the background and behavioural repertoire of the animals is often known, which allows to select as test subjects ecologically-representative individuals that are naïve to the target behavioural form before the onset of the experiments. Ecologically-representative apes are those that have not been enculturated (Henrich & Tennie, 2017). Enculturation refers to rearing conditions "in a human cultural environment, with wide exposure to human artifacts and social/communicative interactions", which socializes the apes to interact with humans (Furlong et al., 2008; see also Henrich & Tennie, 2017; Tomasello & Call, 2004). Importantly, enculturation can induce cognitive skills that would otherwise not be present (so-called cognitive gadgets: Heyes, 2018). Indeed, human training and enculturation is already known to allow apes to copy actions (Buttelmann et al., 2007; Miles et al., 1996), an ability that they do not show spontaneously (Clay & Tennie, 2017; Hecht et al., 2013; Tennie, 2019; Tennie et al., 2009, 2012). Thus, testing unenculturated apes for their natural, spontaneous abilities, is and must be the target of phylogenetic investigations such as the one presented here.

A single experiment to date has tested the sharp-edged stone tool making and tool using abilities of orangutans. Wright (1972) tested the abilities of a captive juvenile male orangutan, Abang, to make and use sharp-edged stone tools in order to cut a rope and access a food reward. During the course of his experiments, Wright performed numerous social demonstrations of how to produce sharp-edged stone tools (using free-hand percussion) and how to use these tools for cutting. Furthermore, Wright (1972) reports that in one occasion, a keeper molded Abang's actions and guiding his hand while he was holding a sharp-edged stone tool, cut the rope of the test box. Regarding the results of the experiment, Wright found that after nine demonstrations, Abang used a (human-made) sharp-edged stone tool to cut the rope keeping closed the testing box. After seven demonstration sessions of how to make sharp-edged stone tools, Abang made a sharp-edged stone tool himself: Abang used a hammerstone to repeatedly strike on the core fixed to a wooden plank, which eventually led to the detachment of several sharp-edged stones. Abang then used these sharp-edged stones to cut the rope and open the box.

Although innovative for its time, the interpretability of Wright's results is limited. As no baseline experiment was performed, Wright did not test for the spontaneous re-innovation of sharp-edged stone tool production and use in orangutans from a naïve state. Furthermore, Abang must be considered somewhat enculturated and so he cannot be representative of either wild orangutans or the LCA of *Pongo* and *Homo* (e.g. Abang was taken for walks as a juvenile by his keeper and scientists entered the enclosure with the orangutan; John Partridge, former keeper of Abang at Bristol Zoo, UK, pers. comm.). Consequently, the spontaneous abilities of ecologically-representative, unenculturated orangutans for making and using sharp-edged stone tools are still unknown. As a result, it is currently not possible to infer these abilities in the LCA of *Pongo* and *Homo*.

In the present study we investigate the spontaneous individual abilities of task-naïve, mother reared and unenculturated orangutans to 1) make and use sharp-edged stone tools to access a reward (Experiment 1; Baseline condition) 2) use human-made flakes to access a reward (Experiment 1; Flake condition) and 3) make sharp-edged stone tools after repeatedly exchanging human-made flakes for rewards (Experiment 2). If enculturation, demonstrations and/or molding had been responsible for the stone tool making and using abilities of the single previously tested orangutan (Wright, 1972), our prediction would be that the orangutans in our study would not show any of these abilities. If these abilities do not spontaneously emerge in the unenculturated orangutans included in our experiments, this would suggest that the LCA of *Pongo* and *Homo* may not have had these abilities either. Alternatively, if at least one orangutan in our study spontaneously shows stone tool making or using abilities, this would support the hypothesis that the LCA of *Pongo* and *Homo* might have had these same (or equivalent) abilities.

2. Methods

2.1 Subjects and housing

Two male orangutans were tested at the Kristiansand Zoo (Kristiansand, Norway). The adult male, Matthieu, was 23 years old at the time of testing and his juvenile son, Loui, was 7 years old at the time of testing. A female orangutan (Nuni, who is also the mother of Loui) had a small dependent infant (Durian, 5 months old, M) at the time of testing. Given that Durian never let go of Nuni, her freedom of movement was restricted, and she avoided getting close to the testing apparatuses (perhaps as a consequence of always carrying the infant). Therefore, Nuni was not the target of the experiments but was sometimes in the room with Loui, the juvenile male, as the keepers were in the process of training Loui to be in a separate room from Nuni. When possible, Loui was tested in a different room from the one where his mother was fed. Both of these rooms where connected through a hatch, which was left open wide enough so that Loui (but not his mother) could pass through.

In order to investigate how novel forms are acquired, it is fundamental to ensure that the target forms are not already present in the subjects' repertoires (Bandini & Tennie, 2017). In our experiment, the orangutan keepers confirmed the naivety of the individuals regarding stone tool making and using before the onset of the experiments. In addition, stones were absent from the outdoor enclosure of the orangutans because the keepers clear them from the outdoor enclosure regularly to prevent the orangutans from throwing them at the visitors.

The orangutans at Kristiansand zoo have access to two enclosures (one indoor and one outdoor), as well as to separate indoor sleeping quarters where the experiments took place. The outdoor enclosure is an island of approximately 1800 m^2 surrounded by a water-filled moat, with natural soil and artificial climbing structures. The indoor enclosure consists of several connected rooms up to 10 m high with multitude of climbing structures and platforms. In addition, the orangutans have access to feeding enrichment both in the indoor and outdoor enclosure such as: tree trunks with holes of different depths filled with honey that the orangutans obtain by using both their fingers and tools; automatic dispensers that release nuts into a maze, which the orangutans obtain by guiding the nuts with tools and PVC tubes and hose fragments approximately 20 cm long with honey smeared inside. The indoor sleeping quarters are out of sight of the visitors and consist of three rooms with two levels each. The sleeping rooms have concrete walls and floor as well as straw as bedding material.

All orangutans participated voluntarily in the experiments as these took place during usual cleaning routines of the indoor enclosure. There were no changes made in the feeding routines during the course of the experiments as the rewards used were part of their regular diet and water was available *ad libitum*. We conducted two experiments in the orangutans sleeping quarters. In Experiment 1 we used two baited boxes, one hammer, a core fixed on a platform and a human-made flake. In Experiment 2 we used a modified fixed core (see below), one hammer, six flakes and no baited boxes.

2.2 Testing materials Experiment 1

Tendon box

In Experiment 1 we used two baited boxes in order to elicit the use of sharp-edged stones as cutting tools: the tendon box and the hide box. Each box was baited with half a piece of fruit before each trial. The tendon box was modeled on an earlier puzzle box described by Wright (1972) and Toth et al. (1993). The tendon box was used to simulate a scenario in which, faced with an animal carcass, a subject must cut through taut tendons (a rope in our experiment) in order to dismember a body. The tendon box consisted of two opaque boxes secured to a wooden board with a rope running between them. The tendon box had a clear Plexiglas window (5cm x 16cm) at the top that allowed for the reward inside to be seen. The door of the box was pulled shut by a rope that ran through the inside and exited through a hole in the opposite end. The rope then ran between the two boxes for approximately 5cm and entered the second (non-rewarded) box. Thus, the rope was only accessible in the area between the two boxes and had to be cut there to allow the door of the front box to open. The rope was a brown twisted hemp rope, approx. 1.5mm thick. Given that cutting the rope itself did not lead directly to the obtention of the reward (but to the opening of the door), the tendon box represented and indirect puzzle box.

Hide box

The hide box was designed based on the box used by Westergaard & Suomi (1994a) to test the sharp-edged stone tool making and using abilities of capuchin monkeys. The hide box was used to simulate a scenario in which, faced with an animal carcass, a subject must cut through taut skin/hide (a silicone membrane in our experiment) in order to access the insides of a body. The hide box consisted of a transparent Plexiglass cylinder (16cm wide x 15.5cm high) with a metallic rim. A silicone membrane 2mm thick was screwed in between the cylinder and the rim, blocking the access to the reward placed inside the cylinder. The hide box was then secured vertically to the bars of the sleeping quarters where the experiments took place.

Contrary to the tendon box, the hide box represented a direct puzzle box in which cutting an object (the membrane) allowed to directly access the food reward contained inside.

Hammer

One artificial hammer made of concrete (ca. 15cm long x 10cm wide, weight 2.2kg) was provided during each trial. The hammer was built around a metallic scaffold linked to a chain that allowed us to fix the hammer to the bars of the sleeping quarters so the orangutans could not carry the hammers into the indoor enclosure. The concrete used to build the hammers included particles of up to 1 cm in diameter. The hammer was covered with non-toxic transparent epoxy resin to prevent the hammer surface from disintegrating upon repeated impacts.

Core

One prepared core (made from Norfolk Chert) was provided to the subjects alongside the hammer in each trial. The cores were prepared in advance to have edges with angles between ~90 and ~40 degrees suitable for flaking. During this reduction process the aim was to produce either i) 3 separate surfaces - with varying angles - from which flakes could potentially be struck from each specimen or ii) a continuous edge around the perimeter of the core with continuously varying angles within the above mentioned range. The cores weighed between 0.8 and 1.5Kg. If the core was not modified during a trial, the core was used in further trials. Due to safety regulations, the core had to be fixed on a metallic platform (20 x 20 x 2cm) to prevent the orangutans from carrying the core into the indoor enclosure (similar to Wright, 1972). The core was attached to the platform using a metallic wired mesh from XTEND (Carl Stahl ARC GmbH, Architectural Cables and Mesh Systems) with a hole width of 50mm and a wire diameter of 3mm.

In the Flake condition a human-made flint flake was provided to the orangutans (see below for details). The flake was made out of sight of the apes by the experimenter (AMR) using freehand percussion. The flake measured 7.6cm x 5cm x 1.7cm and was placed unfixed (loosely on the floor) next to the hammer, core and box(es) before the subjects were allowed into the testing area.

2.3 Testing procedure Experiment 1

We tested subjects in two conditions in Experiment 1: a Baseline and a Flake condition. During the Baseline condition the subjects were provided with the testing materials described above but no additional information (demonstrations, guidance, or artefacts) was provided. A Baseline was included in order to test for the spontaneous individual tool making abilities of the orangutans and if tool making took place, for their spontaneous tool using abilities. The Baseline condition was split into two subconditions (Baseline condition I and Baseline condition II). During the Baseline condition I, the two male orangutans had access to the tendon box, the hide box, a hammer and a fixed core during three trials (condition duration range 00:13:03 to 00:33:31). Trials in all conditions started when the subjects entered the testing room and ended when subjects exited the testing room for more than 10 minutes (in case the hatches connecting to the other enclosures were open, see below) or after 30 minutes, if the subjects stayed in the room. In some cases, due to cleaning routines, trials had to be longer. We included a second baseline (Baseline condition II) in order to focus the attention of the individuals on solving a single task by only providing them with one box. During the Baseline condition II, Matthieu received the tendon box (more robust than the hide box) and Loui was provided with the hide box (less robust) during three trials (condition duration range 00:09:10 to 00:44:53). During the Baseline condition I we observed that Matthieu could force open the hide box by hand, and therefore we gave this box to Loui. The Flake condition was identical to the Baseline condition II except for the provision of a human-made flint flake. This condition was included in order to test for the spontaneous tool-using abilities of the orangutans and for their ability to reverse engineer the production of sharp-edged stone tools. The orangutans were tested in four trials each (condition duration range 00:11:03 to 00:55:36).

If the keepers decided that the animals showed signs of distress during any of the tests, the trial was immediately terminated. This occurred once while testing Loui, who was being trained to be separated from his mother during the time the experiments took place. The duration of the trials varied according to the cleaning routines, as this was the time when tests were conducted. Some keepers kept the doors to the indoor/outdoor enclosure open during trials so the orangutans could go in and out. In some cases (four trials), this led to especially short tests as the subject did not come back to the testing room.

All testing materials (testing box/es, hammer and the fixed core) were placed inside the testing area and secured to the bars of the enclosure before the orangutans were allowed inside the rooms. Two Sony HDR-CX330E Handycams were set-up half a meter from the bars and started recording once the subject entered the testing area. Potential tools were cleared from the testing areas before the tests started. However, the subjects often brought sticks and other objects with them into the testing areas at the start of the tests.

2.4 Testing procedure Experiment 2

In Experiment 2 we conducted a Familiarization phase and a Test condition. In the Familiarization phase we aimed for the orangutans to get used to the exchange of human-made flakes for food rewards in order for them to attribute value to flakes. Ten flint flakes were produced before the start of this condition by the experimenter out of sight of the orangutans, using freehand percussion and a core equivalent to the one used during the trials. These flakes were all placed inside the testing room before the orangutan was allowed inside (see Figure 1). Once an orangutan was inside the testing room, he was asked to exchange each flake for a grape. The experimenter asked for the flakes by showing the hand palm up, verbally encouraging the orangutan and occasionally pointing at the flakes. If the orangutan pushed a flake out of the room, the experimenter gave him a grape. In order to consider the Familiarization phase successful, the apes had to exchange at least eight flakes in ten minutes.

Figure 1: Experimental set up. The top left panel illustrates the set up in the Familiarization phase. The top right panel illustrates the provision of a reward after a flake has been exchanged. The bottom left panel illustrates the core provided during the Test condition together with the two refitted flakes shadowed in blue and red. The bottom right panel illustrates the fixed core as presented to the apes, with the two refitted flakes and the loose flakes placed on top of the core.

After completing the Familiarization phase, the orangutans were further tested in the Test condition. The aim of this condition was to assess if, once orangutans have associated flakes with high value rewards (grapes), they would make sharp-edged stones themselves in order to obtain said rewards. In this condition, a fixed core and two hammers (equivalent to the ones used in Experiment 1), as well as six loose flakes, were placed inside the testing room. The core provided to the orangutans in the Test condition of Experiment 2 had two detached flakes refitted into it (see Figure 1). These flakes were made by the experimenter out of sight of the apes using freehand percussion. One of the flakes was weakly refitted to the core using a sugar-based glue (usually used for decorating cakes). The other flake was strongly glued to the core with clear epoxy adhesive glue. Both glues where transparent and non-toxic. These two flakes were refitted to the core in order to increase the chances of success (flake detachment) if a subject hit the core with the hammer. We predicted that if a flake would detach easily, the orangutans would keep trying to make more. The loose flakes (N=6) were placed around the core structure to reinforce the association that flakes could be detached from the core (see Figure 1). When the subject entered the room in the Test condition, he was once more asked to exchange the flakes, following the method used in the Familiarization phase. The orangutans were tested in four trials during the Test condition, and each trial lasted approximately 30 minutes.

2.5 Coding

From each video-recorded trial we coded i) the number of interactions (events when the orangutans touched a testing material); ii) the duration of these interactions (time spent in physical contact with the testing materials, from when the subject started contact until it paused for more than 3s or changed activity); iii) which testing material the orangutans interacted with and iv) if the interaction was manual or using a tool. As orangutans often use their mouths during tool use (O'Malley & McGrew, 2000), mouth interactions were also coded for.

3. Results

3.1 Experiment 1

None of the two orangutans tested made sharp-edged stone tools during the Baselines or Flake conditions. However, both individuals frequently interacted with the testing materials (N=907) across trials (Figure 2). As there was no significant correlation between trial length and the number of interactions performed by the orangutans (Supplementary Figure 1), the results are displayed as sums of events rather than sums of events divided by trial length.

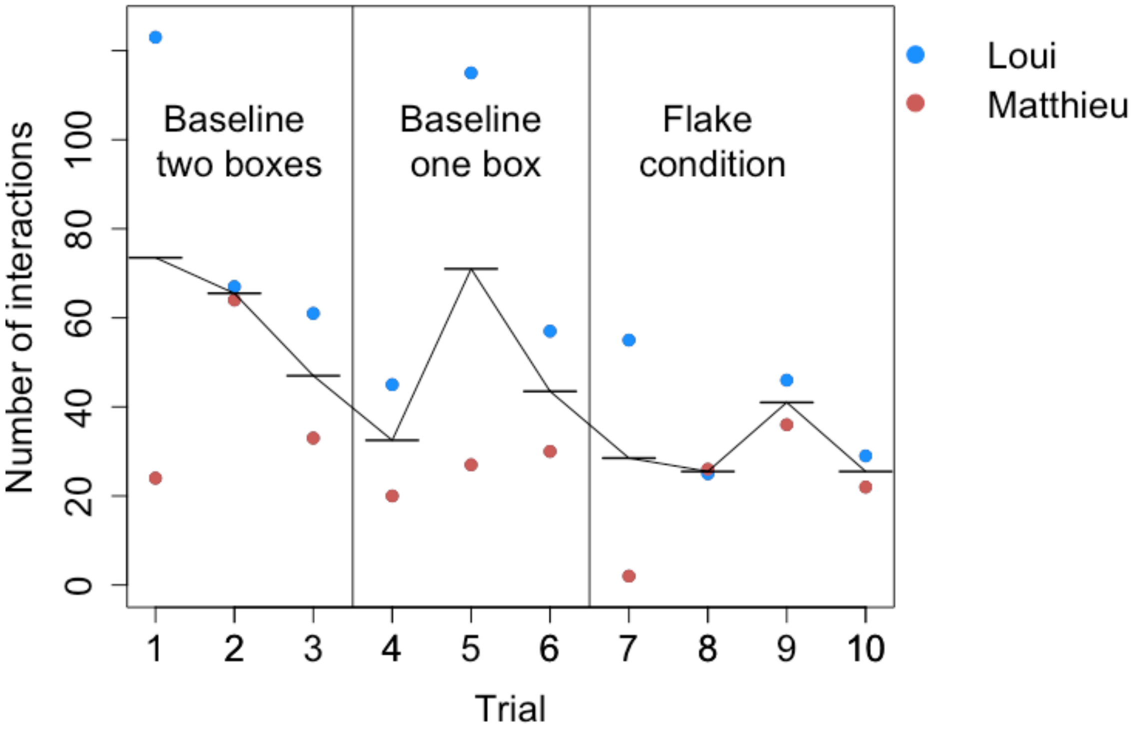

Figure 2: Number of interactions performed by each individual in each trial of the three experimental conditions. Horizontal lines represent mean number of interactions across individuals per trial.

Across all experimental conditions, the orangutans interacted the most with the baited boxes (Figure 3, Table 1). When both baited boxes were available in the Baseline condition I, the orangutans interacted more with the tendon box than with the hide box, but this was inverted in the following conditions (Figure 3). As the orangutans only received one baited box in the Baseline condition II and the Flake condition, it is possible that the orangutan that received the hide box (Loui) was more motivated and interacted more with his box (as it made noise when the membrane was hit) than the orangutan that received the tendon box (Matthieu). Interactions with the hammer increased from the first to the last condition, possibly because the orangutans started using the hammers to hit on the concrete walls and floor of the testing room. In addition, Matthieu, the adult orangutan, was able to break the chain tying the hammer to the room bars, which allow him to manipulate the hammer much more freely and possibly led to a higher number of interactions.

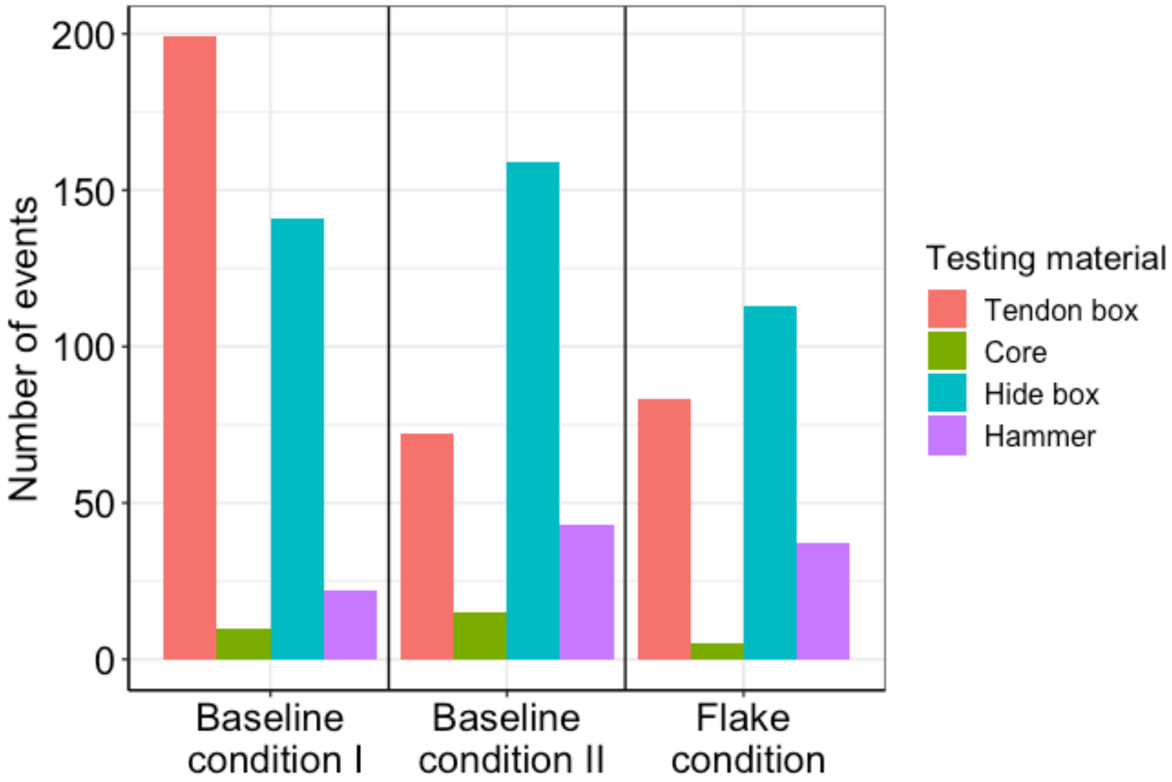

Figure 3: Number of interactions towards the different testing materials in each experimental condition.

Table 1: Frequencies and mean durations in seconds ± SD (between brackets) of the interactions with the different testing elements by individual orangutan.

	Tendon box	Core	Hide box	Hammer	Total
Matthieu	247 (24±46.4)	9 (7.11±10.6)	16 (29.8±29.7)	12 (21±29.2)	284
Loui	107 (6.62±5.80)	24 (3.62±2.32)	397 (10.6±19.0)	95 (8.66±9.44)	623

Interactions with the testing materials were made using the hands (528) and the mouth (166), as well as tools (Table 2). Different tool materials were used to interact with the testing materials: sticks (9), a hose fragment (1) and the provided flakes (4).

Table 2: Frequency and total time of the interactions with different testing materials using a body part (hand or mouth) or a tool.

Testing material	Interact via	N	Total time (seconds)
Touch tendon box	body part	348	6573
Touch tendon box	tool	6	61
Touch core	body part	32	148
Touch core	tool	1	3
Touch hide box	body part	406	4638
Touch hide box	tool	7	54
Touch hammer	body part	107	1075

Tool use to open the boxes

In one occasion, namely on the first session of the Baseline condition II, Loui opened the hide box using a stick that he brought into the testing room. Using his body weight and exerting pressure with the stick, he succeeded in breaking through the silicone membrane covering the hide box and obtained the reward. On the third trial of the Flake condition, Loui tried to open the hide box using a hose fragment that he had brought from the indoor enclosure (these hose pieces were often provided to the orangutans containing honey or peanut butter smeared on the inside as enrichment). After a failed attempt to open the hide box with the hose piece, Loui proceeded to fetch the human-made flake from the floor, approximately 50 cm from where the hide box was fixed. Holding the flake with his mouth, Loui pressed the flake into the hide box membrane, perforating the membrane by pushing with the flake and creating a hole that he then expanded by hand in order to obtain the reward. Therefore, on the third trial of the Flake condition, Loui used the flake as a tool to cut by pressure through a surface (minute 00:24 of video in OSF, see Data availability below). The other three uses of the flake (all performed by Loui) took place during the first trial of the Flake condition: touching the core with the flake for three seconds; pressing the inside of the hide box with the flake for one second and pressing the outside of the hide box with the flake for four seconds.

3.2 Experiment 2

During the Familiarization phase both subjects exchanged the ten flakes provided within the set time limit of ten minutes, therefore both participated in the Test condition (Supplementary Table 1). During the test trials, the orangutans had the possibility to further exchange loose flakes placed around the fixed core for rewards (Supplementary Table 1), which potentially increased the attribution of value to the flakes. The two orangutans exchanged the refitted flakes in addition to the loose flakes. They obtained these flakes by picking at them with their teeth and nails but not by using the hammer.

The orangutans performed four percussive activities (hit floor with core, hit wall with core, hammer on wall and hammer on floor; Table 3 and Figure 4). During two trials, the core was extracted from the fixing platform by the juvenile orangutan, which led to the performance of two previously unavailable behaviours (hit floor with core and hit wall with core).

Table 3: Ethogram of the behaviours performed by the orangutans when interacting with the hammers and core, number of interactions and mean duration of the interaction ± SD.

Behaviour	Description	Number	Mean duration (sec) ± SD
Touch core	Subject places the hand on or touches the core	58	60.6 ± 188
Hit floor with core	Subjects repeatedly strikes the core against the floor	7	7.43 ± 4.54
Hit wall with core	Subjects repeatedly strikes the core against a wall	3	3.67 ± 1.15
Hit hammer on floor	Subject repeatedly strikes the hammer against the floor	33	3.85 ± 1.95
Interact with hammer	Subject places the hand on, touches or holds and lifts the hammer	77	15.4 ± 28.3
Hit hammer on wall	Subject repeatedly strikes the hammer against a wall	4	4.25 ± 2.22

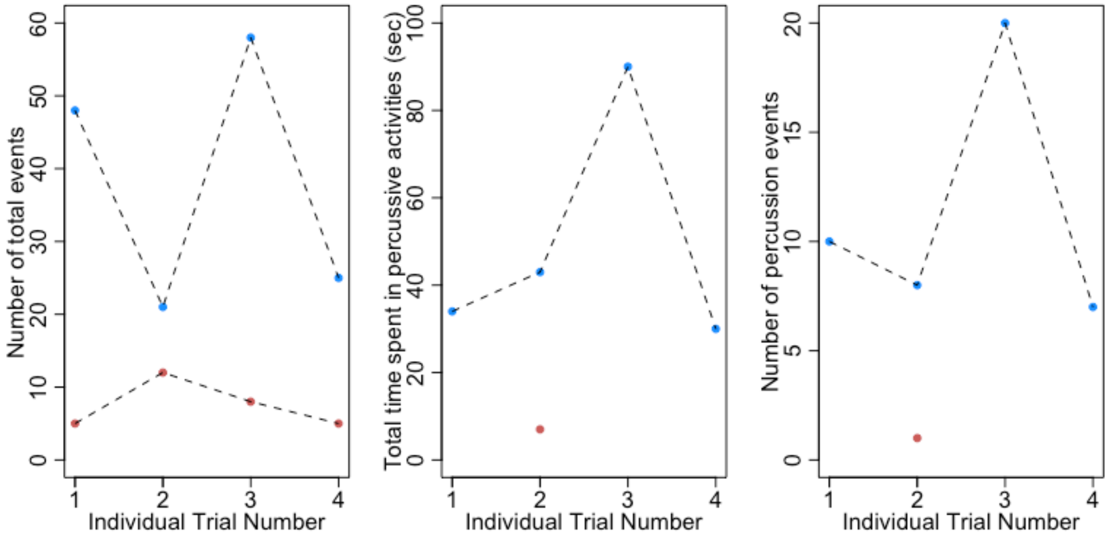

Figure 4: Percussive actions performed by the two individuals. The left panel illustrates the individual variation in the number of events performed by each individual (dotted lines) across trials. Blue dots represent Loui (the juvenile male) and the red dots Matthieu (the adult male). The middle panel illustrates the variation in the duration of percussive behaviours across trials. The right panel illustrates the variation in the number of percussive events across trials. In both the middle and right panels the dotted line represents Loui and the single dot represents Matthieu.

Stone tool making

Loui, the juvenile orangutan, extracted the core from the fixed platform in the second and fourth trial. Once the core was loose, he proceeded to strike the core repeatedly and vertically against the floor (N=7) and walls (N=2) of the room (Table 4 and Figure 5) while holding the core with one hand.

Table 4: Duration type and number of strikes of the percussive events with the core performed by the juvenile orangutan Loui.

Individual trial number	Duration (sec)	Behaviour	Number of strikes
2	10	Hit floor with core	11
2	4	Hit floor with core	6
2	16	Hit floor with core	18
2	5	Hit floor with core	8
2	4	Hit floor with core	4
4	9	Hit floor with core	8
4	3	Hit wall with core	6
4	4	Hit floor with core	1
4	3	Hit wall with core	4

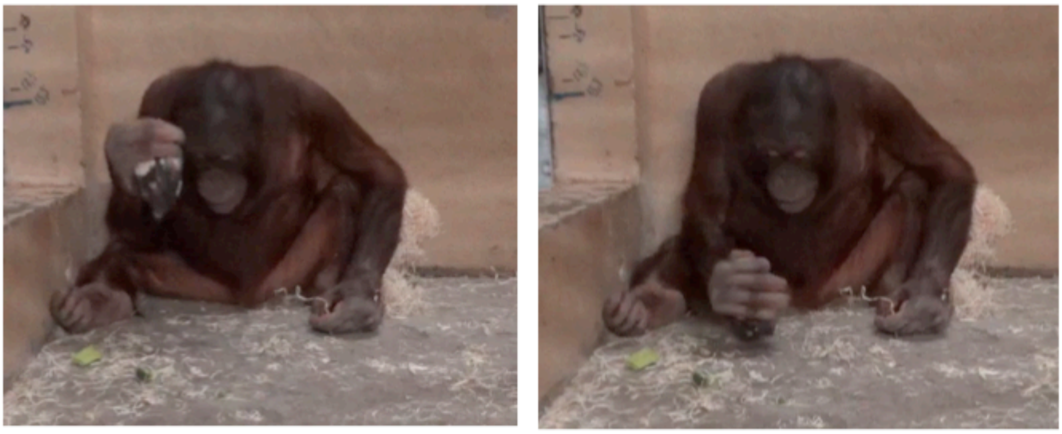

Figure 5: Sharp-edged stone tool making observations. Loui (the juvenile male orangutan) vertically striking the flint core on the concrete floor of the testing room during the Test condition of Experiment 2.

On one trial, the striking of the core (Figure 6) led to the production of three sharp-edged stones (Figure 7). These sharp-edged stones weighed 1.9, 0.6 and 0.3g respectively. The heaviest stone (Figure 7.1) had a platform depth of 2.7mm, a platform width of 6.8mm, a width of 18.8mm and a technological length of 20.3mm (following terminology by Debénath & Dibble, 1994). In the middle-sized stone (Figure 7.2), it was not possible to identify either the impact point or the platform. The maximum length and maximum width perpendicular to the length of the middle size stone were 19.05mm and 11.36mm. The smallest stone (Figure 7.3) had an impact point, but no striking platform could be identified. The width of the smallest stone was 14.9 mm and the technological length 8.8 mm. At the same time that these sharp-edged stones were produced, the two refitted flakes (see above) were also detached. None of these sharp-edged stones (refitted or produced by Loui) were exchanged with the experimenter nor used for any other purpose and were abandoned together with the core once the orangutan was allowed outside the testing room.

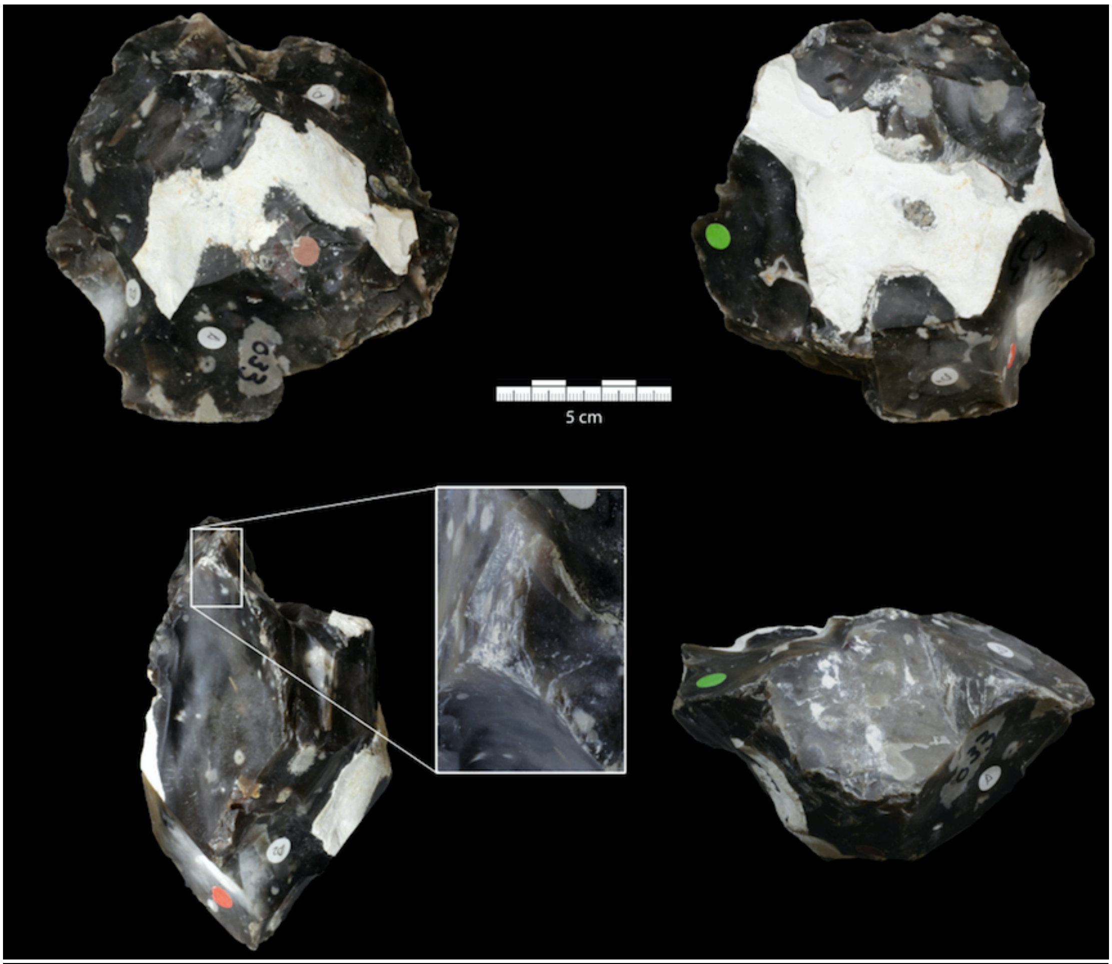

Figure 6: Core from which the sharp-edged stones were detached by the juvenile male orangutan.

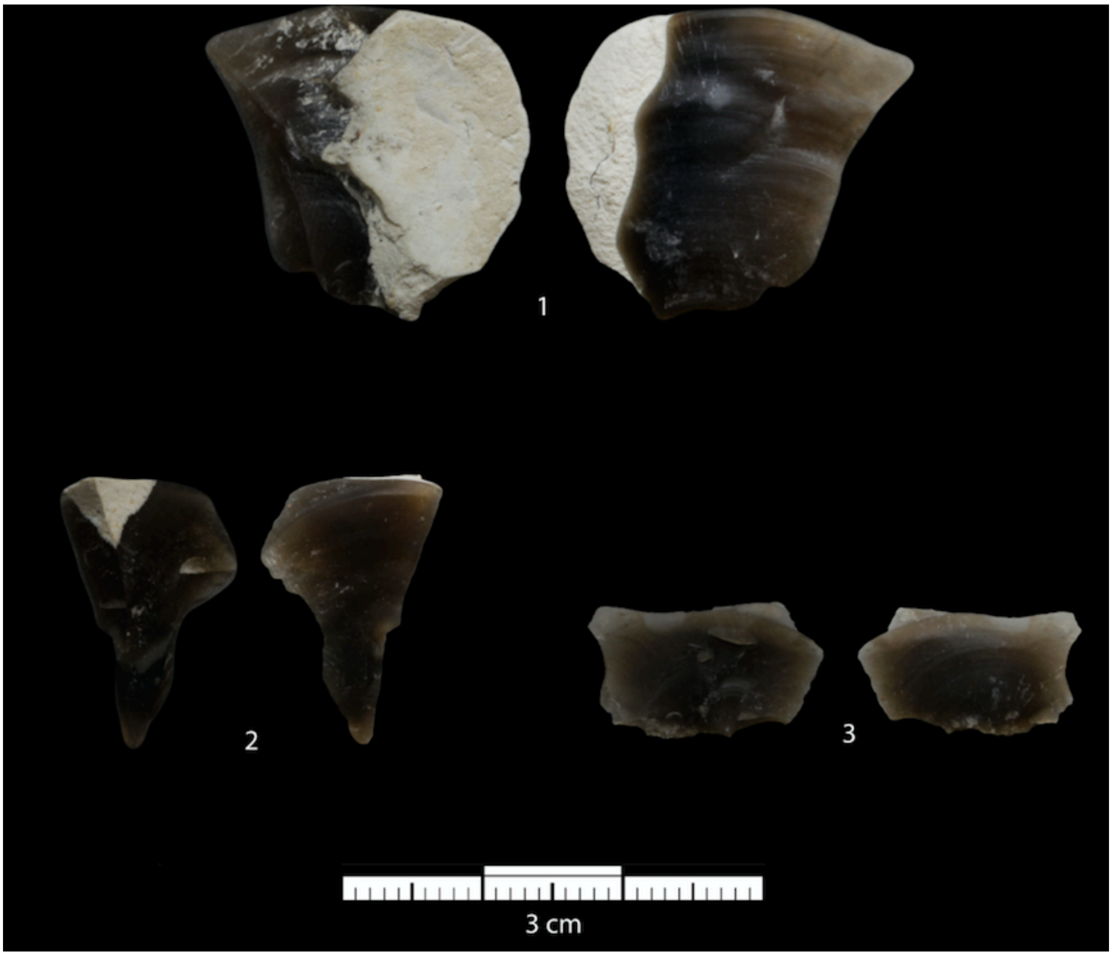

Figure 7: Sharp-edged stones made by the juvenile orangutan.

4. Discussion

We conducted two experiments in which we investigated the spontaneous abilities of two stone tool-naïve, mother-reared (unenculturated) orangutans to 1) make and use sharp-edged stone tools in order to access a reward; 2) use human-made flakes in order to access a reward and 3) make sharp-edged stone tools after attributing value to flakes via previous food exchanges for human-provisioned flakes. None of the orangutans spontaneously produced such stone tools by themselves. However, when a human-made flake was provided, the juvenile orangutan in our sample (7 years old at the time of testing) spontaneously used this flake to cut through an artificial hide. After performing an additional series of experiments aimed at increasing the perceived value of flakes, the same orangutan spontaneously produced three sharp-edged stones as a by-product of percussive actions: the orangutan repeatedly hit the core against a hard surface (similarly to the actions involved in the so-called passive hammer technique), when he could freely manipulate the stone core for a brief period of time. However, he never used the sharp-edged stones that he produced himself as cutting tools. Yet, given that no social demonstrations of how to make or use flakes were given to the orangutans, we conclude that orangutans can spontaneously re-innovate the use of a flake (here: to perforate a hide) and that orangutans can spontaneously re-innovate the unintentional production of sharp-edged stones percussive actions.

4.1 Implications for the evolution of human lithic technology

Our findings support the view that the LCA of *Pongo* and *Homo* also had the necessary cognitive (and physical) abilities to engage in percussive activities that perhaps occasionally led to the production of sharp-edged stones and to use readily available sharp-edged stones to access resources (such as meat behind hides). However, this scenario does not explain the large time gap between the split from the LCA (approximately 13 Ma, Glazco & Nei, 2003) and the appearance of stone tool production in the archaeological record (at least 3.3 Ma, Harmand et al., 2015). One possibility is that hominins (perhaps even hominoids) made and used sharp-edged stone tools continuously throughout this time but that they did so extremely infrequently, with the result that we do not have a continuous record of it (Haslam et al., 2009). A second possibility is that the species living in this time frame did not make or use sharp-edged stone tools because these artefacts were not advantageous within their ecological niches (Koops et al., 2013; Koops et al., 2014; Sanz & Morgan, 2013). A third possibility is that the use and intentional production of sharp-edged stone tools re-emerged separately (i.e. not in combination) long after the split between *Pongo* and *Homo* 13 Ma. Previous studies proposed that sharp-edged stone tool use may have preceded intentional tool making during hominin evolution (McPherron et al., 2010). If that would be the case, the production of sharp-edged stones due to percussive activities and the use of such stones as tools could be independent technical skills, which orangutans (and the LCA of *Pongo* and *Homo*) may simply not combine. Supporting this view, the orangutan in our experiment, who made sharp-edged stones and used a (human-made) flake, did not use the sharp-edged stones that he produced himself. Further supporting the view of the independent emergence of these two abilities, several other species of extant primates that use stone tools in percussive foraging activities, sometimes produce sharp-edge stones unintentionally but do not subsequently use them for cutting. For instance, wild capuchins (*Sapajus libidinosus*) sometimes produce sharp-edged stones when performing stone on stone percussion (SoS, Proffitt et al., 2016); chimpanzees occasionally produce sharp-edged stones during nut-cracking events (Carvalho et al., 2008; Mercader et al., 2002) and macaques sometimes produce sharp-edged stones when cracking oil palm nuts (Proffitt et al., 2018). Yet, none of these species has ever been reported to use the produced sharp-edged stones as cutting tools in the wild.

From a morphological point of view, the sharp-edged stones produced by primates as a by-product of percussive actions (both in the wild and captivity) sometimes overlap with pieces classified as flakes in the archaeological record - some sharp-edged stones produced by primates present both striking points and platforms (Proffitt et al., 2016; this study). Yet, conceptually, sharp-edged stones produced by non-human primates could still be argued to differ from flakes resulting from a process of flaking (Schick & Toth, 2006; Chapter 6). These differences would have to be found not in the physical attributes of the individual artefacts but rather in the context of their production. Flakes are generally considered to be the result of a flaking process, which involves the production of large numbers of flakes in a sequential and systematic manner. In addition, flakes can sometimes be found in association with elements that inform about their function (e.g. bones with cut marks, de Heinzelin et al., 1999), indicating that they were intentionally produced for a specific purpose. Therefore, we do not presume to equate the sharp-edged stones produced by the orangutan in the present study with the conceptual perception of flakes resulting from flaking, despite arguable morphological parallels.

4.2 Phylogenetic inferences on the stone tool use and tool making techniques employed by early hominins

In our study, the orangutan that successfully used a human-made flake to perforate a hide-like structure held the flake with his mouth rather than with his hands (or feet). Such oral tool use was not possible in the study by Wright (1972) because the aperture of the baited box where the rope could be cut was too small. Yet, this may be a preferred way of tool use for orangutans (when possible). Indeed, oral tool use is known to be common both in wild (van Schaik & Fox, 1996) and captive orangutans (O'Malley & McGrew, 2000). But oral tool use is not restricted to orangutans. In a study testing tufted capuchin monkeys, subjects also sometimes held sharp-edged stone tools in their mouth when using them as cutting tools (Westergaard & Suomi, 1994a). Oral tool use (and making) is generally frequent in tool-using primates (Fox et al., 1999; McGrew, 2013) and thus, it could have also played a hitherto undiscussed role in lithic technologies of hominin species.

Another question raised by our data is what kind of behavioural forms, or strategies, early hominins might have employed when using stone tools. Wright (1972) described that the orangutan included in his study "sawed" the cord that kept the baited puzzle box shut (Wright 1972). However, from the video recording of the experiment (https://www.youtube.com/watch?v=3exAOxSKYCE) it seems like the orangutan might have (at least sometimes) merely pressed the flake against the cord instead of using a sawing motion. In accordance with this observation, the unenculturated male juvenile orangutan in our study did not saw the artificial hide of our baited puzzle box. Instead he, too, pressed the flake against the hide (while holding it with his mouth) until the flake perforated it. A similar technique of holding a sharp-edged stone in the mouth and exerting pressure on an equivalent puzzle box to the hide box used in the present study was also described in the abovementioned capuchin study (Westergaard & Suomi, 1994a). Considering the primate data, perforation *by pressure* might be a potentially neglected aspect of ESTs. Davidson (2019) proposed that cutting can be subdivided in different categories according to which element is of interest to the individual cutting. According to Davidson, the type of cutting that the great apes tested in stone tool knapping experiments perform (Wright, 1972; Toth et al., 1993; this study) can be considered *severing* because the individuals are not interested in any of the resulting elements (the two halves of string or rope or the broken membrane pieces of the hide box) but rather in the consequence of the cutting action (the opening of the baited box). Slicing would refer to the use of a cutting tool to obtain a piece out of a bigger object, for example a piece of meat out a carcass (the interesting element is the removed piece; Davidson, 2019). Finally, shaving would refer to the removal of pieces from an object with the goal of shaping or modifying the morphology of the object, such as the removal of wood pieces while making a spear (Davidson, 2019). Therefore, although the tool use actions performed by the juvenile orangutan in this study can be considered cutting actions, these differ from those performed during meat processing or wooden tool making.

The juvenile orangutan that successfully made sharp-edged stones in our study employed a series of percussive actions that resemble those actions associated to the passive hammer technique (where a core is used as an active element to hit the hard surface of an anvil; Shen & Wang, 2000), which has been associated with the production of some of the oldest known stone tools (Harmand et al., 2015; Schick & Toth, 2006). Occasionally, the other (adult) orangutan in our study also struck hard surfaces in the testing room (walls and floor) in similar repeated, percussive actions as those used by the juvenile orangutan using mobile objects (the provided hammers). If such actions would have involved the core instead of the hammers, it is likely that the adult orangutan, too, would have produced sharp-edged stones. However, we could not test this hypothesis because, due to health and safety reasons, the core had to be fixed before it could be provided to the orangutans. The manipulation of a free core, while proving very informative for the potential of orangutan sharp-edged stone production, was due to an accidental malfunctioning of the testing setup. Similarly, the free manipulation of a core as an active element was also not available to the enculturated orangutan (Abang) tested by Wright (1972) as the core in that experiment was also fixed. However, note that Abang performed the same percussive actions we observed in our study when he repeatedly hit the floor of the testing room with the provided hammerstone (see minute 1:38 in video https://www.youtube.com/watch?v=3exAOxSKYCE). Consequently, there is evidence that enculturated and unenculturated orangutans have both the motivation and skill to spontaneously engage in percussive actions involving stones and that these actions do not need to be seen in order to be performed by orangutans.

Regarding the percussive techniques performed by other apes, Toth et al., (1993) found that when free cores and hammerstones were available to the enculturated bonobo Kanzi, he produced sharp-edged stones using several techniques. Most relevant for the aims of the present study, two of these techniques were not previously demonstrated to Kanzi namely, throwing a cobble against a hard surface and throwing a cobble against another cobble. Therefore these throwing techniques were individually re-innovated by the enculturated bonobo. Throwing a cobble against a hard surface somewhat resembles the technique used by the orangutans in our study. However, Kanzi used a stone core as a projectile, whereas the orangutans in our study never released the active element when performing percussive activities (although note reports of orangutans performing aimed throws, Shumaker et al., 2011).

In the only studies that tested the sharp-edged stone tool making and using abilities of primates other than great apes (Westergaard & Suomi, 1994a, 1995b), unenculturated tufted capuchins (*Sapajus apella*) spontaneously produced sharp-edged stones reportedly using three different flaking techniques (stationary anvil technique or passive hammer; portable anvil technique or bipolar and hard-hammer or freehand percussion). The actions described for the first technique employed by the capuchins (stationary anvil technique according to the authors) are identical to the actions used by the orangutans in our study: "striking a stone against a stationary surface" (Westergaard & Suomi, 1994a). This percussive technique is therefore within the individual, spontaneous abilities not only of orangutans, but also of tufted capuchins.

Taken together, studies investigating the production and use of sharp-edged stones by non-human primates in captivity as well as in the wild, suggest that the bodily actions (the action form) involved in the production of sharp-edged stones, are present in a variety of species: some wild chimpanzee populations, capuchin monkeys, captive orangutans and (at least) enculturated bonobos have the physical and cognitive abilities to produce sharp-edged stones as a by-product of percussive activities. Thus, whereas unintentional sharp-edged stone production is present in several primate species, the usage of such pieces as tools is rare (Westergaard & Suomi, 1994a). However, when flakes are provided, our study shows that at least another great ape species – orangutans – can spontaneously use sharp-edged stones as cutting tools to severe an object.

5. Conclusion

The present study is the first to test the spontaneous abilities for sharp-edged stone making and using of naïve, mother reared, unenculturated orangutans. We found that orangutans can spontaneously make and use sharp-edged stones. However, the latter ability was conditional on the external provisioning of these tools by humans. The orangutan in our study produced sharp-edged stones as a by-product of percussive actions which somehow resembled those associated with the passive hammer technique, a technique associated to the production of sharp-edged stone tools in some of the oldest archaeological assemblages (Harmand et al. 2015). The same percussive actions reappeared across both orangutans tested, and have been also described in enculturated orangutans (Wright, 1972). Similarly, we show that the behavioural form of (orally) using flakes as pressure-cutting tools can also be spontaneously re-innovated by orangutans. Based on our results, we conclude that the behavioural forms of unintentionally producing sharp-edged stones as a by-product of percussive actions and the use of sharp-edged stones to pressure-cut a surface are within the individual spontaneous abilities of orangutans. Furthermore, by phylogenetic proxy, these behavioural forms might have also been within the individual re-innovative abilities of the LCA of *Pongo* and *Homo* around 13 Ma. Our results show that these forms do not need to be copied from a model and therefore are latent solutions rather than culture-dependent forms in orangutans. Consequently, these behavioural forms cannot be considered evidence of hominin copying-based cumulative culture.

Data availability

All code, raw data and the 3D scan of the biggest sharp-edged stone produced by the orangutan are available in the Open Science Framework in the folder entitled "Orangutan stone tool project":
https://osf.io/m9qtf/?view_only=8f3f698e22ab40fa8653818586a644e3

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Chapter 5: Great ape stone tool making and using abilities after social demonstrations

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I am the first author of the manuscript corresponding to this chapter. I was the main experimenter and I conducted all data collection and analyses presented in this chapter. The original idea for this study was developed in collaboration with Dr. Tennie and Dr. McPherron. I was the main writer of the manuscript in collaboration with Dr. Tennie. All coauthors provided feedback on the manuscript.

CHAPTER 5

Great ape stone tool making and using abilities after social demonstrations

1. Introduction

Human cumulative culture is composed of behavioural *forms* (physical actions or artefacts), which are successively modified and transmitted within and across generations (Boyd & Richerson, 1996; Tomasello, 1999). Transmission of such forms must be sufficiently detailed to prevent informational slippage, meaning that this transmission must happen via copying social learning mechanisms (henceforth copying: Boyd & Richerson, 1996; Caldwell & Millen, 2009; Heyes, 2018; Tomasello, 1999). A reliance on copying means that isolated individuals cannot spontaneously learn forms constituent of cumulative cultures because these are too complex or causally opaque. Cultural forms that result from cumulative cultural evolution must therefore be acquired by observing a model and/or her products, which makes them culture-dependent (Tennie et al., in press). Culture-dependent forms (after Reindl et al., 2017) resulting from a process of cumulative culture can be found in various behavioural domains, such as food processing, language, rituals, tool making and tool use (Henrich, 2017; Legare & Nielsen, 2015; LeMaster & Monaghan, 2007).

Tool behavioural forms include both the physical actions required to produce/use a tool (*chaîne operatoire* and know-how, e.g. Bar-Yosef & Van Peer, 2009; Pelegrin, 1990) and the resulting artefact or tool forms (typology, e.g. Debénath & Dibble, 1994). Among artefacts, early stone tool forms or ESTs (Tennie et al., 2016; Tennie et al., 2017) are particularly interesting because they offer a window to study early hominin behavioural repertoires and the potential biological, environmental and cultural factors that contributed to shaping their behavioural forms. The oldest purported stone tools are those belonging to the Lomekwian assemblage claimed to be 3.3 Ma (Harmand et al., 2015). This assemblage consists of cores, flakes, hammerstones, passive elements (that could have been used as anvils) and percussors. Experiments have revealed that the most likely knapping techniques used to produce the Lomekwian flake forms were the passive hammer and the bipolar knapping techniques (Harmand et al., 2015). The passive hammer technique consists on the detachment of flakes from a hand-held core by striking the core against a hard surface (passive hammer technique, Shen & Wang, 2000). The bipolar technique involves the detachment of flakes from a stabilized core (on a hard surface) using a hand-held hammerstone. The Lomekwian findings, however, must be interpreted with caution given the controversy surrounding the in situ context of the LOM3 assemblage (Archer et al., 2020; Dominguez-Rodrigo & Alcalá, 2019; Domínguez-Rodrigo & Alcalá, 2016).

The oldest undisputed stone tool forms belong to the Oldowan industries, which oldest sites to date are those of Ledi-Geraru (<2.58 Ma, Braun et al., 2019) and Gona (2.58 Ma, Semaw et al., 1997; Semaw et al., 2003) in Ethiopia. Oldowan assemblages typically consist of various core forms, stone anvils, hammerstones, flakes, and débitage (Roche, 2000; Schick & Toth, 2006). The knapping techniques most commonly associated with the production of Oldowan artefacts are the bipolar technique (described above) but also freehand percussion. The latter consists on the detachment of a flake from a hand-held and/or body stabilized core by striking it with a hand-held hammerstone.

Despite the large body of research dedicated to the analysis of EST artefact forms and *chaïne opperatoires*, how the hominin species that produced these artefacts acquired the behavioural know-how to produce them is still a polarizing debate. Some authors have suggested that Oldowan stone knapping techniques were mainly learnt by direct observation of a behavioural model (copying of behavioural form: Morgan et al., 2015; Stout et al., 2019). Experimental approaches have shown that modern human knappers can learn how to produce Oldowan tools by reverse engineering from artefacts (Morgan et al., 2015), although being taught by an experience knapper was shown to be a more effective learning method. Despite being a less precise learning mechanism than imitation, reverse engineering (also known as end-state emulation, see Chapter 1) has been experimentally shown to sustain culture-dependent forms across transmission chains (Reindl et al., 2017) and has been suggested as an effective mechanisms for the acquisition of stone tool making abilities (Charbonneau, 2019). Yet another possibility is that a mixture of different social learning mechanism contributed to the acquisition of the skills necessary to maintain Oldowan industries. If copying social learning mechanisms were responsible for the acquisition of EST forms, this would mean that the skills of how to produce and use ESTs were learnt in the same way as most modern humans learn novel behavioural forms in the framework of cumulative culture. If evidence were found supporting this scenario, ESTs would be candidate culture-dependent forms and therefore the result (and perhaps the origin) of cumulative culture in our lineage.

Alternatively, the behavioural forms underlying EST production and use might have been learnt individually, without the need to observe behavioural models or their products (latent solutions approach: Reindl et al., 2018; Tennie et al., 2016; Tennie et al., in press; Tennie et al., 2017). The latent solutions approach for EST production and use proposes that the behavioural or physical skills necessary to produce the Oldowan industrial complex were learnt in the same way as modern non-human great apes in the wild learn their tool forms: via individual learning catalysed by non-copying variants of social learning (Chapter 2; Bandini & Tennie, 2017; Tennie et al., 2009; Tennie et al., in press;). Thus, the latent solutions approach takes into account the effect of non-copying social learning mechanisms on the distribution of behavioural forms within and across populations.

Great apes are phylogenetically relevant models to test hypotheses of early hominin behaviour (Carvalho & McGrew, 2012; Haslam et al., 2009; Rolian & Carvalho, 2017; Wynn et al., 2011). In addition, great apes (particularly chimpanzees and orangutans) posses the broadest tool repertoires among non-human animals (Nishida et al., 1999; van Schaik et al., 2003; Whiten et al., 2001) and some great ape tool behaviours (e.g. USO extraction, pounding, hunting) have also been identified in the archaeological record as being performed by early hominins (Hernandez-Aguilar et al., 2007; Pruetz & Bertolani, 2007; Wynn et al., 2011). As in the case of ESTs, the role that copying social learning plays in the formation of great ape tool behaviours is debated (Chapter 2; Galef, 1992; Tennie et al., 2009; Tomasello, 1996). However, several sources of evidence suggest that great apes do not copy often nor reliably. First, when the pattern of behavioural distribution across populations and species is analysed, it can be observed that the vast majority of great ape behavioural forms appears in unconnected populations, meaning that these forms can be individually re-innovated by naïve individuals without the need of observing a model performing the behaviour in question (Chapter 2). Previous studies have further suggested that wild-representative apes cannot learn new behaviours (by any means) beyond their species-specific repertoire, meaning that they cannot learn anything that they could not have learnt individually (Reindl et al., 2018; Tennie et al., 2009).

Second, several baseline experiments have been conducted in order to test the spontaneous abilities of captive, unenculturated (Furlong et al., 2008; Henrich & Tennie, 2017) great apes to re-innovate behaviours outside of their individual/group repertoire but performed by their wild conspecifics. Several such experiments have revealed that great apes do not need to observe demonstrations of these behaviours in order to learn them. Instead, given the right environmental conditions many wild ape behaviours re-appear in baseline experiments (Allritz et al., 2013; Bandini & Tennie, 2017; Lonsdorf et al., 2009; Menzel et al., 2013; Neadle et al., 2017; Tennie & Hedwig, 2009). Previous studies conducting baseline experiments have suggested that when testing complex behaviours (for example those that involve behavioural sequences with multiple objects), a single re-innovation of the target behaviour by a single individual is sufficient to conclude that the species tested can spontaneously and individually learn the target behaviour (Bandini & Tennie, 2017).

Great apes' non-copying based cultures represent a null hypothesis of the type of culture present in early hominins. Testing great apes for their abilities to produce and use ESTs can inform us about the behaviours that would have been within the cognitive reach of early hominins with great ape-like cultures. Furthermore, exposing great apes to social demonstrations of EST production and use can elucidate if hominins that possessed non-copying based cultures (like great apes, Chapter 2) could socially acquire stone tool making and using abilities.

Two previous studies have tested the abilities of great apes (one orangutan and two bonobos) for making and using stone tools (Schick et al., 1999; Toth et al., 1993; Wright, 1972). All three subjects included in these studies succeeded in making and using sharp-edged stone tools using techniques (reportedly) resembling bipolar knapping (Wright, 1972), freehand percussion and throwing (Toth et al., 1993). Furthermore, the authors of these studies claimed that the great apes had acquired sharp-edged stone tool making abilities by observing the human models (Toth et al., 1993; Savage-Rumbaugh & Fields, 2006; Wright, 1972). Although these experiments opened a new line of research using great apes as behavioural models for the production and use of sharp-edged stone tools in early hominins, these studies presented an important limitation. All apes included in those experiments were enculturated to some degree, meaning that they were exposed to frequent human contact and training (Furlong et al., 2008). These apes were therefore not wild-representative, as it has been shown that enculturation alters ape's cognitive and imitative abilities (Call, 2001; Call & Tomasello, 1996; Tomasello & Call, 2004; Tomasello et al., 1993) as well as their brain connectivity (Pope et al., 2018).

Overall, there remain several open questions regarding the abilities of great apes to make and use sharp-edged stone tools: 1) Can enculturated apes make or use sharp-edged stone tools spontaneously in the absence of social demonstrations?; 2) Can unenculturated apes make or use sharp-edged stone tools spontaneously in the absence of social demonstrations?; 3) Can unenculturated apes also make or use sharp-edged stone tools after social demonstrations?. Regarding question 1, there does not exist much data on the spontaneous sharp-edged stone tool making abilities of enculturated apes. To the best of our knowledge, the only report to date refers to the techniques (throwing and directed throwing) innovated by the language-trained bonobo Kanzi (Toth et al., 1993). Regarding question 2, in two previous studies, we evaluated the spontaneous sharp-edged stone tool making and using abilities of chimpanzees (Chapter 3) and orangutans (Chapter 4). Our previous results showed that unenculturated chimpanzees do not spontaneously produce nor use sharp-edged stone tools. However, we found that one juvenile orangutan spontaneously used a human-made flake as a cutting tool to open a puzzle box that contained a food reward inside. In addition, after performing a series of exchanges of human-made flakes for food, the same orangutan (unintentionally) produced three sharp-edged stones as a by-product of striking a flint core against a hard surface.

Here we address and expand on question 3 (the social acquisition of sharp-edged stone tool making and using abilities of great apes) by testing the abilities of human-reared and mother-reared chimpanzees and orangutans to make and use sharp-edged stone tools after seeing social demonstrations performed by a human model. Our prediction is that mother-reared, wild-representative apes are less likely to socially acquire sharp-edged stone tool making and using abilities because, as proposed by Reindl et al. (2018), great apes might only learn behaviours that are already within the species-typical latent behavioral repertoire (Chapters 3,4; Reindl et al., 2018). Given their exposure and contact with humans, we expected human-reared individuals to have a higher degree of enculturation than mother-reared individuals. Enculturation has been proposed to allow great apes to learn behaviors outside of their latent behavioral repertoire (Reindl et al., 2018) and thus we expect human-reared individuals to be more likely to socially acquire sharp-edged stone tool making and using abilities.

2. Materials and Methods

2.1 Subjects and housing

The subjects of the experiments presented here were orangutans (N_{adults}=3F; $N_{infants}$=1F and 1M) and chimpanzees (N_{adults}=7F and 6M) housed at Twycross Zoo (Atherstone, UK). Demographic data on the tested subjects can be found in Table 1. The chimpanzees were housed in social groups while the orangutans were housed in pairs at several interconnected (but independent) enclosures. All orangutan pairs had visual contact with each other and could interact through meshes. The composition of the pairs in which the orangutans were housed changed every two to three days. This housing arrangement was implemented in order to reduce the levels of aggression from the adult male towards the infants. All apes at Twycross Zoo have access to indoor and outdoor enclosures as well as to quarters off-sight from the visitors. Indoor enclosures are equipped with environmental enrichment such as climbing frames, bedding materials, platforms and containers where food can be placed for the apes to retrieve. The floor of the indoor enclosures was covered with wooden chips and straw. Outdoor enclosures consisted on grassed areas surrounded by glass walls from where visitors could observe the apes. The outdoor enclosures included climbing frames and huts. Feedings took place several times a day, when food (fruit, vegetables, primate pellets and nuts) was scattered in the indoor and outdoor enclosures. Food was often placed inside enrichment devices such as hanging balls and boxes attached to the meshes. Water was available *ad libitum* in all enclosures.

Table 1: Demographic data of the apes included in the study.

Species	Subject	Birth year	Rearing	Sex
Chimpanzees	CH1	1965	Unknown	F
	CH2	1986	Human-reared	M
	CH3	1995	Human-reared	F
	CH4	1982	Mother reared	F
	CH5	1982	Human-reared	M
	CH6	1990	Human-reared	M
	CH7	1988	Human-reared	F
	CH8	2003	Mother reared	M
	CH9	1973	Unknown	M
	CH10	1976	Human-reared	F
	CH11	2007	Mother reared	F
	CH12	1980	Unknown	M
	CH13	1990	Human-reared	F
Orangutans	O1	2017	Mother reared (O4)	M
	O2	2017	Mother reared (O3)	F
	O3	1977	Human-reared	F
	O4	1994	Mother reared	F
	O5	2011	Mother reared	F

The experiments took place in the off-sight quarters connected to the indoor enclosures. During the experiments, chimpanzees could access the off-sight quarters as well as both the indoor and outdoor enclosures as a group. Orangutans did not have access to the enclosures during tests. The experiments with the orangutans took place during cleaning routines, when the orangutans were individually housed in the off-sight quarters (mothers and dependent infants were housed and tested together) and could not exit until cleaning routines in the enclosures finished.

2.2 Testing materials

We used two puzzle boxes to elicit the use of sharp-edged stone tools as cutting tools: the tendon box and the hide box (see also Chapters 3 and 4).

Tendon box

The tendon box was modeled on an earlier version described by Wright (1972) and Toth et al. (1993). The tendon box was used to simulate a scenario in which, faced with an animal carcass, a subject must cut through taut tendons (a rope in our experiment) in order to dismember a body. The tendon box consisted of two opaque boxes secured to a wooden board. The tendon box had a clear Plexiglas window (5cm x 16cm) at the top that allowed the apes to see the reward inside. The door of the box was pulled shut by a rope that ran through the inside and exited through a hole in the opposite end. The rope then ran between the two boxes for approximately 5cm and entered the second (non-rewarded) box. Thus, the rope was only accessible in the area between the two boxes, and had to be cut there to allow the door of the front box to open. The rope was a braided brown twisted hemp rope, approximately 3mm thick. Given that cutting the rope did not grant direct access to the reward but that instead led to the opening of the box door, the tendon box represented an indirect puzzle box.

Hide box

The hide box was designed based on the apparatus used by Westergaard & Suomi (1994a) to test the sharp-edged stone tool making and using abilities of tufted capuchin monkeys. The hide box was used to simulate a scenario in which, faced once more with an animal carcass, a subject must cut through taut skin/hide (a silicone membrane in our experiment) in order to access the inside of a body. The hide box consisted of a transparent Plexiglass cylinder (16cm wide x 15.5cm high) with a metallic rim. A silicone membrane 2mm thick was screwed in between the cylinder and the rim, blocking the access to the reward placed inside the cylinder. The hide box was then secured to the same wooden board where the tendon box was placed. The hide box represented a direct puzzle box because the use of a tool to cut through the membrane granted access to the food rewards contained inside the cylinder directly.

Each box was baited before the onset of each trial with 5 peanuts or a small container with approximately 100g of quick oats without shell soaked in water. These rewards were chosen because the keepers considered that they were highly valued by the apes. The type of reward was chosen depending on the daily availability of each product.

Hammers

Three artificial hammers made out of concrete were used during the demonstrations and the tests (small: 12cm length x 9cm width, 2 Kg; medium: 15cm length x 10cm width, 2.5Kg; large: 18cm length x 11cm width, 3Kg). The hammers had an overall potato shape and were built around a metallic scaffold linked to a chain that allowed fixing the hammer to a wooden platform (see Appendix). The metallic scaffold was necessary for security reasons in order to fix the hammers and prevent the apes from hitting the glass windows (or each other) with them. Although the metallic scaffold made the artificial hammers considerably heavier than those found in Oldowan sites (de la Torre, 2006), it clearly did not reduce their functionality given that an inexperienced knapper (AMR) could use them to make flakes (>100) during the demonstrations. The concrete used to build the hammers included particles of up to 0.5 cm in diameter. The concrete composition was altered from the previous experiments in Chapters 3 and 4 to strengthen the hammers and prevent their fracture after repeated impacts.

Cores

Retouched Norfolk Chert cores were used for the demonstrations and tests. The cores were modified to display angle variability between ~90 degrees and ~40 degrees (see also Chapters 3 and 4). During the reduction process the aim was to produce either i) 3 separate surfaces - with varying angles - from which flakes could potentially be struck from each specimen or ii) a continuous edge around the perimeter of the core with continuously varying angles within the above mentioned range. Different cores were used for the demonstrations and the tests. If a core was not modified during a test, the core was used in further tests. Due to safety regulations, the core had to be fixed on a metallic platform (20cm x 20cm x 2cm) to prevent the apes from carrying the core into the indoor enclosure (similar to Wright, 1972). The core was attached to the platform using a metallic wired mesh with a hole width of 50mm and wire diameter of 3mm from XTEND (Carl Stahl ARC GmbH, Architectural Cables and Mesh Systems).

All materials were mounted onto two wooden platforms with a metallic frame that allowed us to fix the materials to the walls of the testing quarters. In the first platform we fixed the core and the hammers while in the second platform we fixed the two testing boxes. During the orangutan tests, the platforms were fixed in opposite walls od the testing room separated by 1.8m, whereas the platforms in the chimpanzee quarters were in parallel and 30cm apart. The same testing materials were used during the demonstrations and tests.

2.3 Experimental procedure

Demonstrations

The demonstrations to the chimpanzees took place in the service aisle in front of the quarters where the tests took place and which the chimpanzees were free to access outside of cleaning hours (see Figure 10 in Neadle et al., 2020). The demonstrations to the orangutans took place in a room that had a glass wall connecting with the room where the tests took place and a wall of rigid metal mesh connecting to the indoor enclosure of the orangutans (Figure 1). When demonstrations took place during cleaning hours of the enclosures, these were directed to the orangutan inside the testing room that could observe the demonstrations through the glass window. When demonstrations took place outside of cleaning hours, these were directed to the orangutans in the indoor enclosure that could observe the demonstrations through the metal mesh. During the demonstrations, the chimpanzees and orangutans could be as close as 1 m from the testing apparatuses. An individual was considered to have observed a demonstration when his/her head had been oriented with eyes open towards the demonstrator during the entire demonstration. If the individual moved away or stopped looking during the demonstration, the demonstrator stopped and started again from the beginning when the individual was paying attention. A spreadsheet of which individuals had observed which demonstrations was continuously updated after each demonstration (this was necessary to ensure that the chimpanzees saw a minimum of three demonstrations before their first trial and to count how many demonstrations each orangutan saw). The identity of the individuals that observed each demonstration (specially of the chimpanzees as they were housed as a group) was confirmed by the keepers present during the demonstrations. If the experimenter was not sure if an individual had seen a full demonstration, it was assumed that he/she had not and the demonstration was repeated. During all demonstrations, the wooden platforms where the testing materials were fixed were place on the floor between the apes and the demonstrator, so the actions of the demonstrator were clearly visible from where the apes were.

Figure 1: Experimental set up. Panel A depicts how the puzzle boxes were fixed onto the wooden board and presented to the apes. Panel B depicts how the fixed core and the three artificial hammers were fixed onto the wooden board and presented to the apes. Panel C depicts the room in which the demonstrations were given to the orangutans during cleaning routines. During actual demonstrations, the wooden platforms where the materials were placed were oriented towards the apes.

Each demonstration consisted on the production of one flake using a hand-held artificial hammer to strike a stabilized core on the fixing platform later presented to the apes and the subsequent use of the produced flake to open the test apparatus and obtain the food reward. This knapping technique was employed in order to demonstrate to the apes the flake production method that later was going to be available to them. One flake was made in each demonstration and flakes were not reused between demonstrations. After the detachment of a flake, the demonstrator held it in front of the observing apes to make sure that they saw it. The demonstrations of flake use did not start until all apes present had seen the flake (i.e. their head was oriented towards the demonstrator). Demonstrations of flake use were conducted with both puzzle boxes (see below). When demonstrating how to open the tendon box, the demonstrator used the flake she had produced immediately before to cut the rope that kept the door of the box closed. When the demonstrations of how of to open the hide box took place, the demonstrator used a flake she had produced immediately before to cut through a plastic sheet placed in the same position as the silicone membrane would be placed during the actual tests. We used plastic sheets instead of silicone membranes during the demonstrations due to the limited availability of the silicone membranes. When obtaining the reward, the demonstrator made sure that the ape saw it by taking the reward out of the box and showing it to the observing apes. After each demonstration, the boxes were re-baited with the same reward and closed.

The demonstrations involved all possible combinations (N=9) between hand (left, right, both) and hammer type (small, middle, large) and were performed both with the tendon box and the hide box. Each of the nine combinations was demonstrated twice per test box (3 hand combinations x 3 hammers x 2 boxes x 2 rounds of demonstrations = 36 demonstrations) before the start of Test 1. As all demonstrators had to be made in the presence of a keeper, each round of demonstrations was spread between at least two days depending on the keeper's availability. Demonstrations were made to the chimpanzees as a group and to the orangutans in pairs (the pairs were set by the keepers according to their housing rotation routine, see above).

Chimpanzee testing

The experiments were structured into the following phases for the chimpanzees: A priori Demonstrations (N=36) - Test 1 - Test 2 - Repeated Demonstrations (N=18) - Test 3 - Test 4 - Test 5 - Test 6. That is, AMR performed 36 demonstrations to the chimpanzees before the start of the tests and 18 demonstrations between Tests 2 and 3. As some of the chimpanzees rarely entered the off-sight quarters where demonstrations were taking place, we proceeded to Test 1 when at least 80% of the chimpanzees had seen a minimum of three demonstrations. Each phase took place 24h after the previous phase and the testing materials were only available to the apes during the tests.

Orangutan testing

Adult orangutans were tested individually or with their dependent offspring. Tests and demonstrations focused on the adult orangutans because the infants were considered too young to participate in the tests (i.e. it was not clear that they were strong enough to hold the artificial hammers). Each adult orangutan saw at least 27 demonstrations (three repetitions of the nine combinations) before the start of the tests (see Supplementary 1 for the individual demonstrations seen and the delays between tests and demonstrations). Each adult was tested in three trials per condition (see below). except one orangutan (O5) that was tested in a fourth trial due to the promising results obtained in her previous trials.

The orangutans participated in a second experimental condition (Flake condition) where a human-made flint flake was provided to the orangutans alongside the testing materials. This flake was made out of sight of the orangutans by the experimenter (AMR) using freehand percussion. The flake measured 7.6cm x 5cm x 1.7cm and was placed unfixed (loosely on the floor) next to the hammers and core before the subject was allowed into the testing area. This condition could not be implemented with the chimpanzees due to the risk of the individuals carrying the flake into the indoor enclosure. No new demonstrations were given to O5 between conditions due to the short delay since she had seen the initial demonstrations and given her high motivation to interact with the testing materials. After the first set of tests, new demonstrations (N=18) were given both to O3 and O4 before entering the Flake condition. New demonstrations were given to these two individuals because they did not show any promising behaviour in the initial tests, which could have been due to the long delay since they were exposed to the a priori demonstrations. Following these new demonstrations, these two individuals were also tested in the Flake condition.

Tests and coding

Tests took place in the off-sight quarters, where the testing materials were fixed to the walls in the case of the orangutans and to the mesh in the case of chimpanzees (Figure 2). Chimpanzees participated in one test each day for several hours (between 2 and 3 hours) on a voluntary basis. The testing materials were placed inside the testing quarter and all individuals were free to participate. In the case of the orangutans, the tests lasted between 23 and 60 minutes and a maximum of two tests were conducted per day (one in the morning and one in the afternoon). In one occasion and due to repair works in the indoor enclosure one test lasted 90 minutes (the third trial of O4 in the Flake condition).

Figure 2: Experimental set up inside of the testing room of the orangutans. Observations and video recordings were made from the window visible in both pictures.

From each video recording of each test we coded all active interactions that the chimpanzees and the orangutans performed with the testing materials. An interaction started when the ape entered in physical contact with the testing materials and finished when the contact a) ceased, b) paused for more than three seconds or c) the interaction type changed. We only considered active interactions, meaning that stationary contact (such as placing and resting a hand on the materials or siting on the materials) was not coded. From each interaction we coded: 1) the identity of the individual; 2) the testing material that the individual interacted with (core, flake, hammer, hide box, tendon box); 3) if the interaction took place manually, using the mouth or a tool, 4) the type of tool and 5) the duration of the interaction.

All demonstrations and tests were recorded with two Sony HDR-CX330E Handycams video cameras.

3. Results

3.1 Chimpanzees

Twelve chimpanzees interacted at least once with the materials during the tests. The total number of interactions across all subjects was 1025. The total number of interactions per individual varied from 2 to 199 (Table 2) and the number of interactions per test varied from 473 during Test 1 to 68 during Test 5 (Figure 3).

Table 2: Individual interactions of the chimpanzees performed in each test.

Test	CH1	CH2	CH3	CH5	CH6	CH7	CH8	CH9	CH10	CH11	CH12	CH13	Total
1	1	62	98	15	63	68	52	4	0	37	70	3	473
2	36	29	16	0	23	45	1	29	1	4	15	1	200
3	0	11	35	0	7	17	2	4	0	31	8	3	118
4	23	5	28	0	3	22	2	0	0	8	4	0	95
5	0	8	0	3	7	36	3	2	1	4	3	1	68
6	2	4	22	0	1	6	1	5	0	14	15	1	71
Total	62	119	199	18	104	194	61	44	2	98	115	9	

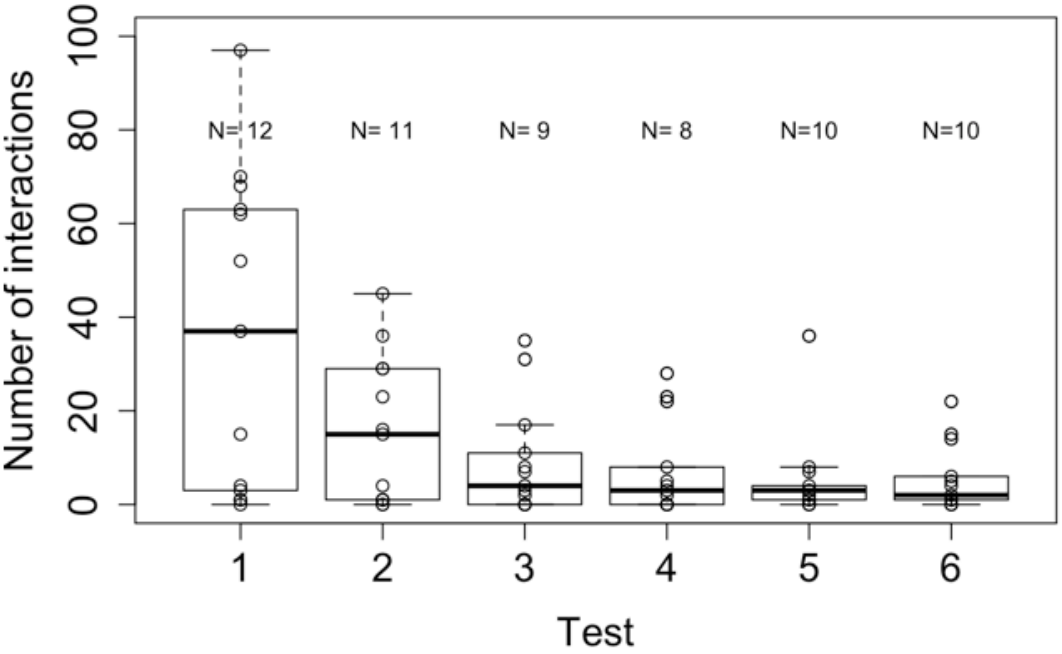

Figure 3: Number of interactions performed in each of the tests. N indicates the number of individuals that interacted with the testing materials in each test and each data point corresponds to one individual.

No correlation was found between the duration of the test (Test duration) and the number of interactions the chimpanzees performed in each Test (Figure 4). However, a strong correlation was found between the number of demonstrations an individual had seen and the number of interactions that same individual performed (Figure 5).

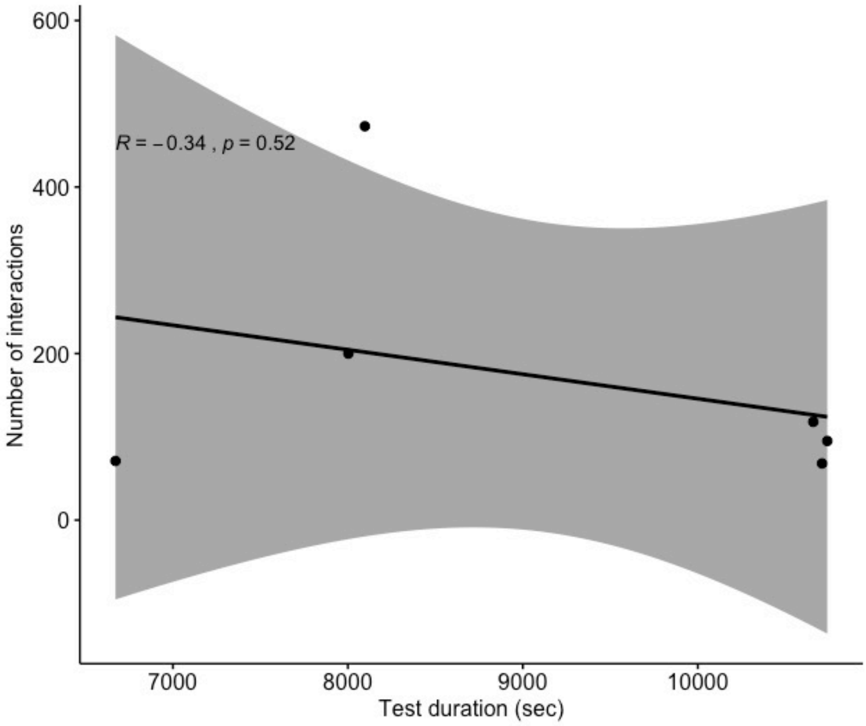

Figure 4: Pearson correlation between the Test duration in seconds and the number of interactions observed. Each data point is one test. R denotes the correlation value and p the p value of the correlation.

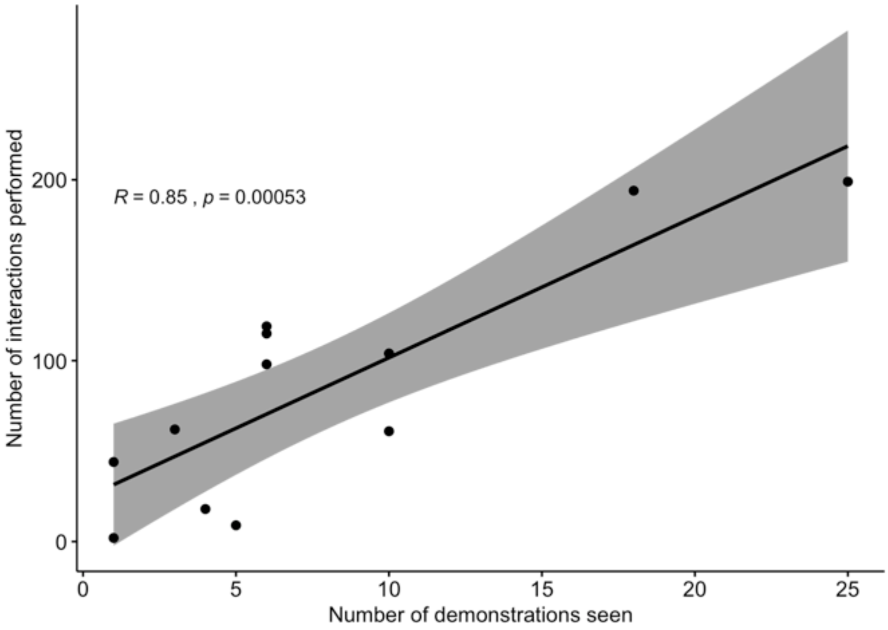

Figure 5: Pearson correlation between the number of demonstrations an individual chimpanzee was recorded to observe and the number of interactions that the

individual performed during the tests. Each data point corresponds to one individual. R denotes the correlation value and p the p value of the correlation.

The chimpanzees interacted the most with the baited boxes (hide and tendon box, Figure 6). One of the chimpanzees learnt to open the hide box manually by pulling on the edge of the silicone membrane, and did so in several tests. Despite being open and unbaited, most chimpanzees interacted often with the hide box (including the individual that learnt how to open it manually, Figure 6).

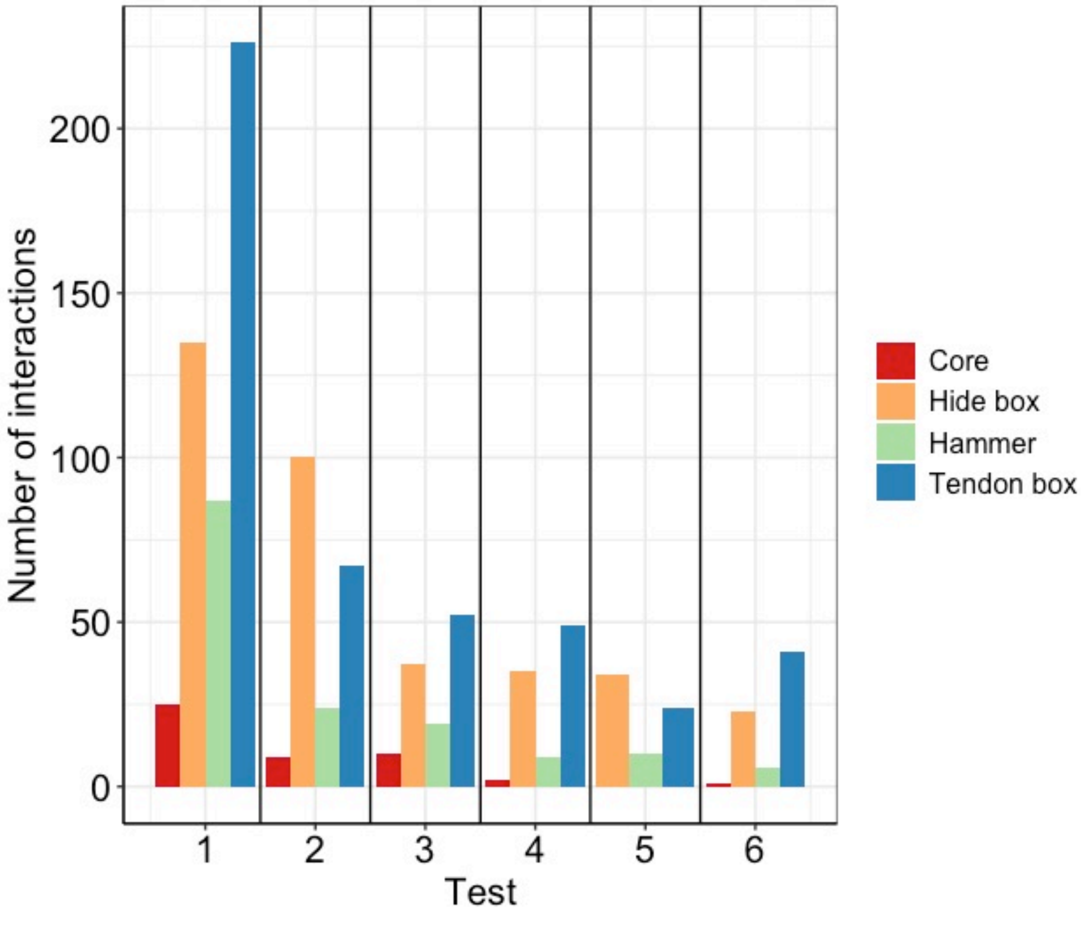

Figure 6: Frequencies of interaction with the different materials across tests.

Most of the interactions performed by the chimpanzees with the testing materials were manual (N=970), although the chimpanzees also used their mouths to try to open the boxes (N=5) as well as several tools that they brought from the indoor enclosure (N=50). The chimpanzees performed 20 interactions using sticks and five using pieces of straw obtained from the indoor enclosure. The nature of the tools used in the remaining 25 interactions could not be identified from video recordings.

Twelve chimpanzees touched the rope of the tendon box a total of 52 times. Of these, only two individuals (CH3 and CH11) interacted with the rope more than five times (13 and 10 times respectively). The rope was the single element keeping the box closed and it was necessary to cut this rope in order to access the food reward. Most interactions with the rope took place by hand (N=45) and using the teeth (N=5), but in two occasions a piece of straw was used to try to break the rope.

The chimpanzees interacted with the hammers a total of 155 times. Of these interactions, 12 involved percussion, defined as the use of tools to strike surfaces or objects (Whiten et al. 2009). In nine occasions the chimpanzees used a hammer to hit on the metal platform holding the core and four times to hit another hammer. The chimpanzees also forcefully rolled the hammers on their side without lifting them (N=6), which occasionally caused the impact of a hammer with the core. Eight times, the chimpanzees made contact with the core with a (hand-held) hammer. Two of these interactions involved percussion. CH7 (F, 32 years old at the time of testing) was the first individual to use the small hammer to hit the middle section of the core once during Test 1. During Test 3, CH12 (M, 40 years old) struck four times the core with the middle hammer hitting the middle section of the core (Figure 7). In none of these interactions, a flake was detached. This is likely due to the fact that the percussive actions were directed towards the middle section of the core rather that the edges. In addition, the strikes were barely forceful.

Figure 7: CH12 striking the middle section of the fixed core while holding the middle hammer with the right hand during test 3.

3.2 Orangutans

The orangutans interacted with the materials 425 times. Of these interactions, 48 took place using the mouth and the rest were manual interactions. Unlike the chimpanzees, the orangutans could not access the indoor enclosure during the tests and therefore could not bring tools to the test room. The frequency of the interactions (Figure 8) was highest during test 1 (mean=28.2, range=1-62) and lowest during test 4 (mean=0.6, range=0-3). Figure 8 shows that although there was a progressive decrease in the number of interactions with time, there was also substantial inter-individual variation. For instance, the young female O5 (9 years old) presented different interaction frequencies between trials (from 62 to 0) whereas the adult female O4 (26 years old) always presented low interaction frequencies (Figure 8).

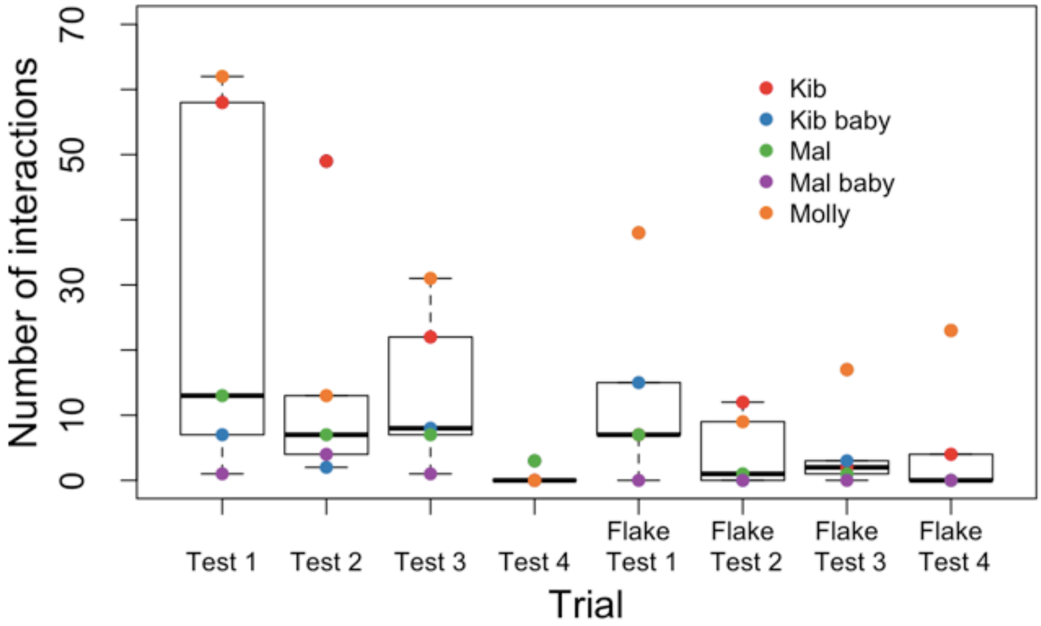

Figure 8: Individual interaction frequencies in each experimental trial.

No correlation was found between test duration and the number of interactions the orangutans performed in each task (Figure 9).

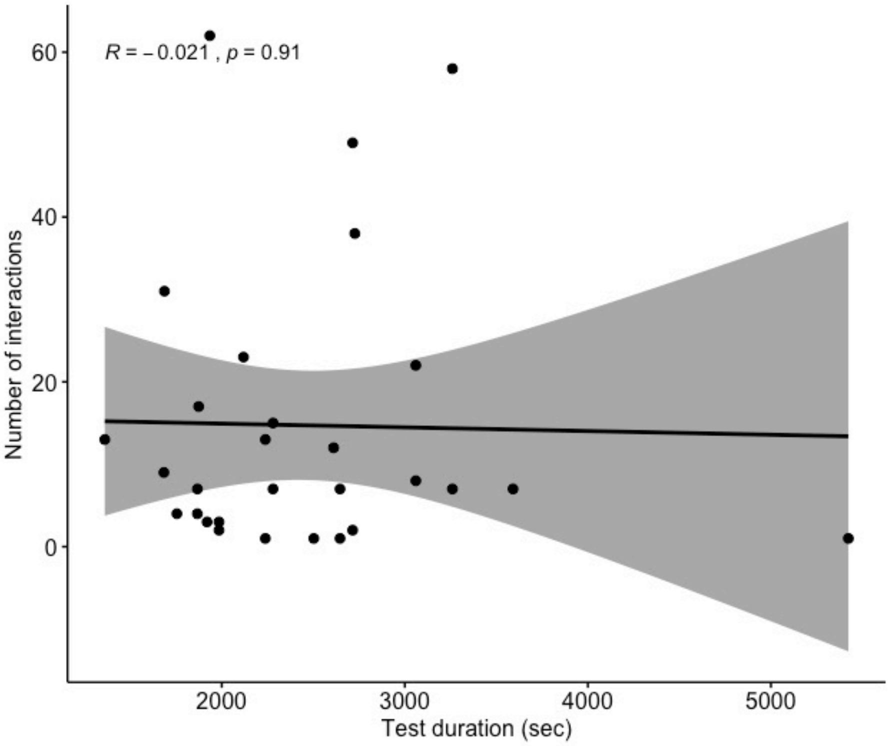

Figure 9: Pearson correlation between the Test duration in seconds and the number of interactions observed. Each data point is a test. R denotes the correlation value and p the p value of the correlation.

Regarding the testing materials, the orangutans interacted the most with the tendon box (N=137) and the hide box (N=168). Of the interactions with the tendon box, 23 involved touching the rope which needed to be cut in order to open the box and obtain the reward. The adult orangutans could manually open the hide box by ripping the silicone membrane and therefore the only box that remained baited during tests was the tendon box. In an attempt to strengthen the hide box, the silicone membranes were substituted by two types of vinyl membranes (2 and 5mm thick) and the attachments of the membrane were reinforced with metal rings. Unfortunately, the orangutans could still open the box after these modifications and therefore, although the hide box was baited and closed for every test, it was not operative. The orangutans interacted with the hammers a total of 82 times, a total 22 times with the core and during the Flake condition, a total of 19 times with the human-made flake (Figure 10).

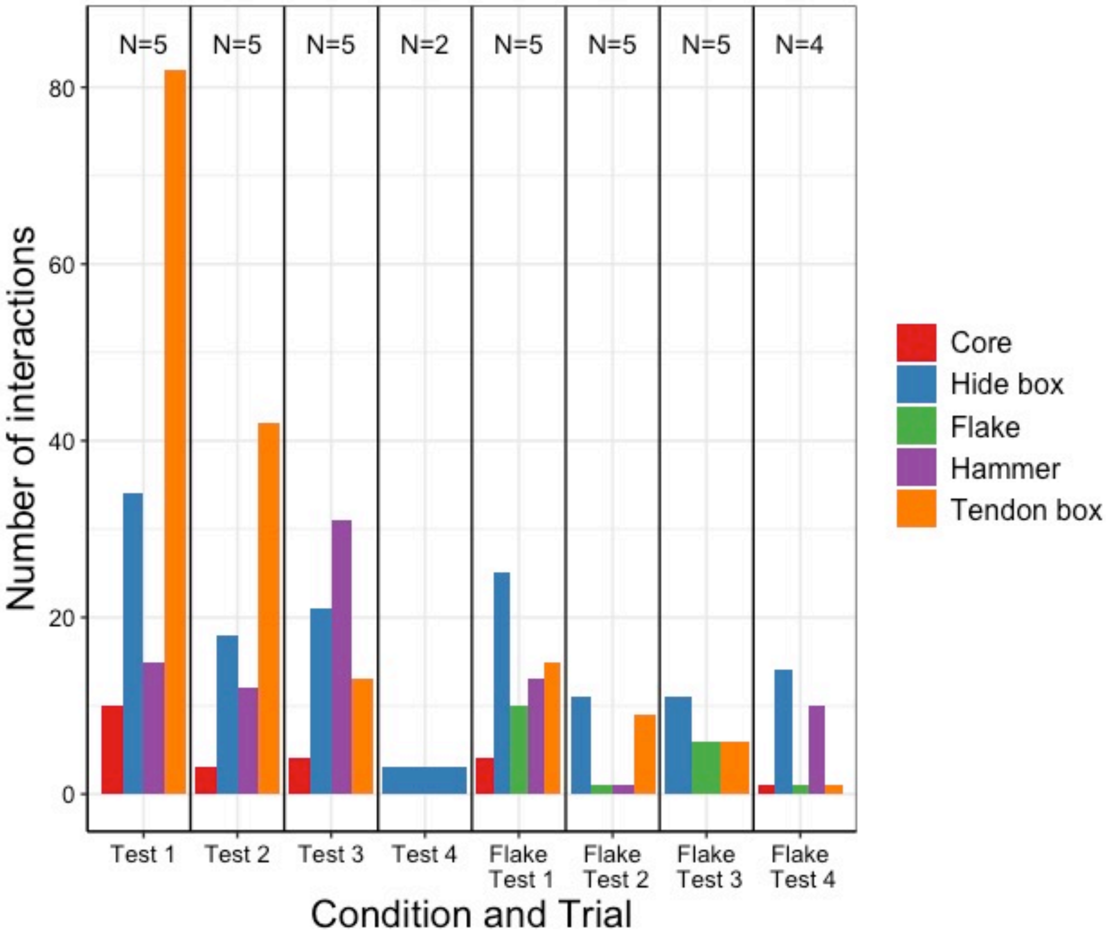

Figure 10: Number of interactions with each of the testing materials in each of the experimental trials. N represents the number of individuals tested.

The young female O5, was the individual who interacted the most with the hammers (Table 3).

Table 3: Individual number of interactions of each orangutan with the different testing materials.

	Core	Hide box	Flake	Hammer	Tendon box	Total
O1	0	3	0	2	1	6
O3	5	38	0	20	91	154
O2	1	23	0	4	7	35
O4	5	18	1	3	12	39
O5	11	55	17	53	57	193
Total	22	137	18	82	168	

Of O5's (F, 9 years old) interactions, 38 involved percussive actions in which an object was stricken against another. Most percussive actions (36) were directed towards the floor, but also the wooden platform where the hammers and core were secured, the wall and the other hammers. In these cases, O5 held a hammer with one hand and repeatedly struck these surfaces, often changing the hand with which she held the hammer. These percussive actions with a (hand-held) hammer were performed both in a downward vertical motion and in a horizontal motion when the wall was stricken. As a consequence of these percussive actions, six pieces of concrete were detached from a hammer, which were licked and sniffed but not used (Figure 11).

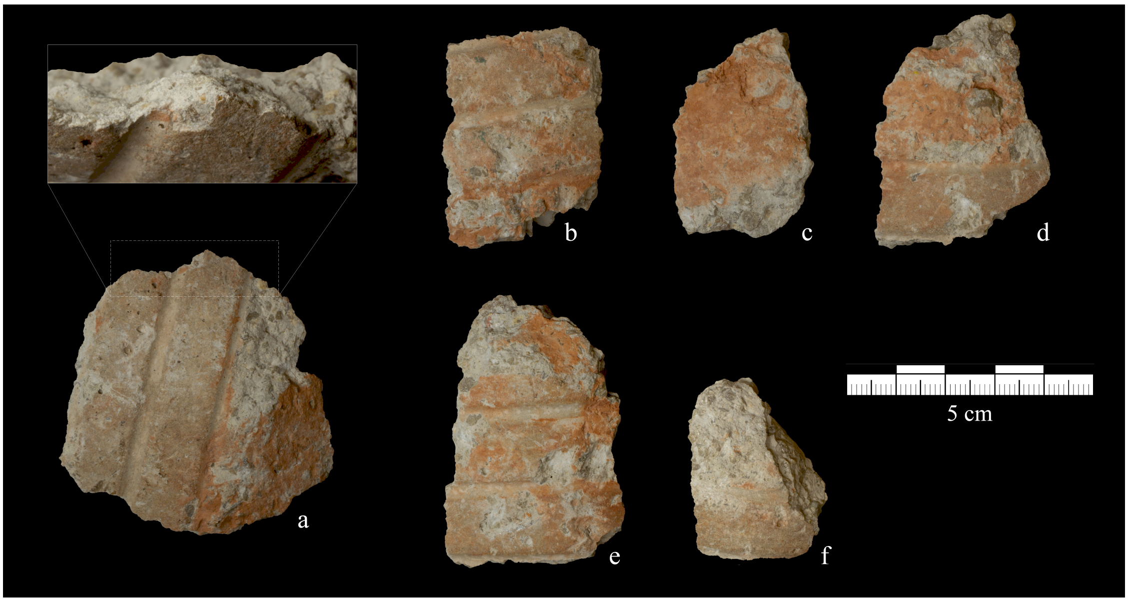

Figure 11: Concrete pieces detached by the female orangutan O5 (9 years old) as a by-product of percussive actions in which a hand-held core (initially provided to act as a hammer) was repeatedly hit against a hard surface. Some sections of the concrete pieces (enlarged in detail in the picture) were sharp enough to cut the rope closing the tendon box (tested by AMR).

At least two out of the six pieces produced as a by-product of the percussive actions had sharp enough edges that qualified them as potential cutting tools (which AMR tested by successfully cutting the rope of the tendon box with these hammer pieces).

Three times (once during test 1, Figure 12, and twice during the first test of the Flake condition), O5 used a hammer to hit on the fixed core. The first instance occurred 18 minutes after the start of test 1 and lasted 14 seconds during which O5 hit the core 12 times holding the middle hammer with the right hand. The second instance occurred 11 minutes after the start of the first test of the Flake condition. O5 struck the core 3 times in the span of 7 seconds holding the larger hammer with the left hand. The third and last instance of percussion with a hammer on the core took place 38 seconds later, when O5 struck the core 4 times during 10 seconds while holding the middle hammer with the right hand. Although no sharp-edged stones were detached, all 17 strikes on the core were directed to its exposed area (one edge), from which no sharp-edged stones could have potentially been produced. This area is the one from which the flakes were detached during the demonstrations. Thus, from the 1117 strikes performed in total by O5, 1.5% were directed towards the core.

Figure 12: Picture of the first percussive actions performed by O5 during test 1 using a hand-held hammer to strike the edge and exposed area of the core.

4. Discussion

Our results show that two chimpanzees (potentially enculturated given that they were human-reared) and one unenculturated orangutan used a hand-held artificial hammer to strike a fixed core. In addition, the orangutan detached six pieces from one of the hammers by vertically striking it against a hard surface (floor). Two of these pieces had sharp enough edges to be used as a cutting tool (though the orangutan did not use them). Although it is not possible to derive from the experiments presented here that the apes copied the actions or physical outcomes demonstrated to them by a human model, our results suggest that some of the tested apes may have socially acquired information from the actions or objects employed during the demonstrations.

Although none of the apes produced flakes using the demonstrated knapping technique in this experiment, one orangutan detached stone pieces from an artificial hammer by vertically striking the floor with a hand-held hammer, a technique not demonstrated by the human model. Two orangutans used this same technique in a previous study exploring the spontaneous stone tool making and tool using abilities of stone tool naïve orangutans (see Chapter 4). In both studies, sharp-edged pieces were detached from the hand-held object (a flint core in the first study and a concrete structure in the present study). The results from the experiments reported in Chapter 4 show that percussive actions that occasionally lead to the detachment of stone pieces as a by-product (including those performed by O5 in the present experiment), can be individually learnt by orangutans in the absence of specific demonstrations. However, contrary to the previous study reported in Chapter 4, O5 directed some of the strikes towards the exposed area of the core as demonstrated by the human model. In addition, the strength used to strike the core could have been sufficient to detach a sharp-edged stone. However, given that no flake detachment took place, either one or both of these variables (target and strength) did not match accurately enough the demonstrations. Furthermore, percussive actions were only performed by one of the three adult females tested (the youngest), which was the only one without dependent offspring (a factor that might have affected the performance of the other two females).

Similarly, two chimpanzees in this study also performed the correct mechanical actions (striking a fixed core with a hand-held artificial hammer) to produce a flake grossly using the actions previously demonstrated to them. Contrary to the orangutan, however, the target point where the chimpanzees hit the core was not the exposed area (as demonstrated) but the center, which was covered by a metallic mesh. In addition, the force employed for percussion did not match the one used in the demonstrations and it was insufficient to detach a sharp-edged stone. Furthermore, these actions occurred in very low frequency (only 2 out of 1025 interactions involved striking the core with a hammer) and were only performed by two out of the 13 tested chimpanzees.

Based on the results of the present study, it cannot be safely concluded that the orangutan and the two chimpanzees copied the demonstrated actions (and they clearly did not copy the demonstrated outcomes). In the wild, several species of primates engage in percussive activities that involve the use of stones. Several populations of chimpanzees and some capuchin monkeys (*Cebus apella*) in Brazil and Panama use stone hammers and anvils to crack nuts (Barrett et al., 2018; Boesch & Boesch, 1983; Carvalho et al., 2008; Proffitt et al., 2016). Certain subspecies of long-tailed macaques (*Macaca fascicularis*) in Thailand also use stone hammers and anvils to crack oil palm nuts and stone hammers to forage on marine crustaceans (Luncz et al., 2017). Thus, given that the percussive actions employed by the two chimpanzees resembled those used by wild conspecifics to crack nuts (Boesch & Boesch, 1983; Carvalho et al., 2008), it is likely that chimpanzees are prone to such activities and that they did not copy them from the model. Similarly, captive orangutans spontaneously perform percussive actions involving the use of artificial hammers to strike on hard surfaces in the absence of a model (Chapter 4), suggesting that these are activities in which captive orangutans engage in if the necessary materials are available. Further supporting the interpretation that the apes in this study did not acquire percussive actions from the model, the vast majority of studies on ape spontaneous copying abilities (reviewed in Chapter 1; Neadle et al., 2020; Tennie et al., 2009; Tennie et al., 2012) show that apes do not copy demonstrated actions without previous training.

An alternative explanation for our results besides action copying would be that the two chimpanzees and one orangutan in our experiment that engaged in stone percussion, socially learnt from the demonstrations what was the target of percussion (rather than the percussive actions themselves) via non-copying social learning mechanisms such as local enhancement, stimulus enhancement or social facilitation. The use of the artificial hammers as active elements could be then readily explained by the fact that these were the only mobile materials available. Furthermore, the results of the orangutan experiment reported in Chapter 4 suggest that percussive actions are spontaneously produced by orangutans. Thus, the performance of percussive actions per se does not directly imply that the apes (specially the orangutan) copied these actions from the demonstrator.

Nevertheless, our experimental design cannot completely exclude the (unlikely) possibility that the chimpanzees that engaged in percussive activities copied the demonstrated actions. Contrary to the present study, a previous study investigating if the very same population of chimpanzees could socially learn to crack nuts using a wooden hammer by observing a human demonstrator cracking nuts, failed to find any instance of subsequent tool percussion (Neadle et al., 2020). Thus the theoretical possibility remains that the two chimpanzees that performed percussive actions in the present study, acquired this behavioural form as a consequence of observing the human model. However, this performance most likely does not translate to wild chimpanzees.

Of the two chimpanzees that performed percussive actions targeted towards the core, one of them (CH7) had been hand-reared by keepers as an infant and the other (CH12) had "unknown background". It is therefore possible that both (or at least one) of the two chimpanzees that performed percussive activities were somehow enculturated due to extensive exposure to human contact (Henrich & Tennie, 2017). Extensive human contact has been shown to affect both brain connectivity and cognition – including motivation and/or ability to copy behavioural forms (Pope et al., 2018; Tomasello & Call, 2004). Enculturated apes have been repeatedly shown to possess enhanced copying abilities compared to unenculturated apes (Call, 2001; Call & Tomasello, 1996; Custance et al., 1995; Tomasello et al., 1993). The only two studies that reported that great apes could acquire sharp-edged stone tool making skills by copying a human model, tested enculturated individuals who had extensive human training (Toth et al., 1993; Wright, 1972). The enhanced attention towards humans could thus explain why the hand-reared individual (CH7) acquired social information about the target of percussion (and perhaps even the physical percussive actions). If this was the case, it remains unanswered why the other hand-reared individuals in the group did not performed percussive activities after being exposed to demonstrations. A potential explanation for this latter result could be that a combination of human exposure during rearing and a more neophilic personality led only two individuals to perform percussive actions.

Our finding that there was a correlation between the number of observed demonstrations and the number of individual interactions with the testing materials in chimpanzees could have several explanations. It is possible that observing a higher number of demonstrations would have caused an increase in curiosity and frequency of exploration of the testing materials. Alternatively, the same outcome could have also been obtained without a causal link. More naturally curious and less neophobic individuals could have been more explorative than other group members and consequently approached more often the experimenter *and* the testing materials (Damerius et al., 2017; Forss et al., 2019). This would have led both to the observation of a higher number of demonstrations and to a higher number of interactions with the testing materials.

5. Conclusion

Our results show that three great apes (two chimpanzees and one orangutan) performed some of the behavioural actions involved in the production of sharp-edged stone tools after being exposed to social demonstrations. Unfortunately, it remains unclear the nature of the information that was socially acquired. Given that wild and captive primates engage in percussion and as described above, even in stone percussion (see also Chapter 4), it is unlikely that percussive actions were learnt from the demonstrations. However, contrary to wild behaviours, the percussive actions in the present study did not grant immediate access to food, suggesting that these actions might have been performed in a play context, perhaps somehow elicited by the social demonstrations. Social demonstrations could have also provided information regarding the target of the percussive actions, namely the core (but note that other hard surfaces were also used as targets). The fact that one orangutan produced stone pieces as a by-product of percussive activities, adds to previous studies (Chapter 4) showing that some behaviours that can lead to the unintentional production of stone tools are within the physical and cognitive abilities of orangutans. Intentional production of sharp-edged stone pieces, however, seems to be beyond what orangutans (and chimpanzees) can learn, even when provided with full social demonstrations.

Data availability

All raw data, supplementary material, videos and R code employed to analyse the data and create the figures of this chapter can be found in the OSF project titled "Demonstration experiments (Chapter 5)": https://osf.io/vdkga/?view_only=53a2cee101f840e2bc64b3662085cde9.

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CHAPTER 6

General discussion

1. Summary of findings

The goal of this thesis was to evaluate which potential learning mechanisms underlay the acquisition of early stone tool (EST, in particular sharp-edged stone tool) making and using skills in early hominins, using non-human great apes as behavioural models. This evaluation was a necessary step towards postulating which type of culture was more likely present in the hominin species that possessed the oldest known lithic industrial complexes. Broadly, the null hypothesis tested was that individual learning was sufficient to spontaneously acquire sharp-edged stone tool making and using abilities by naïve individuals (H0) and thus these abilities were latent solutions potentially available to all individuals of the species (Tennie et al., 2017). The alternative hypothesis (H1) was that these abilities could not be acquired without directly copying a model or her artefacts. In this scenario, sharp-edged stone tool making and using skills would represent culture-dependent forms (after Reindl et al., 2017) that no single individual could learn on her/his own (Charbonneau, 2015). If sharp-edged stone tool making and using abilities could have been acquired individually by naïve chimpanzees and orangutans in the studies presented here (H0), this would have suggested (via cognitive cladistics, e.g. Haun et al., 2006) that the last common ancestor of hominins and these great ape species could have also learnt these skills individually. In turn, such finding would have suggested that the hominins that made and used sharp-edged stone tools most likely possessed a non-copying based culture, which would have been constituted primarily by latent solutions (Tennie et al., 2009). This result would have equated the type of culture present in early hominins with the type of culture supposedly present in modern great apes. Alternatively, if sharp-edged stone tool making and using abilities could only have been learnt by the chimpanzees and orangutans tested here after receiving social information about the target behavioural forms (H1), this would have suggested that the last common ancestor of early hominins and the tested great ape species (chimpanzees and orangutans), could have also had the necessary cognitive abilities to acquire novel behaviours via copying social learning mechanisms. Such a result would have suggested that sharp-edged stone tool making and using abilities potentially constitute the earliest detectable instance of a copying-based, cumulative culture like our own.

The focus of this thesis on stone tools is a direct consequence of their high degree of preservation in the archaeological record. Although sharp-edged stone tool production and use are employed here as representative of early hominin material culture, other tool behaviours might have been learnt via different learning mechanisms. Early hominin material culture included other types of artefacts such as bone and (most likely) wooden tools (see section 6.5), which making and using skills might not have been learnt in the same way as sharp-edged stone tool production and use were learnt. Thus, it is theoretically possible that the type of culture that early hominins had included both culture-dependent forms and latent solutions.

1.1 Great ape cultures

The interpretations of the potential outcomes of the two hypotheses tested in this thesis assumed *a priori* that great ape cultures were fundamentally different from human cultures due to the different learning mechanisms (non-copying versus copying, respectively) that underlie the acquisition of behaviours in these species (Galef, 1992; Tennie et al., 2009). However, prior to the work presented in this thesis, this specific assumption had not been tested at a large scale but only in individual experiments, testing single behaviours. Therefore, the first question that I addressed was: which type of culture do great apes have? I addressed this question by conducting a meta-analysis (Chapter 2) where I applied a novel method (The Method of Local Restriction) to investigate whether there is any evidence of a copying-based culture in great apes. A copying-based culture in great apes would have become evident by producing locally restricted behavioural forms in single populations as the unavoidable result of local lines of transmission via copying social learning mechanisms. These local lines of transmission would have been locally restricted due to copying errors (Eerkens & Lipo, 2005) and innovations (Bandini & Harrison, 2020; Charbonneau, 2015) that take place in one population but are unlikely to re-occur in the same form in other unconnected populations. Copying errors unavoidably accumulate when inexperienced individuals acquire information by copying experienced individuals and/or their artefacts (Eerkens & Lipo, 2005). Therefore, if great apes had copying-based cultures, we should observe numerous locally restricted behavioural forms across domains and species. Alternatively, if great apes had non-copying based cultures the same behavioural forms would re-appear repeatedly across unconnected populations of the same and (probably) different great ape species via socially mediated re-innovations (Bandini & Tennie, 2017).

After analyzing 78 potentially locally restricted forms reported in the literature (out of the likely thousands ape behaviours), I found that only 27 forms across great ape species and behavioural domains were locally restricted to a single population. Of these 27, only seven forms were found in a single population of a single species (locally unique), whilst the other 20 also appeared in the same form in additional primate species. The results of this meta-analysis demonstrate that the vast majority of great ape behavioural forms are actually latent solutions: these behaviours appeared in unconnected populations (even of different species) indicating that at least some individuals in these populations acquired the behaviours not by copying each other but rather via individual learning fostered by non-copying social learning mechanisms (Bandini & Tennie, 2017; Tennie et al., 2009). Therefore, using the Method of Restriction, I found supporting evidence for a non-copying based culture in great apes mainly constituted by latent solutions.

Regarding the remaining seven locally unique forms found in the meta-analysis, their distribution pattern corresponds to that of a behaviour that was acquired via copying (see Chapter 2 for a detailed explanation). Thus, the seven locally *unique* behaviours identified by the Method of Local Restriction represent the best candidates for culture-dependent forms in great apes. However, given the very low number of locally unique behaviours found, it is possible that at least some of these cases (if not all) are false positives (behaviours that appear to be culture-dependent forms but in reality they are not, see Chapter 2 for an in depth discussion of the method). To keep track of possible new results of the Method of Local Restriction, I created and online resource where new behavioral observations can be reported (at https://sites.google.com/view/group-specific-ape-behaviours/home). I believe that the method and website created for this project constitute useful contributions to the fields of primatology, primate archaeology and cultural evolution that will help us better understand both great apes' and our own cultures.

1.2 Baseline stone tool experiments

Once the type of culture present in great ape was assessed, the next step was to evaluate which type of culture (human- or great ape-like) was most consistent with sharp-edged stone tool production and use in early hominins. The first experiments reported in this thesis tested the spontaneous abilities of chimpanzees and orangutans to make sharp-edged stone tools in baseline conditions (Chapters 3 and 4). These baselines did not include any social information regarding the form of the target behaviours or artefacts, namely no information was provided regarding how to make or use stone tools. However, some other types of information were unavoidably provided during these experimental conditions as a consequence of giving novel objects to the test subjects. For example, just by placing testing apparatuses and other objects into the enclosures, information was provided regarding the *location* where the target behavioural form was expected to take place (local enhancement) and which *elements* the target form was expected to include (stimulus enhancement, Bandini et al., under revision). Nevertheless, although certain types of enhancement likely took place even during the baselines reported in Chapters 3 and 4, no information about the physical actions or outcomes involved in sharp-edged stone tool production and use were provided. Consequently the apes remained naïve to the target behavioural forms and did not have any opportunity to copy the target behavioural actions or results.

Despite ample testing time and the apes being motivated to explore the novel objects provided (see Chapters 3 and 4), no chimpanzee and no orangutan made sharp-edged stone tools during the baseline conditions. Consequently, the results from these experimental conditions show that chimpanzees and orangutans could not individually learn how to make sharp-edged stone tools.

In the case of the chimpanzees, these negative results could be explained by the potential existence of a sensitive learning period. It has been found that wild chimpanzees start to hit nuts using (blunt) stone hammers at the age of 1.5 years

(Estienne et al., 2019). However, it is not before they are 3.5 years old that they can successfully crack nuts open (Inoue-Nakamura & Matsuzawa, 1997; Biro et al., 2006) and their nut-cracking performance (percentage of cracked nuts divided by failed attempts and number of cracked nuts per minute spent nut-cracking) does not start to rise until they reach 5-6 years of age (Estienne et al., 2019). Crucially, chimpanzees that do not learn the basic actions for nut-cracking (i.e. placing nuts on an anvil, pick hammers and hit a nut placed on a anvil with a stone hammer) before they are 7 years old, do not perform nut-cracking behaviour in adulthood (Biro et al., 2006). In agreement with these findings, a previous study that tested the ability of adult chimpanzees to learn to crack nuts both individually and after social (human) demonstrations of actions and results, found that none of the chimpanzees performed the target behaviour. Given that most of the chimpanzees tested in the baseline condition (Chapter 3) for their abilities to produce sharp-edged stone tools were adults (only one juvenile was 7 years old) it is possible that chimpanzees possess a sensitive learning period not only for nut-cracking, but generally for percussive behaviours that involve the use of active elements. Future studies should therefore test the spontaneous stone tool making and using abilities of juvenile chimpanzees under 7 years of age.

Although they did not produce sharp-edged stones during the baseline conditions, the orangutans did engage in percussive actions. Both the juvenile and the adult male included in the study (Chapter 4) performed frequent percussive actions using the artificial hammers as active elements to strike both the concrete floor and walls of the testing room. The finding that orangutans (regardless of age) engage in percussive behaviours involving stones when suitable materials are available (a behaviour not reported in wild orangutans to the best of my knowledge), suggest that orangutans do not posses a sensitive learning period to develop percussive behaviours. These findings also suggest that percussive actions in orangutans are spontaneously performed when the appropriate elements are available (i.e. active mobile objects and hard surfaces), perhaps also as a consequence of genetic predispositions for object manipulation (Bandini et al., in press).

1.3 End-state stone tool experiments

In order to test if the apes could reverse engineer (a type of emulative learning called end-state emulation: Whiten et al., 2004) the production of sharp-edged stone tools by observing a ready-made sharp-edged stone tool and if they could spontaneously use sharp-edged stones as cutting tools, the subjects where provided with a human-made flake (Chapters 3 and 4). As in the baseline condition, neither chimpanzees nor orangutans produced their own sharp-edged stone tools. However, the juvenile orangutan (Loui, male, 7 years old at the time of testing) did use the provided flake as a cutting tool to successfully press through the occluding membrane of the hide box (severing, Davidson 2019). This result shows that the orangutan could use the sharp-edge of a flake as a cutting tool despite never having been in contact with a sharp-edged stone tool before.

1.4 Exchange experiments

In an attempt to increase the value attributed to the flakes, a series of trials in which the chimpanzees and orangutans exchanged human-made flakes for small food items (grapes) were conducted (Chapters 3 and 4). The aim of these experiments was to motivate the apes to produce their own sharp-edged stone tools so they could then exchange these tools directly for food items. As in the previous experiments, chimpanzees did not produce their own sharp-edged stone tools but contrary to the baseline conditions, one orangutan did produce sharp-edged stones. Due to a failure in the metallic mesh that held the core fixed on a platform for health and safety reasons, the juvenile orangutan was able to freely manipulate the core during one trial (for approximately 12 minutes). This event led to an increase in the range of actions that the juvenile could perform with the core, as this had now become a potential active, mobile element. Almost immediately after the core was released, and similarly to how the artificial hammers had been used to strike the walls and floor of the test rooms in previous trials, the juvenile orangutan started to strike the flint core against the floor and the walls of the room while holding it in his hand. This repeated percussive actions eventually led to the detachment of three small sharp-edged stones.

One of this stones presented morphological characteristic typically resulting from a conchoidal fracture, namely striking platform, striking point and bulb of percussion (Figure 1). Therefore, from a typological point of view (Debénath & Dibble, 1994), at least one of the stones produced by the orangutan could be considered as a flake.

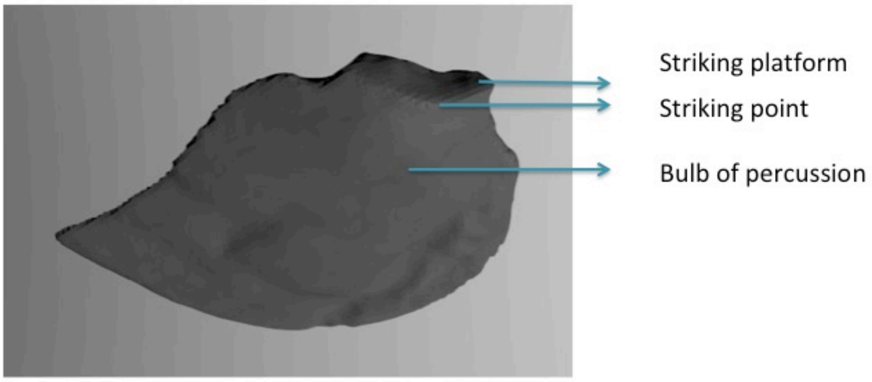


Figure 1: 3D scan of one of the sharp-edged stones made by the juvenile, male orangutan (Chapter 4). The arrows indicate several characteristic features found in flakes that often result from a conchoidal fracture (Debénath & Dibble, 1994).

However, it is important to acknowledge the distinction between a typological flake (product) and a flake resulting from flaking as a process. Neither are all flakes the result of flaking processes (Barnes, 1939), nor do flaking processes always produce flakes. Even if we referred to the sharp-edged stone produced by the orangutan depicted in Figure 1 as a typological flake (Debénath & Dibble, 1994), this would not imply that the orangutan engaged in a process of flaking. Oldowan flaking has been described as "intentional, controlled, and [showing] a basic sense of skill in lithic reduction" (p. 25; Schick and Toth, 2006), which was never observed in any of the experiments reported here. Indeed, given that the sharp-edged stones produced by the orangutan were not used for any purpose nor were they exchanged for a food reward, it is not possible to assess the intentionality (nor the goal) behind their production. Furthermore, the extremely low frequency of sharp-edged stones suggests that their production was unintentional (although it is not clear what the frequency of typological flakes in a site should be in order to be indicative of a process of flaking). Overall, the results of the exchange experiment demonstrate that typological flakes can be produced by orangutans. However, regarding the underlying process of production, the limited data available suggests that the sharp-edged stones (including the piece with signs of conchoidal fracture) were unintentional by-products of (perhaps exploratory) percussive activities.

Capuchin monkeys (*Sapajus libidinosus*) in Serra da Capivara National Park (Brazil) have also been found to occasionally produce sharp-edged stones that qualify as typological flakes (Proffitt et al., 2016). These sharp-edged stones are produced as a consequence of a behaviour called stone on stone (SoS) (Proffitt et al., 2016) in which a hand held cobble is struck against another cobble that is fixed in a natural conglomerate. The hypothesized proximate function of this behaviour is to create stone dust or access lichen that is then licked by the monkeys. This behaviour has attracted archaeologists' attention because it often leads to the fracture of the hand-held cobble, the fixed cobble, or both. As in the case of the orangutan mentioned above, the capuchin monkeys do not seem to intentionally engage in flaking: the frequency of sharp-edged stones qualifying as typological flakes produced via SoS is very low and they are not subsequently used for any purpose. Consequently, it is likely that the production of sharp-edged stones by capuchins is an unintentional by-product of the SoS behaviour (Proffitt et al. 2016).

1.5 Demonstration experiments

Chimpanzees and orangutans from different populations to the ones tested in Chapters 3 and 4 were exposed to a human model performing a series of demonstrations of flake production and use (Chapter 5). The demonstrator (AMR) used different hammers to detach flakes from a fixed core and then proceeded to use the flakes thus produced to open one of the two puzzle boxes (hide box or tendon box) in order to obtain the food reward contained inside. Following these demonstrations, chimpanzees and orangutans were provided with the testing materials (fixed core, artificial hammers and puzzle boxes) to investigate their sharp-edged stone tool making and using abilities. Although none of the apes tested detached sharp-edged stones from the core, one orangutan (and to a lesser degree two chimpanzees) engaged in percussive activities, some of which involved striking the core with an artificial hammer.

In two occasions, chimpanzees (N=2) struck the fixed core while holding one of the artificial hammers in their hand (Chapter 5). These observations could theoretically be explained recurring to several copying social learning mechanisms (see Chapter 1). Imitation and object movement re-enactment are unlikely to be responsible for the observed percussive actions during the tests. In the wild, chimpanzees as young as 1.5 years old engage in percussive actions involving stone hammers and by 3.5 years they hit nuts with stone hammers (Hayashi, 2015). At Gombe (Tanzania) chimpanzees open hard-shelled orange-size fruits by hitting them repeatedly against a stone anvil (McGrew et al., 1999). Wild and captive chimpanzees have been shown to pull shoots from the crown of oil palms in order repeatedly hit and soften the palm heart in order to eat it (Yamakoshi & Sugiyama, 1995; Bandini & Tennie, 2019). Chimpanzees in Assirik (Senegal) have been also reported to crack open baobab fruits by smashing them against stationary stone anvils (Marchant & McGrew, 2005). Indirect evidence suggests that chimpanzees in the Nimba Mountains (Guinea) open *Treculia* fruits by hitting them with clubs and stone cleavers as well as by smashing the fruits against stationary anvils (Koops et al., 2010). Furthermore, some of these behaviours that involve percussive actions (e.g. anvil use to pound open fruits) have been found to re-appear in unconnected chimpanzee populations (Whiten et al., 2001), suggesting that their acquisition is not dependent on copying social learning mechanisms (Chapter 2). Consequently, percussive actions (including those observed in Chapter 5) can most likely be learnt by chimpanzees without relying on the observation of actions (imitation: Galef, 1988) or object movements (object movement re-enactment, Whiten et al., 2004) performed by behavioural models. However, it is a possibility that the chimpanzees engaged in end-state emulation and that they performed percussive actions in order to recreate the noises resulting from the percussive actions performed during the demonstrations. Therefore, although our experimental design does not allow us to directly exclude the possibility that the chimpanzees engaged in copying social learning mechanisms, this scenario is not the most parsimonious. The percussive actions performed by the chimpanzees could be alternative be explained by a process of individual learning catalysed by non-copying social learning mechanisms (stimulus and/or local enhancement, Chapter 1, Heyes, 1994). This alternative explanation would be further supported by a broad body of literature showing that apes do not spontaneously copy novel actions (see Chapter 1 for a review of the literature on chimpanzee copying).

After being exposed to social demonstrations, one young adult female orangutan also performed the demonstrated percussive actions when she used the artificial hammer as an active element to strike the core (Chapter 5). The target of these percussive actions was the exposed area at the edge of the core rather than the center of the core as it was the case in the chimpanzees. As mentioned above, although it is theoretically possible that these actions were learnt via copying variants of social learning (imitation or object movement re-enactment), such a scenario is highly unlikely for two reasons. First, previous studies have shown that unenculturated orangutans do not spontaneously copy demonstrated actions (Call & Tomasello, 1995). Second, in the previous orangutan experiments (Chapter 4) it was found that naïve orangutans spontaneously engage in percussive actions when hard, mobile materials are provided. Consequently, orangutans can learn percussive behaviours without the need of copying the actions performed by a model (imitation) and without seeing the movements of the objects involved in the target behaviour (object movement re-enactment). The orangutan, however, could have engaged in end-state emulation reproducing the noises produced while flaking during the demonstrations. Alternatively, the female orangutan could have individually learnt to perform the percussive actions (as was probably the case in chimpanzees), prompted by non-copying social learning mechanisms, which increased the likelihood of expression of these actions already present in the behavioural repertoire of the orangutan (Tennie et al. 2009). Via stimulus or local enhancement the female orangutan might have been drawn towards the fixed core as a target of percussion and used the only mobile elements available (the artificial hammers) as active elements.

2. Implications for the evolution of lithic technologies

Figure 2 summarizes the current state of knowledge regarding the presence and absence of necessary behaviours for the emergence of lithic technologies in different primate lineages, as well as it highlights the contributions of the present thesis to this topic.

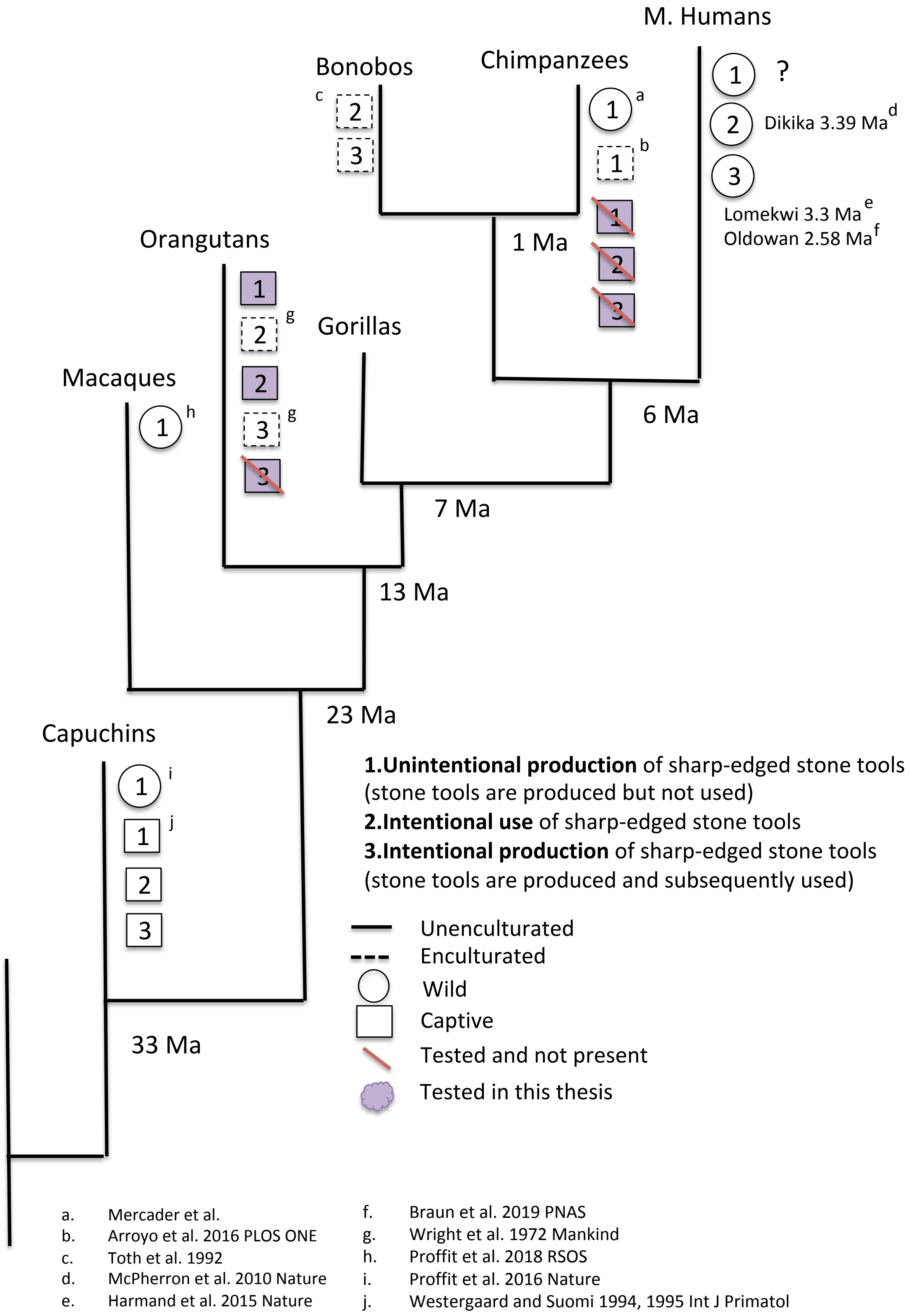


Figure 2: Simplified phylogenetic tree indicating the sharp-edged stone tool making and using abilities of the different great apes and other primate species that engage in tool use. Next to each branch it is indicated if the species in question has been shown

to unintentionally produce (1), intentionally use (2) or intentionally produce (3) sharp-edged stone tools. It is also indicated if these findings were reported in captive or wild settings and if they refer to enculturated or unenculturated subjects. Symbols in purple represent the contributions of this thesis to the literature on primate stone tool studies. Finally, those symbols that are crossed with a red line represent studies that were conducted but produced negative results (i.e., the behaviour was not found).

The experiments included in this thesis inform us about three behaviours involved in the emergence and maintenance of lithic technologies: the unintentional production of sharp-edged stone tools, the use of already-made sharp-edged stone tools and the intentional production of sharp-edged stone tools (Davidson, 2019; Panger et al., 2002).

2.1 Unintentional production of sharp-edged stones

Percussive activities in the broad sense of "forceful, muscle-driven striking of one solid body against another" (p. 342, Marchant & McGrew, 2005) are present in a variety of animal species (reviewed by Marchant & McGrew, 2005). However, percussive activities that involve the use of stones as active elements are rarer (Carvalho et al., 2008; Hall & Schaller, 1964; Luncz et al., 2017; Proffitt et al., 2016; Thouless et al., 1987). Several species of primates unintentionally produce sharp-edged stones as a by-product of percussive activities. Some populations (see list in Carvalho et al., 2008) of West African chimpanzees (*Pan troglodytes verus*) sometimes detach sharp-edged stones from the anvils they use to stabilized hard-shelled nuts when they mishit them with stone hammers (see examples in Carvalho et al., 2008). No reports so far exist of chimpanzees using the resulting sharp-edged stones as cutting tools, although in a few cases these stones have been subsequently used as hammers (Carvalho et al., 2008). Similarly to chimpanzees, long-tailed macaques (*Macaca fascicularis*) sometimes unintentionally detach sharp-edged stones from the hammerstones that they use to crack nuts in Thailand by mishitting the stone anvils (Proffitt et al., 2018). Capuchin monkeys (*Sapajus libidinosus*) also sometimes produce sharp-edged stones (see above) when engaging in SoS behaviour (Proffitt et al., 2016).

The experiments reported in this thesis contribute novel data on the unintentional production of sharp-edged stones as a by-product of percussive activities in orangutans and chimpanzees, namely by showing that this behaviour spontaneously emerges in orangutans but not in chimpanzees (Figure 2). Percussive frequencies strongly differed between species, with orangutans engaging in percussive activities both spontaneously (Chapter 4) and after being exposed to demonstrations (Chapter 5) of the target behaviours, whereas chimpanzees only anecdotally engaged in percussion after seeing demonstrations (Chapter 5). In light of the results presented here and the literature on chimpanzee percussive behaviours, stone-tool percussion may only systematically emerge in chimpanzees under specific combinations of environmental conditions, rearing background (e.g. exposure to the behaviour during a sensitive learning period, se also Neadle et al., 2020) and (potentially) genetic predispositions.

The finding that orangutans spontaneous perform percussive actions using stones shows that this behaviour is individually learnt in this species, even though not (yet) reported in wild orangutan populations. Wild orangutans have been reported to "hammer" with wooden sticks to access termite or bee nests (Fox et al., 1999) but no reports exist (to the best of my knowledge) of stone tool use in the wild. Orangutans are the most arboreal great ape species and in the wild they are rarely found on the ground (sensu Fox et al., 1999). The fact that captive orangutans spontaneously performed percussive actions using stones (Chapter 4) shows that these actions are in the latent repertoire of orangutans (Tennie et al. 2009). However percussive actions seem not to be expressed unless the right environmental affordances are present, namely when arboreality is partly substituted by terrestriality, as it is the case in captive settings (see also Marchant & McGrew, 2005; Meulman et al., 2012), and/or the right materials (i.e. mobile stones) are available.

It has been hypothesized that the unintentional production of sharp-edged stones as a by-product of percussive activities in a foraging context was the first step in a series of innovations that eventually led to the emergence and stabilization of lithic technologies (Carvalho & McGrew, 2012; Davidson & McGrew, 2005; Panger et al., 2002). The results presented in this thesis are the first to find this ability (unintentional production of sharp-edged stone tools) in orangutans, who share the oldest common ancestor among great apes with our lineage. This finding suggests that the cognitive and physical abilities involved in percussive activities, which might lead to the unintentional production sharp-edged stones, could have also been present in the last common ancestor of *Pongo* and *Homo* 13 Ma.

2.2. Sharp-edged stone use

The systematic use of sharp-edged stones as cutting tools has so far only been described in the hominin lineage (Bunn, 1981; McPherron et al., 2010). This behaviour has been deemed critical for hominin evolution, as it has been suggested to have expanded our ancestors' capacity to obtain food resources (Davidson, 2019; Davidson & McGrew, 2005). Only one previous study reported a non-human, unenculturated animal (tufted capuchins; *Sapajus apella*) using sharp-edge stone tools to cut an acetate membrane of a puzzle box to access a food reward (Westergaard & Suomi, 1994a). The results from the Flake condition reported in Chapter 4, are the first to show this ability in a non-human great ape, namely in an orangutan.

In the archaeological record, the oldest indications of the use of sharp-edged stones as cutting tools date from 3.39 Ma at Dikika, Ethiopia (McPherron et al., 2010), where two bones were found with surface marks that had been produced before fossilization. After analyzing these marks, the authors concluded that they were produced by the use of stone tools to cut flesh of an animal carcass (but see Domínguez-Rodrigo et al., 2010). These findings were interpreted as suggesting that stone tool production might be 800 ky older than previously thought and that stone tools dating from the period between 3.39 and 2.58 Ma had perhaps not been found due to low densities in the landscape (McPherron et al. 2010). However, it could also be possible that the hominins that produced the Dikika cut-marks (presumably *Australopithecus afarensis*) did not make themselves the sharp-edged stones that they used.

Sharp-edged stones can be produced involuntarily as a by-product of percussive foraging behaviours (see above) but also by natural abiotic processes (Barnes, 1939). Stones can acquire sharp-edges due to falls (from a cliff for example), fluvial transport, solifluxion, cryofracture, thermal fracture and other natural events (Barnes, 1939). If sharp-edged stones produced by natural processes were available in the landscape, it is possible that early hominins occasionally collected and used them for foraging activities without yet knowing (or needing to know) how to intentionally produce sharp-edges (see the niche construction hypothesis by Davidson, 2019). Similarly, sharp-edged stones produced as a consequence of cracking nuts using stone hammers and anvils could have eventually been collected and used for other purposes, such as meat processing (Carvalho & McGrew, 2012; Marchant & McGrew, 2005; Panger et al., 2002).

Both these scenarios would have necessarily required the identification of sharp-edges as potential cutting tools as well as the ability to use them as such. The recognition of sharp-edged stones as cutting tools was shown in the enculturated bonobo Kanzi, who was trained to repeatedly select one sharp flake among an array of blunt human-made flakes (Toth et al. 1993). In addition, Kanzi was trained in the identification of sharp-edged stone tools by being provided with human-made flakes, which he used as cutting tools to severe the cord of the tendon box and open it. Therefore, given Kanzi's training, his abilities to identify sharp-edged stones among an array of tools cannot be taken as representative of the species as a whole (let alone all great apes). The experiments presented in this thesis show that the ability to use a human-made flake as a cutting tool is present in unenculturated orangutans. This flake use (Chapter 4) seemed to be the result of a process of trial and error learning in which the orangutan used the available materials in the testing room to try to open the hide box (i.e. before using the flake the orangutan tried to open this box by pressing with a foot and pressing with a piece of hose on the membrane). Therefore, given that orangutans seem to be able to individually learn to use sharp-edged stones as cutting tools, it remains parsimoniously possible that the last common ancestor of all great apes (including hominins) would have also possessed this ability 13 Ma.

2.3 Intentional production of sharp-edged stone tools

None of the chimpanzees or orangutans tested in the experiments presented here produced and then subsequently used a sharp-edge stone. Therefore, the detachment of sharp-edged stones reported in Chapter 4 cannot be deemed intentional. On the other hand, the two previous studies that tested enculturated apes found that (after seeing demonstrations) the apes (two bonobos and one orangutan) eventually produced and subsequently used sharp-edged stones (Toth et al., 1993; Wright, 1972). Consequently, intentional sharp-edged stone production in non-human apes, and their subsequent use as cutting tools, seems only possible if a great ape subject has been extensively exposed to human training and given demonstrations of the target behaviours. Unenculturated chimpanzees and orangutans do not seem to be able to acquire intentional sharp-edged stone tool production neither via individual learning nor via copying variants of social learning. However this does not seem to be the case in capuchin monkeys.

A study investigating the spontaneous abilities of captive, unenculturated tufted capuchin monkeys (*Sapajus apella*) to produce and subsequently use sharp-edged stones, revealed that these abilities can be individually learnt by these monkeys (Westergaard & Suomi, 1994a). In their first experiment, Westergaard & Suomi, (1994a) presented two groups (N_{total}=11) of stone-naïve capuchins with quartzite stones of different sizes that could be used as hammers or anvils (but with no baited puzzle box where the stone tools could be used). Three capuchins in each group (N=6) spontaneously produced sharp-edged stones using several techniques. All six monkeys detached sharp-edged stones by striking a stone against a hard surface (i.e. the floor of the enclosure and an anvil). Four of the six capuchins produced sharp-edged stones by striking a hand held hammer against a passive stone (core). Finally, two of the six capuchins produced sharp-edged stones by hitting together two hand-held stones. In a second experiment, three groups of capuchins (the two previously tested groups and an additional, previously untested group, N_{total}=15) were provided once more with quartzite stones of different sizes as well as a baited transparent puzzle box (this box was the model used to build the hide box included in the experiments of this thesis). As in the first experiment, several monkeys (N=3, two monkeys from the same group and a monkey from a different group) spontaneously produced and subsequently used sharp-edged stones to cut the membrane of the hide box. In summary, these experiments show that unenculturated, naïve and captive tufted capuchin monkeys can individually learn how to make and subsequently use sharp-edged stones (Westergaard & Suomi, 1994a) and that these behaviours are reliably reproduced in follow-up studies (Westergaard & Suomi, 1995b).

Contrary to capuchins, the studies presented here suggest that unenculturated great apes do not spontaneously make and then use sharp-edges stones. It has been suggested that chimpanzees represent poor stone toolmakers and -users because their wrist and finger motion, power and precision are not sufficient to effectively manipulate cores and hammers (reviewed by Rolian & Carvalho, 2017). Therefore, there might exist an anatomical limitation to the production of stone tools by apes using certain knapping techniques that involve handholding both the hammer and the core. However, the methodology employed in this thesis did not require the apes to perform freehand percussion but rather a behaviour that some wild chimpanzee populations (and presumably the last common ancestor of *Pan* and *Homo*) naturally perform, namely the use of a hand-held hammerstone to strike an object stabilized on a surface (Carvalho et al., 2008). Thus, the studies presented in this thesis tested behaviours that are physically possible for chimpanzees to perform.

Rolian and Carvalho (2017) argued that extant primates possess the basic necessary requirements to accomplish tool manufacture and use. Cognitive abilities such as causal reasoning, technical understanding of object properties and physical understanding of object interactions are present in several species of tool using primates (reviewed by Rolian & Carvalho, 2017). However, more complex abilities such as the mental representation of tools, the process of their manufacture and their future application (future planning) are less common in non-human primates and perhaps only present certain species (chimpanzees, orangutans and capuchins; Rolian & Carvalho, 2017). After reviewing the evidence for the presence of these abilities in tool using/making primates, Rolian & Carvalho, (2017) concluded that (at least) the last common ancestor of *Pan* and *Homo* already presented all the necessary cognitive abilities to make and use tools 7 Ma. However, the intentional production of sharp-edged stones presents the added difficulty that the product in their final shape (the tool itself) is not visible at the onset of the behavioural sequence and to date, there is no evidence that unenculturated non-human primates can solve such a task.

The evolutionary forces that might have led to the transition from unintentional sharp-edged stone tool production to intentional, goal-directed, sharp-edged stone tool production are still unknown. Marchant and McGrew (2005) hypothesized that the evolution of stone tool technologies started when the level of terrestriality increased in early hominins and they gained access to both hard and stable substrates as well as hard and mobile tools. The consumption of highly caloric food items that were too hard to consume just using the teeth (such as nuts), might have led early hominins to systematically use stones for food processing. Access to novel food resources, such as large game or hard tubers which need to be processed before they can be consumed, might have later prompted the need to use sharp cutting tools (Marchant & McGrew, 2005; Schick & Toth, 1994). It has also been hypothesized that the transition from quadrupedal to bipedal locomotion strongly influenced the wrist and hand anatomies allowing the performance of new types of grips perhaps necessary for at least some knapping techniques (Marzke, 2013; Rolian & Carvalho, 2017).

3. Synthesis

Figure 2 and Table 1 illustrate the contributions of this thesis towards advancing our knowledge on the emergence and evolution of behavioural forms relevant for the development of lithic technologies. To the best of my knowledge, only one previous study (Bandini, 2018) investigated the abilities of four chimpanzees to learn how to produce and use sharp-edged stone tools. This represents the first report of the abilities of unenculturated and stone-naïve orangutans to learn sharp-edged stone tool making and using skills. The studies presented here broaden the window through which we can investigate the behaviours that presumably preceded the emergence of intentional stone tool production in our lineage. The results of these studies corroborate that sharp-edged stone tool production is composed of a series of simpler behaviours, some of which can be individually learnt by great apes and some of which seem to be outside their cognitive or physical reach. Unenculturated naïve orangutans can spontaneously use a human-made flake as a cutting tool despite never having been exposed to sharp-edged stones before. Similarly, orangutans spontaneously perform percussive activities using cores and hammers as active elements and these activities sometimes lead to the detachment of sharp-edged stones. After seeing social demonstrations performed by a human on how to make and use flakes, an individual in a second population of orangutans also performed percussive activities striking a stone (originally envisioned as a hammer) both against the core and against hard surfaces, which in the second case led to the detachment of several stones from the hammer (some of which were sharp). Contrary to orangutans, chimpanzees in the studies reported here, did not produce or use sharp-edged stones neither spontaneously nor after seeing social demonstrations. However, stimulus and/or local enhancement (which most likely also influenced the orangutan's behaviour in Chapter 5) could have led two chimpanzees to explore the hammers and eventually non-forcefully strike a fixed core.

Table 1: Summary of findings of the stone tool experiments conducted with naïve, unenculturated chimpanzees and orangutans reported in this thesis.

	Orangutans	Chimpanzees
Spontaneously use sharp-edged stone tools	**Yes**	No
Spontaneously make sharp-edged stone tools	No	No
Make sharp-edged stones after attributing value to flakes	**Yes**	No
Make sharp-edged stones after human demonstrations	**Yes**	No
Use sharp-edged stone tools after demonstrations	No	Not tested

The studies reported in this thesis provide evidence for the view that the intentional production of sharp-edged stone tools is outside the cognitive reach of unenculturated, stone-naïve great apes given that these behaviours did not even appeared after full (human) demonstrations. These results, together with the findings from previous experiments with enculturated, non-naïve apes that found positive evidence for intentional sharp-edged stone production, suggest that enculturation (together with full behavioural demonstrations) is necessary for apes to develop intentional sharp-edged stone tool making. Human exposure seems to elicit the development of key cognitive abilities (Rolian & Carvalho, 2017) that allow apes to engage in this behavior (see also Heyes, 2018).

Returning to the original goal of this thesis of investigating the learning mechanisms underlying stone tool production and use in early hominins to investigate which type of culture (copying or non-copying based) early hominins might have had, the puzzle seems to be more complex than expected. On the one hand, intentional sharp-edged stone tool production (for subsequent use) might require the development of learning mechanisms such as copying variants of social learning (e.g. imitation) not found in unenculturated great apes (see Chapter 1). On the other hand, more basic behaviours such as the unintentional production of sharp-edged stones and the use of already made (by other individuals or naturally produced) flakes as cutting tools, can be individually learnt by naïve orangutans (Chapter 4) but not chimpanzees (Chapter 3). Overall, intentional sharp-edged stone tool production could be a culture-dependent form (after Reindl et al., 2017) in great apes whereas unintentional sharp-edged stone production and (independently) sharp-edged stone use are latent solutions in some great ape species (orangutans) but not others (chimpanzees).

4. Limitations of the stone tools studies

4.1 Available techniques

It could be argued that the target behaviours (spontaneous production and use of sharp-edged stone tools) did not emerge during the baseline conditions because the techniques that the subjects could use to produce stone tools were too limited. Namely, chimpanzees and orangutans could only perform one type of knapping in which (somehow similar to the actions involved in the bipolar technique), a core is stabilized on a hard surface and struck with a hand-held hammerstone. Given health and safety protocols at the testing institutions, it was not possible to provide subjects with loose hammerstones and loose cores (which would have maximized options of object manipulation). The experimental set up was designed to eliminate the risk that the subjects might take the testing materials to the enclosures and potentially damage the enclosures, harm visitors and/or themselves. Therefore, the core had to be fixed on a platform and the hammers had to be artificially built so that they could be secured with a chain. These security measures meant that the core could only act as a passive element. By design, subjects could therefore not produce stone tools with any technique that involved the use of the core as an active element (such as the passive hammer technique or the throwing and directed throwing techniques, Toth et al., 1993) or that involved holding the core in the hand (such as in some modalities of freehand percussion). Thus, the only technique available to the apes with the experimental set up was the detachment of sharp-edged stones from the core by striking the exposed area on the edge of the core with the artificial concrete hammerstone.

However, when the experimental design failed and the core was extracted from the fixing platform, interesting observations were made. Given that the only positive results of sharp-edged stone production took place when the core could be manipulated as an active element, this would suggest that the necessary safety measures undertaken might have prevented the apes from using more effective techniques. Nevertheless, in a previous study (Bandini, 2018), where four chimpanzees were provided with loose hammerstones and flint cores, the chimpanzees also did not produce sharp-edged stones. Therefore, it seems that the absence of sharp-edged stone tool production (at least in chimpanzees) is not the result of the more restrictive experimental set up used in this thesis. The movement restrictions imposed on the hammers and cores could however have affected the results of the orangutan experiments.

4.2 Conditions' length and motivation levels

All the experimental trials that included individual tests were conducted during the cleaning routines of the indoor enclosures. This meant that the trial length was not under the control of the experimenter. Although an effort was made to test the apes for a minimum of 30 minutes in each trial (the keepers often waited after the cleaning routines were completed), sometimes trials had to be shortened and sometimes they lasted much longer due to maintenance and repairs of the ape enclosures (see examples in Chapters 3, 4 and 5).

Thus, it could be possible that the chimpanzees and orangutans did not perform the target behaviours during the baselines due to time constraints. This possibility is however unlikely. Although most individuals interacted with the testing apparatuses in each trial, the number of interactions decreased as the experiments progressed. This reduction in the interaction frequencies suggests that the individuals started to become familiar/bored with the testing materials and progressively reduced their explorative behaviours. In other words, the motivation of the individuals started to decrease. In order to increase the length of the conditions, I would have had to add more trials or to extend the duration of each trial. Regarding the first option, it is debatable if adding even more trials to each condition would have increased the likelihood of finding the target behaviours, as the motivation levels were already decreasing with three trials per condition. However, in those cases where interaction frequencies did not decrease (Chapter 4) or the apes showed promising behaviours such as sticking the core with the hammers (Chapter 5), the number of trials was increased (generally by one) to increase the possibilities of finding the target behavioural forms. Regarding the extension of trials, this option could not have been implemented because it would have involved, during individual tests, keeping the apes isolated for long periods of time, which could have potentially compromised their welfare.

A potential improvement on the testing methodology used here would be to alternate test trials with motivational trials that would increase the interest of the subjects on the testing materials (Bandini et al. in press). Motivational trials might include small tests (such as a memory task) that the subjects can easily solve and be rewarded for. These trials would have to be designed to ensure that no additional information about the target behaviours would be unintentionally provided.

4.3 Sample sizes

One other potential limitation of the studies presented here is that the number of individuals tested was relatively small. In Chapter 3, seven chimpanzees were initially tested, and only four completed all experimental conditions. Yet, although limited in absolute numbers, this is the largest sample size ever used to test the abilities of great apes to learn sharp-edged stone tool production and use. Indeed, all published previous great ape knapping studies only included one (Wright, 1972) or two individuals (Schick & Toth, 2006). Only one unpublished study (Bandini, 2018) tested chimpanzees housed at an African sanctuary (N=4) in a similar task to the one used here (Chapters 3) following (among other experimental conditions) the extended baseline methodology. Similar to the findings presented in Chapter 3, Bandini found that none of the tested chimpanzees learnt to make or use sharp-edged stone tools neither individually nor socially even when full demonstrations by a human were provided. Therefore, the negative results regarding the spontaneous abilities of chimpanzees to produce and use sharp-edged stone tools are consistent across eleven individuals and two facilities (Bandini et al., under review). Although it is always problematic to provide evidence of the absence of a behaviour because the possibility always remains that the next individual tested shows the behaviour, the probability that we did not find the target behaviours with our sample size, was very low. We estimated this probability using the findings of the only previous study that tested unenculturated primates for their ability to spontaneously produce and use stone tools (Westergaard & Suomi, 1994a). This study found that 55% of the tested capuchin monkeys (6/11 monkeys) spontaneously produced sharp-edged stone tools when presented with the materials necessary to perform the behaviour (e.g. stones of different sizes; see also above). If this incidence rate is extrapolated to chimpanzees, the probability that we would not find a single case of spontaneous stone tools production in our combined sample size of eleven individuals would be smaller than 0.001 (Figure 3 and Bandini et al., under review). Therefore, it is very unlikely that the target behaviour was present in the tested chimpanzee population but we did not detect it with our experiments.

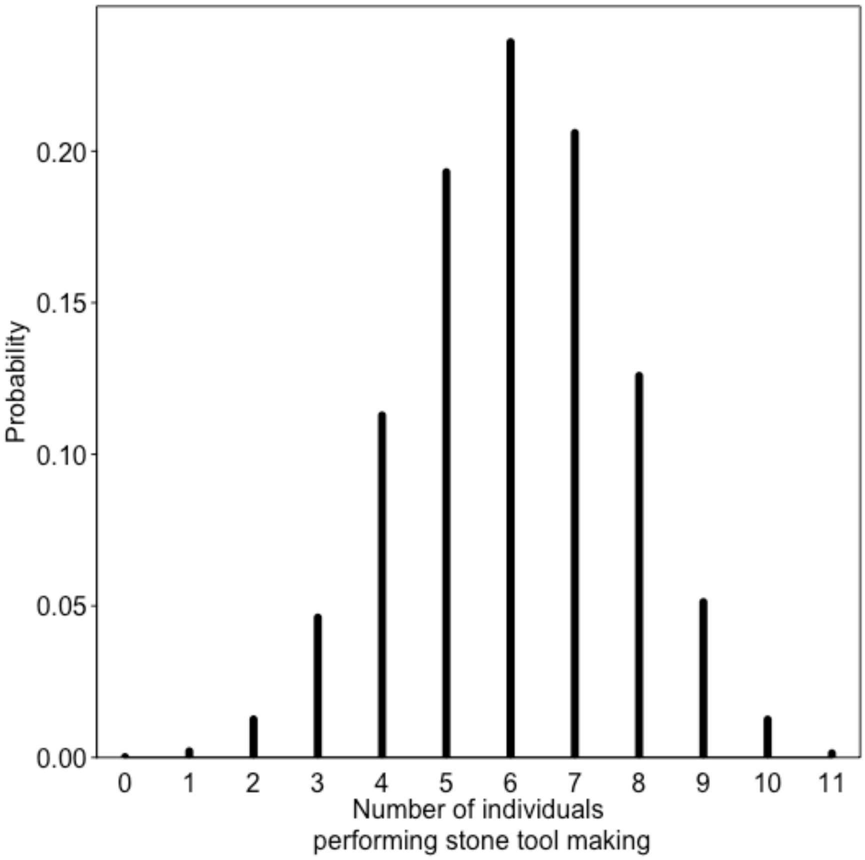


Figure 3: Probabilities of finding different numbers of individuals performing sharp-edged stone tool making behaviour with a sample size of eleven (Bandini et al., under review) based on the incidence rate reported by Westergaard & Suomi (1994a).

We extrapolated the incidence rate from capuchins to chimpanzees based on the fact that both populations were captive and unenculturated. Furthermore, both of these species similarly engage in percussive behaviours in the wild that involve the use of stones (nut cracking, Visalberghi et al., 2015) and sometimes unintentionally produce sharp-edged stones in the wild as a by-product of percussive activities (Proffitt et al., 2016; Mercader et al., 2002).

In Chapter 4, the results of the experiments testing the stone tool making and using abilities of two orangutans are reported. In this case, despite the small sample size (N=2), positive results were found regarding sharp-edged stone tool use and stone tool making. Similarly, in Chapter 5, despite only testing three adult orangutans and two infants, positive results were found. Therefore, although it would be interesting to test more orangutans in order to draw conclusions at the species level and to study which factors influence the emerge of sharp-edged stone tool making and using abilities in this species, our sample size proved sufficient to show that the unintentional production of sharp-edged stones and the use of human-made flakes as cutting tools is within the cognitive reach of orangutans (as at least one individual could perform these behaviours, Bandini & Tennie, 2017).

Regarding the social acquisition of sharp-edged stone tool making by chimpanzees, it was found that none of the 13 chimpanzees tested learnt to perform the demonstrated behaviours after social demonstrations. Taken together, the study presented in Chapter 5 and Bandini (2018) tested the abilities of a sample of 16 chimpanzees from two institutions to produce and use stone tools after observing social demonstrations.

Although bigger sample sizes allow to obtain more robust conclusions (specially about negative results, ManyPrimates et al., 2019), finding great ape populations where experimental studies can be conducted is always challenging. Despite this fact, the great ape studies presented in this thesis include the largest samples tested in sharp-edged stone production studies. In addition, the samples tested proved sufficient in orangutans (where positive results were obtained) and were arguably sufficient in the case of chimpanzees to shed meaningful negative results.

4.4 Testing institutions

The experiments reported in this thesis took place in two institutions: Kristiansand zoo in Norway and Twycross zoo in the UK. Tests needed to be conducted in captivity to be able to provide the testing materials to the chimpanzees and orangutans and to control for the naivety status of the subjects. We changed the test populations that participated in the baselines and the demonstration conditions in order to control for so-called carryover effects from previous experiments. After conducting the baseline conditions and the exchange experiments in Kristiansand zoo, some of the individuals tested there (the orangutans) had already performed some of the target behaviours (sharp-edged stone use and production). Therefore, in order to test the effect of social demonstrations on the emergence of the target behaviours, it was necessary to test naïve populations in which the target behaviours were not present. Consequently, we conducted the demonstration experiments for chimpanzees and orangutans at Twycross zoo. Due to time limitations we could not conduct additional baseline conditions with the chimpanzees and orangutans at Twycross, which would have helped interpret the results from the demonstrations experiments (Chapter 5). However, we did have some previous information on the percussive behaviour of the apes housed at Twycross zoo.

One previous study had applied the extended baseline methodology (Chapter 1) to investigate the abilities of the chimpanzees housed at Twycross zoo to learn nut-cracking behaviour (Neadle et al, 2020). Neadle et al. (2020) conducted both baseline and social conditions to test if the chimpanzees could individually or socially learn how to crack open nuts using wooden anvils and hammers. Despite the considerably large sample size (N=13), no chimpanzee ever attempted to crack a nut with the materials provided and no percussive activities ever took place. Therefore, using the study by Neadle and colleagues as a behavioural baseline, it was determined that the chimpanzee population did not spontaneously engage in percussive activities before the onset of the experiments (Neadle et al., 2020).

Regarding the orangutans housed at Twycross zoo, no previous study had tested their spontaneous percussive abilities and therefore, no baseline was available for this population (a baseline was conducted for the orangutans at Kristiansand, Chapter 4). Ideally, a behavioural baseline would have also been conducted at Twycross, but due to time limitations, only the demonstration experiments could be conducted. Consequently, it is difficult to directly determine how much of the behaviour performed by the orangutan that engaged in percussive activities after seeing human demonstrations of how to make and use sharp-edged stone tools was performed spontaneously and how much was elicited by the social demonstrations (Chapter 5). Nevertheless, it is important to note that the two orangutans tested in Kristiansand (Chapter 4) never used the hammers to strike the fixed core whereas the orangutan at Twycross performed this behaviour 15 minutes into her first trial after having seen 27 demonstrations (Chapter 5). The finding that the orangutan at Twycross (but not those at Kristiansand) performed percussive actions on the core after seeing social demonstrations, suggests that some social learning mechanism might have played a role in the emergence of this particular behavioural variant that involved striking the exposed area of the core. However, it would be necessary to test more individuals in order to unravel which social learning mechanism in particular led to the performance of this behavioural variant.

Finally, two of the adult orangutans that were tested at Twycross zoo (Chapter 5) had dependent offspring with them in the testing room. Although these two females manipulated the testing materials, they never performed any percussive activities. These negative results stand in stark contrast to the younger female O5 (without offspring), who performed percussive actions in every trial (Chapter 5). This disparity could result from the mothers adapting their behaviour to the presence of the infants in order to not engage in any activity that could be potentially dangerous for them. Supporting this hypothesis, the mothers were observed in several occasions during the trials actively discouraging the infants from touching the testing materials by pulling them away (similar observations were made of the female orangutan with dependent offspring at Kristiansand zoo). Consequently, the fact that two of the test subjects in the study reported in Chapter 5 had dependent offspring could have affected their performance in the demonstration experiments.

4.5 Testing materials

Although the positive results obtained during the Flake condition (Chapter 4) represent a proof of concept regarding the spontaneous use of human-made flakes by orangutans, an open question remains on why the orangutans tested in the demonstration experiments did not use the provided flake (Chapter 5). The main difference between the set up of these two experiments (Chapters 4 and 5) was that in Kristiansand (Chapter 4), the juvenile orangutan could not manually open the hide box whereas in Twycross (Chapter 5), all adult orangutans could break open the membrane of the hide box. The fact that the box could be opened without a tool might have eliminated the most immediate motivation to use a flake as a cutting tool to access the food rewards contained inside the hide box. The hide box was transparent and represented a *direct* puzzle box in which the use of a cutting tool to break the membrane granted access to the food rewards directly. The tendon box on the other hand, was opaque and *indirect*, meaning that the use of a cutting tool to severe the rope did not grant direct access to the food rewards but instead led to the opening of the box's door, which then granted access to the food reward. Therefore the tendon box was a more indirect puzzle box. However, the fact that the hide box could be manually opened does not mean that the need for using a cutting tool completely disappeared in the demonstrations experiments reported in Chapter 5. The orangutans (at both facilities) could not open the tendon box manually or using their teeth, despite trying often to do so. Therefore, in every trial reported in Chapter 5 there was a baited box present (the tendon box) that required the use of a cutting tool to access a food reward.

Whether the apes included in the studies presented in this thesis (especially during the demonstration experiments where the hide box was opened manually; Chapter 5) understood the working mechanism of the tendon box is debatable (see also Bandini, 2018). A similar tendon box was used by Wright (1972) and Toth et al. (1993) to test the sharp-edged stone tool using abilities of enculturated orangutans and bonobos. All three enculturated apes previously tested with this box successfully managed to open it using a cutting tool. However, as mentioned above, the tendon box is an indirect box which functioning mechanism might prove to be too complex for unenculturated apes to solve even when demonstrations are provided.

It is thus possible that flake use did not emerge in the orangutan group housed at Twycross zoo because the more direct and transparent hide box could be manually opened and/or because the mechanism of the tendon box was too opaque. In future studies the hide box should be adapted to withstand the strength of adult individuals (especially adult orangutans). Although several modifications were applied to the original design of the hide box (the silicone membrane was substituted both by a nylon and vinyl membranes, the number of membranes used was increased from one to up to three and the attachment points of the membranes were reinforced by additional metal plates), none of these modifications proved efficient.

4.6 Human demonstrators

Another potential shortcoming of the demonstration experiments (Chapter 5) could have been the use of a human demonstrator instead of a conspecific. A human demonstrator was used due to the impossibility of training an orangutan and a chimpanzee to make and use stone tools in such a short time period. Furthermore, such extensive training is strongly discouraged by the zoos as it often involves very close contact between the apes and the experimenters, which is generally considered to be against health and safety protocols. Furthermore, the evidence in favor of using conspecific demonstrators over human demonstrators is not yet very clear. Some studies have shown that chimpanzees socially learn more readily when watching videos of conspecifics than videos of human demonstrators (Hopper et al., 2015). Yet other studies show that apes can be induced to express behaviours after watching demonstrations performed by human models (Ross et al., 2010; Toth et al., 1993). Therefore, there is no convincing evidence to date showing that human demonstrators are less effective than conspecifics (although this possibility remains open).

5. Learning mechanisms underlying other hominin tool behaviours

Most of the studies that have investigated how early hominins acquired technological behaviours have focused on stone tool production and use (e.g. Schick & Toth, 1994; Stout & Semaw, 2006; Stout et al., 2008; Stout et al., 2006; Tennie et al., 2017; Toth

& Schick, 2018). The interest in understanding how stone tool-related behaviours were learnt comes as no surprise given the abundance of lithic artefacts in archaeological assemblages and their ubiquitous presence across millions of years of human evolution (Ambrose, 2011). Indeed, this thesis has contributed to the efforts of numerous scientists across disciplines to advance our knowledge on the emergence of lithic technologies. However, in all likelihood, early hominins did not only make stone tools.

Bone tools have also been found in the archaeological record, dating as far back as 2 Ma (Brain & Shipman, 1993; d'Errico & Backwell, 2009). Bone tools consist of both unmodified bones and sharp bone fragments produced using hammerstones. Unmodified bones were supposedly used as tools to access underground storage organs of plant (USOs), termite and bee nests and to process encased fruit (Backwell & d'Errico, 2001; d'Errico & Backwell, 2009). The only study, to date, that aimed to investigate the emergence of bone tool behaviours using primates as models was conducted with capuchin monkeys in 1994. Westergaard and Suomi (1994b) found that three capuchins (*Sapajus apella*) from two different groups spontaneously used bone fragments as pounding tools to crack open nuts and as cutting tools to break through the membrane of a baited box (resembling the hide box used in the experiments presented in this thesis). With this experiment, Westergaard and Suomi (1994b) showed that these abilities can be individually learnt by uncneculturated capuchin monkeys without the need for observing behavioural demonstrations. Unfortunately, no such studies have been yet conducted assessing these abilities in great apes (but see Kitahara-Frisch et al., 1987) and thus, the phylogenetic inferences about early hominin bone tool behaviour that can be drawn from experimental studies are still limited.

In addition to bone tools, it has been long hypothesized that early hominins probably used tools made of other perishable materials, which generally did not last in the archaeological record (Backwell & d'Errico, 2001; d'Errico & Backwell, 2009). Much as great apes do today, especially chimpanzees, early hominins could have consumed insects as well as other food sources that did not require the use of stone tools. This hypothesis, strongly influenced by observations of primate tool making and use, has led to the novel discipline of "Archaeology of the perishable" (Pascual-

Garrido, 2018). This novel subfield investigates, using archaeological methods, past animal behaviour associated to the production and use of plant tools (Pascual-Garrido, 2018). By tracing the sources of chimpanzee plant tools, Pascual-Garrido has been able to infer transport distances, time since tool manufacture, sites of material sourcing, plant species and raw material preferences (Pascual-Garrido, 2018).

Regarding the learning mechanisms that underlay the acquisition of these plant tool behaviours, several studies have been conducted using great apes as phylogenetically relevant behavioural models. Lonsdorf et al. (2009) investigated the abilities of captive chimpanzees (N=7) and gorillas (N=13) to spontaneously retrieve a food reward from a recently built artificial termite mound using plant tools. In both species, at least the first subject that obtained the food rewards using plant tools, must have individually learnt how to perform the target behaviour without the need of observing a behavioural model. It must be noted however, that these results refer to a simpler behavioural form than that described in some wild populations. For example, in the Goualaougo triangle (DRC, Africa), chimpanzees employ tool sets (a sequence of different tools) in order to gather termites (Sanz et al., 2004), which differ depending on the structure of the nest (epigeal or subterranean). The learning mechanisms underlying the acquisition of these tool set sequences has not yet been investigated experimentally.

Another plant tool behaviour present in extant apes and human populations that has also been associated to early hominins is tool excavation of underground food sources (Laden & Wrangham, 2005). Purported digging sticks have been recovered from Neanderthal sites in Spain dating approximately 90 ka (Rios-Garaizar et al., 2018) and Italy dated to 171 k BP (Aranguren et al., 2018). In extant apes, two populations of wild chimpanzees have been described to use plant tools in order to excavate underground storage organs of plants during periods of food scarcity (Hernandez-Aguilar et al., 2007). These reports, however, were based on indirect evidence (e.g. footprints, half eaten tubers, feces, excavated holes and abandoned tools) and thus no direct observations of this behaviour have been made.

Several studies have investigated the learning mechanisms behind the acquisition of tool excavating forms testing captive primates. Westergaard and Suomi (1995a) investigated the spontaneous abilities of two groups of unenculturated, task-naïve captive tufted capuchin monkeys (N1=5, N2=5) to use sticks as excavating tools when presented with sticks and a container with buried food items under compacted soil. Individuals in both groups (N1=3, N2=1) used the sticks provided as excavating tools to obtain the buried food items. These results showed that tool excavation can be individually learnt in capuchin monkeys without requiring the observation of behavioural models. Roffman et al. (2015) conducted the first study on tool excavation in great apes. In this study two groups of bonobos (N1=8, N2=7, rearing background not reported) were presented with different raw materials (sticks and antlers) that they could use as excavating tools as well as buried food items under compacted soil and rocks. Roffman et al. (2015) found that bonobos in both groups individually learnt how to use tools of different materials to excavate in the absence of social demonstrations. Finally, together with others, I conducted a study investigating the excavating abilities of two groups of captive chimpanzees (N1=5, N2=4, one enculturated individual). Similarly to the previous studies, the chimpanzees were provided with tools that they could use to excavate in several locations in their outdoor enclosure where food had been previously buried under compacted soil (Motes-Rodrigo et al., 2019). As in the two previous studies, we found that chimpanzees in both groups spontaneously used the tools provided, as well as tools that they gathered themselves, to excavate the buried food items.

Taken together, the primate studies on tool excavation show that this behaviour can be individually learnt by naïve unenculturated subjects and that tool excavation is most likely a latent solution in capuchins, bonobos and chimpanzees. Therefore, it is parsimonious to infer that the same learning mechanisms that underlie the acquisition of tool excavation in extant *Pan* species (namely individual learning) also underlay the acquisition of this behavioural form (but not its frequency, Tennie et al., in press) in the last common ancestor between *Pan* and *Homo* 7 Ma.

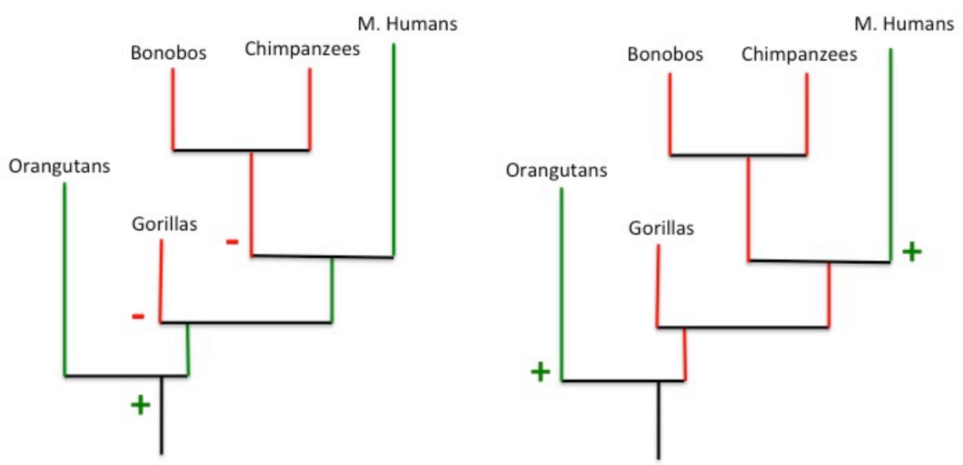
6. Conclusion

Identifying the learning mechanisms responsible for the emergence and sustenance of lithic technologies is a necessary step in order to elucidate which type of culture stone tool making and using hominins had. If sharp-edged stone tool production and use can only be learnt via the direct observation of a behavioural model and/or her products, this would imply that stone tool making hominins already possessed the learning abilities necessary to produce and sustain a copying-based culture such as the one present in modern humans. However, if stone tool behaviours can be spontaneously and individually learnt by naïve individuals who are not familiar with these behaviours beforehand, this would suggest that sharp-edged stone tool production and use are part of a non-copying based culture like that of extant great apes. Consequently the main goal of this thesis was to indirectly (via cognitive cladistics) investigate how early hominins could have learnt sharp-edged stone production and use by studying these abilities in our closest living relatives, the great apes.

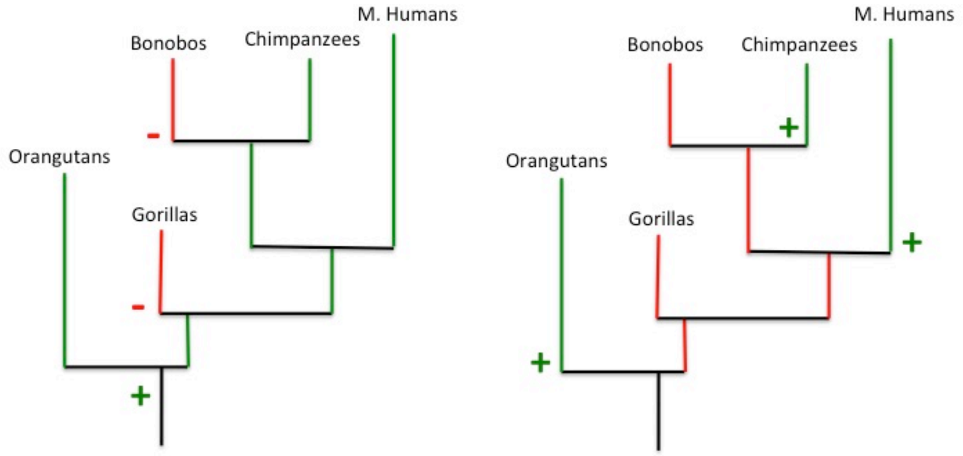
One of the premises of this research project was that great ape cultures are sustained by non-copying social learning mechanisms. However, despite being long suggested that great apes have a fundamentally different type of culture than modern humans do (e.g. Galef, 1992), this hypothesis had not been previously tested taking into account the full extent of great ape repertoires across behavioural domains and species. Therefore, the first step towards unraveling which cultural model stone tool making hominins had, was to assess which cultural model great apes have. To this end, the Method of Local Restriction was developed in order to indirectly detect evidence of copied behaviours by analyzing their pattern of presence and absence across great ape populations (Chapter 2). The rationale behind the Method of Local Restriction is that behaviours that are transmitted via copying must cumulate copying errors and innovations over time that must result in a large number of population-specific behavioural forms. Therefore, if great ape behavioural forms are copied, they should reflect this underlying learning process by being locally restricted (only appearing in one single population in a given form). After analyzing published reports of potentially population-specific behaviours in great apes across behavioural domains, I found that only seven behaviours are locally unique, i.e. they (currently) appear to occur in just one population of just one species. Given the rarity of these cases (incompatible with a widespread reliance of copying), great ape behavioural repertoires appear to be re-innovated by each individual as part of each species latent repertoire (Chapter 2). However, the frequency in which these re-innovations happen is likely under social control (Bandini & Tennie, 2017), explaining the presence of culture (but not cumulative culture) in apes (Tennie et al., in press).

After establishing that great ape culture differs from modern human culture in its underlying mechanisms, I investigated if and how modern great apes can learn sharp-edged stone tool production and use. The experiments conducted with chimpanzees and orangutans revealed that both species likely differ in their ability to learn behaviours related with sharp-edged stone tool production and use. The results of these experiments showed that orangutans can spontaneously use a human-made flake as a cutting tool (holding it with their mouth), spontaneously perform percussive actions and unintentionally produce sharp-edged stone tools as a by-product of percussive actions. Chimpanzees on the other hand, did not acquire stone tool making or using abilities neither spontaneously (Chapter 3) nor socially (although see Chapter 5 for two potential exceptions).

Based on these results, several scenarios are possible for the development of sharp-edged stone-related behaviours in hominoids (Figure 4). Given the abilities shown by orangutans, it is likely that the last common ancestor between orangutans and our lineage could also unintentionally produce sharp-edged stones as a by-product of percussive activities in other foraging contexts (Davidson, 2019; Panger et al., 2002). In addition, it is possible that this last common ancestor could also spontaneously use readily available flakes from anthropogenic (unintentional sharp-edged stones produced as a by-product of percussive activities) and/or non-anthropogenic origins (e.g. cliff falls; Barnes, 1939) as cutting tools. Some of these abilities were maintained, or evolved independently, in terrestrial great apes such as chimpanzees, which unintentionally produce sharp-edged stones as a by-product when cracking nuts, as well as in hominins. Why captive unenculturated chimpanzees do not (often) engage in percussive activities (Neadle et al., 2020; this thesis) but capuchins do is unclear. Lack of genetic predispositions or ecological requirements could be partly responsible for the absence of percussive behaviours in multiple captive chimpanzee groups, whereas some capuchin species might have strong genetic predispositions for stone or object manipulation (Hayashi, 2015). Similarly, the stone tool abilities shown by captive orangutans might not be expressed in their wild counterparts due to their high degree of arboreality, which reduces the possibilities and need of engaging in percussive foraging using stone tools.



Stone tool use



Unintentional stone tool production

Figure 4: Possible evolutionary scenarios resulting in the distribution pattern of sharp-edged stone tool use and unintentional sharp-edged stone production observed among great apes. Plus (+) symbols indicate the emergence of the trait whereas negative symbols (-) indicate the disappearance of the trait in the designated clade. The trees on the left represent evolutionary scenarios in which the last common ancestor of all

great apes presented the trait and it was subsequently lost (red lines) in some species. The trees on the right represent scenarios in which the last common ancestor did not present the trait but it converged (the same behaviour independently evolved) in several species (green lines).

The results presented in this thesis suggest that different learning mechanisms underlay the acquisitions of different behaviours that probably preceded the intentional production of sharp-edged stone tools: some suggested prerequisites for the emergence of intentional knapping (percussive activities that unintentionally produce sharp-edged stones and use of readily available sharp-edged stones for cutting) can be individually learnt and might have been present in hominoids 13 Ma. The intentional production of sharp-edged stones to be used as cutting tools, likely evolved much later after the split of *Homo* and *Pan* 6 Ma. Possibly, these abilities emerged when the degree of terrestriality increased and the foraging niche expanded, including the exploitation of larger prey and processing of hard USOs (e.g. Marchant & McGrew, 2005). Given that the intentional production of sharp-edged stone tools does not emerge in unenculturated chimpanzees and orangutans even after social demonstrations, it is possible that the intentional production of sharp-edged stone tools represented the starting or crystallization point of copying-based cultures in our lineage.

7. Outlook

The results of this thesis provide further support for the hypothesis that unenculturated great apes do not spontaneously learn behavioural forms via copying social learning mechanisms. Indeed, the results of the meta-analysis conducted in Chapter 2 suggest that the vast majority of great ape forms across behavioural domains are in fact latent solutions acquired via individual learning mechanisms which frequency is catalysed via non-copying forms of social learning. To the best of my knowledge, only one study to date has reported spontaneous imitation in chimpanzees (Persson et al., 2017). Persson and colleagues studied the interactions that took place between captive chimpanzees in a zoo and the zoo visitors in order to identify potential imitative events. After conducting live observations, the authors' conclusion was that the chimpanzees imitated the actions performed by the humans at a similar rate that the humans imitated the chimpanzees. However, this study presented several limitations that might have confounded the results. First, the authors did not conduct video recordings of the interactions between the chimpanzees and the visitors, and therefore it is not possible to check the reliability of their observations or their data. Video recordings would have also allowed assessing if the chimpanzees really imitated the humans (chimpanzee imitation) or if in fact it was the humans who were performing behaviours previously expressed by the chimpanzees (human imitation). Second, the authors did not conduct a behavioural baseline in order to determine which behaviours were already within the chimpanzees' repertoire and thus they were familiar with. Determining if the chimpanzees already knew the supposedly imitated actions was a crucial step in evaluating the social learning mechanisms at play during these interactions (i.e. imitation would have involved the acquisition of novel behaviours). Due to these limitations, the study by Persson et al. (2017) needs to be replicated.

In order to investigate chimpanzees' imitative abilities and attempt to replicate the results by Persson et al., (2017), I (together with collaborators) have designed and written a registered report that has recently received in principle acceptance in the journal Royal Society Open Science. The aims of this registered report entitled "Evaluating the influence of action- and subject-specific factors on chimpanzee copying" are: 1) to assess if chimpanzees spontaneously imitate any actions performed by zoo visitors, (2) to test if human biases exist in perceiving that the chimpanzees imitate visitors even when action matching does not actually take place and to (3) assess if chimpanzees imitate actions performed by human demonstrators when tested individually. If enough evidence for imitation of demonstrated actions is found, we will further assess (4) if the rearing background influences chimpanzees' imitative abilities (following Tomasello et al., 1993), (5) if chimpanzees engage in contextual imitation of familiar actions, production imitation of unfamiliar actions or both (following Byrne & Tanner, 2006), (6) if actions are imitated depending on the actions being "anchored," (i.e., actions involving contact with the subjects body, Call, 2001), and finally, (7) if actions are imitated depending on the presence of an environmental effect (sound) or not – as sound reproduction can be done via emulation instead of imitation (following Tomasello et al., 1997). Our study will provide valuable data regarding the factors eliciting imitation (or failing to do so) in chimpanzees, which will, in turn, help interpret the results presented in this thesis.

Both archaeology and ethology face the limitation that they cannot ask questions directly to the subjects of their studies. Often, these fields conduct comparative research in order to draw phylogenetic inferences about how certain abilities evolved and under which evolutionary pressures they developed. However, comparative studies are especially powerful when they include a wide variety of species from different taxa. Thus, the line of research of this thesis is far from completed. A logical continuation of the work presented in this thesis is to test bonobos and gorillas (*Gorilla gorilla*) for their ability to spontaneously make and use stone tools. These experiments will produce valuable additional data that will help create a clearer picture of how sharp-edged stone tool behaviours evolved. Bonobos are (together with chimpanzees) our closest phylogenetic relatives and although they do not often use tools in the wild, their tool using abilities in captivity are similar to those of chimpanzees (Gruber & Clay, 2016). Only one previous stone tool project has been conducted with this species focusing of the sharp-edged stone tool making and using abilities of the enculturated bonobo Kanzi (Toth et al., 1993; Schick et al., 1999). Kanzi's half-sister (Panbanisha) and her two offspring were also later included in the project and they reportedly acquired knapping skills by observing human models. However no detailed accounts of the learning process were published. In addition, all individuals included in the abovementioned project were heavily enculturated, meaning that their results cannot be extrapolated to the species as a whole (Henrich & Tennie, 2017). Similar to bonobos, gorillas very rarely use tools in the wild (Breuer et al., 2005) but they often do so in captivity (e.g. Herrmann et al., 2008). Furthermore, the abilities of gorillas to make and use sharp-edged stones have never been tested before. Therefore, it would be interesting to determine if (similar to orangutans) bonobos and gorillas, which do not use stone tools in the wild, have the cognitive and physical abilities to make and/or use sharp-edge stone tools when the appropriate environmental affordances are present. Testing unenculturated naïve bonobos and gorillas who are not familiar with the target behaviour before the onset of the experiments will be an important contribution to understanding the development of stone tool making and using abilities in our lineage.

If we want to understand the cultural environment in which our hominin ancestors developed, we need to foster collaborative work between disciplines. Such interdisciplinary projects might include 1) primate studies (both in controlled, captive settings and in more ecologically-representative wild settings), 2) anthropological investigations of the learning mechanisms underlying the acquisition of behaviours across different human populations, 3) archaeological projects that can give us insights into the artefacts produced by early hominins and 4) modeling approaches in order to predict and identify patterns of variation in the abovementioned fields. I believe that only by considering together the advances from fields such as the ones outlined above, we will get closer to understanding the minds and cultures or our ancestors. I look forward to contributing to that endeavor in the years to come.

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Chapter 2 Supplementary Table 1: Compiled results of the studies that have reported gestural repertoires in great apes.

<table>
<tr><th>Species</th><th>Setting</th><th>Location</th><th>Total repertoire size</th><th>Total N of hours</th><th>N of subjects</th><th>N of groups</th><th>Repertoire size per group</th><th>N of hours per group</th><th>Idiosyncratic behaviors</th><th>Asymptote</th><th>Reference</th></tr>
<tr><td>Chimpanzee</td><td>captivity</td><td>Yerkes</td><td>17</td><td>~ 240</td><td>5</td><td>1</td><td></td><td></td><td></td><td></td><td>Tomasello et al., 1985</td></tr>
<tr><td>Chimpanzee</td><td>captivity</td><td>Yerkes</td><td>17</td><td>180</td><td>7</td><td>1</td><td></td><td></td><td></td><td></td><td>Tomasello et al., 1989</td></tr>
<tr><td>Chimpanzee</td><td>captivity</td><td>Yerkes</td><td>25</td><td>160</td><td>8</td><td>1</td><td></td><td></td><td></td><td></td><td>Tomasello et al., 1994</td></tr>
<tr><td>Chimpanzee</td><td>captivity</td><td>Yerkes</td><td>27</td><td>75</td><td>19</td><td>1</td><td></td><td></td><td></td><td></td><td>Liebal et al., 2004</td></tr>
<tr><td>Chimpanzee</td><td>captivity</td><td>Yerkes</td><td>30</td><td>240</td><td>11|9</td><td>2</td><td>23|20</td><td>120</td><td>5|4</td><td></td><td>Tomasello et al., 1997</td></tr>
<tr><td>Chimpanzee</td><td>captivity</td><td>Yerkes</td><td>38</td><td>815</td><td>28</td><td>NA</td><td></td><td></td><td>13</td><td></td><td>Call & Tomasello, 2007a</td></tr>
<tr><td>Chimpanzee</td><td>wild</td><td>Budongo</td><td>66</td><td>120</td><td>82</td><td>1</td><td></td><td></td><td>0</td><td>15h active gesturing</td><td>Hobaiter & Byrne 2011a</td></tr>
<tr><td>Bonobos</td><td>captive</td><td>Apenheul| Planckendael</td><td>20</td><td>245</td><td>4|3</td><td>2</td><td>19|13</td><td>140|105</td><td>3</td><td></td><td>Pika et al., 2005</td></tr>
<tr><td>Bonobos</td><td>wild</td><td>Wamba</td><td>68</td><td>1159</td><td>36|29</td><td>2</td><td>55|48</td><td>671|488</td><td>13</td><td>2000 gesture events</td><td>Graham et al., 2016; Graham PhD thesis</td></tr>
<tr><td>Gorillas</td><td>captivity</td><td>Apenheul| Howletts</td><td>33</td><td>195</td><td>7|6</td><td>2</td><td>32|29</td><td>105|90</td><td>3</td><td></td><td>Pika et al., 2003</td></tr>
<tr><td>Gorillas</td><td>captivity and wild</td><td>Basel|Zürich| La Valleé| Mbeli Bai</td><td>102</td><td>365-415</td><td>10|11|9|130</td><td>3</td><td>88|101|68|47</td><td>125-175</td><td>1</td><td>1200 gesture events</td><td>Genty et al., 2009</td></tr>
<tr><td>Orangutans</td><td>captivity</td><td>Leipzig| Zürich</td><td>44</td><td>160</td><td>7|9</td><td>2</td><td>36|38</td><td>70|90</td><td>4</td><td></td><td>Liebal et al., 2006</td></tr>
<tr><td>Orangutans</td><td>captivity</td><td>Twycross|Apenhaul|Durrell</td><td>62</td><td>>900</td><td>8|12|4</td><td>3</td><td>56|50|48</td><td>>300</td><td>1</td><td></td><td>Cartmill & Byrne, 2010</td></tr>
<tr><td>B Orangutans</td><td>wild</td><td>Sabangau</td><td>21</td><td>681</td><td>16</td><td>NA</td><td></td><td></td><td></td><td>not reached</td><td>Knox et al., 2019</td></tr>
</table>

Chapter 2 Supplementary Table 2: List of behaviours analysed. Type C includes behaviours that were reported as locally restricted by the Original reference but were later found in additional populations of the same or other species. Type B includes behaviours that are locally restricted in one population of one species (Original population) but also found in populations of other species (Other species). Type A (in bold) includes behaviours that are locally unique, meaning that they are only found in one population (Original population) of one species. N refers to the number of individuals reported performing a behaviour. When the number was not available, the number is referred as unknown.

The original reference is the study in which the behaviour was deemed population-specific. The name of the behaviour is the one used by the Original reference. The definitions of the behaviours are quoted from the Original reference and when a definition was not available, we defined the behaviour (indicated by *). Chimp/c= chimpanzee, S ora/o= Sumatran orangutan, B ora/o= Bornean orangutan, Bon/b= bonobo; W gor/g= Western Lowland gorilla; M gor/g= Mountain gorilla; sm= spider monkey; gi=gibbon; crm= crested macaques; Sp=species; G= gesture; T=tool; O=other; V=vocalization; ER= environment-related; FP= food processing

Type	Behaviour	Definition	Domain	Sp	N	Original reference	Original population	Additional population 1 (same species)	Reference 1	Additional population 2 (same species)	Reference 2	Other sp	Reference
C	Arm shake	Small repeated back and forth motion of the arm	G	Chimp	>1	Hobaiter & Byrne, 2011	Sonso (Uganda)	Leintal Zoo (Germany)	Motes-Rodrigo (pers. obs.)	Yerkes Primate Center (USA)	Liebal et al. 2004	gor, bon	g: Genty et al. 2009; b: Pika et al. 2003, M. Surbeck (pers. comm.)
B	Branch-hook	Branch used to hook branch	T	Chimp	unk	Whiten et al. 2001	Bossou (Guinea)					orang	Russon et al. 2009
C	Comb	Stem used to comb through hair	T	Chimp	unk	Whiten et al. 2001	Budongo Forest (Uganda)	Goualougo triangle (Republic of	Sanz & Morgan, 2007				

								Congo)				
C	Container	Object used as a container	T	Chimp	unk	Whiten et al. 2001	Gombe (Tanzania)	Arnhem Zoo (The Netherlands)	Takeshita et al. (1996)	Kristiansand Zoo (Norway)	Motes-Rodrigo (pers. obs.)	bon, orang	b: Gruber et al. 2010; o: Galdikas, 1982b
C	Drum other	Short hard audible contact of alternate palms against recipient's body	G	Chimp	>1	Hobaiter & Byrne, 2011	Sonso (Uganda)	Kanyawara (Uganda), Taï (Côte d'Ivoire)	Fröhlich et al. 2016	National Center for Chimpanzee Care (NCCC), Bastrop	S. Watson (pers. comm.)	gor, bon	g: Genty et al. 2009; b: M. Surbeck and C. Hobaiter (pers. comm.)
C	Feet shake (1)	Repeated back and forth movement of feet from the ankles	G	Chimp	>1	Hobaiter & Byrne, 2011	Sonso (Uganda)					gor	Genty et al. 2009
C	Foot present (2)	Sole of the foot is presented to the recipient	G	Chimp	>1	Hobaiter & Byrne, 2011	Sonso (Uganda)	Kanyawara (Uganda), Taï (Côte d'Ivoire)	Fröhlich et al. 2016			bon, orang	b: Graham PhD thesis; o: M. Fröhlich (pers. comm.)
C	Head butt	Head is briefly and firmly pushed into the body of the recipient	G	Chimp	>1	Hobaiter & Byrne, 2011	Sonso (Uganda)	Kanyawara (Uganda), Taï (Côte d'Ivoire)	Fröhlich et al. 2016	National Center for Chimpanzee Care (NCCC), Bastrop	S. Watson (pers. comm.)	gor, bon, orang	g: Genty et al. 2009; b: Graham et al. 2016; o: M. Fröhlich (pers. comm.)
C	Head stand	Signaller bends forward and places head on the ground	G	Chimp	>1	Hobaiter & Byrne, 2011	Sonso (Uganda)	Mahale (Tanzania)	Roberts et al. 2014			orang, bon	o: Cartmill & Byrne, 2007, 2010; b: Graham et al. 2016
C	Hide face	Face is hidden by the hands and/or arms	G	Chimp	>1	Hobaiter & Byrne, 2011	Sonso (Uganda)	Kanyawara (Uganda), Taï (Côte d'Ivoire)	Fröhlich et al. 2016			gor, bon, orang	g: Genty et al. 2009; b: M. Surbeck (pers. comm.); o: C. Fryns (pers.

													comm.)
C	Insect-pound	Probe used to mash insect	T	Chimp	unk	Whiten et al. 2001	Bossou (Guinea)	Chimfunshi Wildlife Orphanage (Zambia)	Bandini, 2018			bon	M. Surbeck (pers. comm.)
C	Inspect (3)	Break off leave audibly and turn it in hands	O	Chimp	>1	Roberts et al. 2014	Sonso (Uganda)	Budongo Forest (Uganda)	Nishida et al. 2010	Mahale and Gombe (Tanzania)	Nishida et al. 2010		
C	Leaf-brush	Leaf used to brush away bees	T	Chimp	unk	Whiten et al. 2001	Gombe (Tanzania)	Goualougo triangle (Republic of Congo)	Sanz & Morgan, 2007	Ngogo (Uganda)	Watts, 2008		
C	Leg swing (4)	Large back and forth movement of the leg from the hip	G	Chimp	>1	Hobaiter & Byrne, 2011	Sonso (Uganda)	Kanyawara (Uganda)	Fröhlich et al. 2016			gor, bon	g: Genty et al. 2009; b: Graham et al. 2016, M. Surbeck (pers. comm.)
A	**Liana scratch**	**Grasping a growing liana, pulling it downwards or sideways in order to hold the flexible stem taut, and then rubbing his body back-and-forth against the taut liana**	**T**	**Chimp**	**>1**	**Hobaiter & Byrne, 2010**	**Sonso (Uganda)**						
B	Nasal probe	Clear nasal pasage with stick	T	Chimp	2	Whiten et al. 2001	Mahale M (Tanzania)					capu	Haslam & Falotico, 2015

A	**Nest tying**	**Tie nest into trunk when no strong weight-bearing structures support the nests**	**ER**	**Chimp**	**unk**	**McLennan, 2018**	**Bulindi (Uganda)**						
B	Nipple stimulate	Press digit tip(s) against own nipple(s)	G	Chimp	>4	McGrew & Marchant, 2001	Mahale M (Tanzania)					bon	M. Surbeck (pers. comm.); de Waal & Lanting, 1997
C	Object in mouth approach	Signaller approaches recipient while carrying an object in the mouth (e.g. a small branch)	G	Chimp	>1	Hobaiter & Byrne, 2011	Sonso (Uganda)	Kanyawara (Uganda)	M. Fröhlich (pers. comm.)	Bossou (Guinea), Gombe (Tanzania), Taï (Côte d'Ivoire), Mahale (Tanzania), Kibale (Uganda)	As "Play start (invite play holding stem in mouth)"; Whiten et al. 1999	orang	M. Fröhlich (pers. comm.)
C	Pounce	Signaller displaces through the air to land quadrupedally on the body of the recipient	G	Chimp	>1	Hobaiter & Byrne, 2011	Sonso (Uganda)	Kanyawara (Uganda)	M. Fröhlich (pers. comm.)			gor, bon, orang	g: Genty et al. 2009; b: Graham et al. 2016; o: C. Fryns (pers. comm.)
B	Rub	Hand makes back-and-forth movement on another's body without losing contact	G	Chimp	>1	Roberts et al. 2014	Sonso (Uganda)					bon	M. Surbeck (pers. comm.)

C	Side roulade	Body is rotated around the headfeet axis while lying on the ground with horizontal displacement along the ground	G	Chimp	>1	Hobaiter & Byrne, 2011	Sonso (Uganda)	Leintal Zoo (Germany)	Motes Rodrigo (pers. obs.)	Chimfunshi Wildlife Orphanage (Zambia), Yerkes Primate Center (USA), National Center for Chimpanzee Care (USA)	K. Liebal and S. Watson (pers. comm.)	gor, bon	g: Genty et al. 2009; b: Graham et al. 2016; M. Surbeck (pers. comm.)
C	Spit water	Subject spits water at other to invite play	G	Chimp	>1	Tomasello et al. 1989, 1994; Pollick & de Waal, 2007 in Hobaiter & Byrne, 2011	Yerkes Primate Center (USA)	Kristiansand Zoo (Norway)	Motes Rodrigo (pers. obs.)				
B	Tap object	Movement of the arm from the wrist or elbow, with firm short contact of the fingers to the object (single/multiple)	G	Chimp	>1	Hobaiter & Byrne, 2011	Sonso (Uganda)					gor, bon, orang	g: Genty et al. 2009; b: Graham et al. 2016; o: Motes-Rodrigo (pers. obs.)
C	Touch self	Hand make contact with own body	G	Chimp	>1	Roberts et al. 2014	Sonso (Uganda)	Chester Zoo (UK)	Fletcher & Weghorst 2005			all great apes	Motes-Rodrigo (pers. obs.)
C	USO digging	Use sturdy plant part to dig up underground storage organs such as tubers	T	Chimp	unk	Kühl et al. 2019	Issa (Tanzania)	Kristiansand Zoo (Norway)	Motes-Rodrigo et al. 2019a	Bandafassi (Senegal)	Gaspersic & Pruetz, 2011		

C	Foam leaf body	Chewing leaves into pulp then smearing foam over body (selected parts chosen) until fur all wet	T	B Ora	>1	van Schaik et al. 2009	Sabangau (Borneo)	Leipzig Zoo (Germany), Dortmund Zoo (Germany)	Orangutans chewing leaves into their fur - not as foam, but in form of a knobble K. Liebal (pers. comm)		
C	Leaf scoop	Drinking water from ground or strem using leaf as vessel	T	B Ora	unk	van Schaik et al. 2009	Gunung Palung (Borneo)	Rehabilitants in Borneo	Russon et al. 2009	chimp	Sousa et al. 2009
C	Leaf-wipe	Wiping face with fistful of squashed leaves, then drop (in kiss squeak context)	T	B Ora	>1	van Schaik et al. 2009	Tanjung Putin (Borneo)	Suaq Balimbing (Sumatra)	Meulman PhD thesis	chimp	Whiten et al. 1999, 2001
C	Leave gloves (bite)	Use gloves to get into ants' nests (and avoid being biten)	T	B Ora	unk	van Schaik et al. 2009	Sabangau (Borneo)	Ketambe (Sumatra)	Meulman PhD thesis		
C	Lip smile (tense)	Sender opens its mouth slightly with the corners of the mouth pulled back and the teeth scarcely visible between the lips; teeth can be either closed or slightly	G	B Ora	2	Cartmill & Byrne, 2010	Apenhaul Zoo (The Netherlands)	Leipzig Zoo (Germany), Zürich Zoo (Switzerland)	Liebal et al. 2006 ("grin")		

		opened											
C	Moss cleaning	Cleaning hands with moss	T	B Ora	>1	van Schaik et al. 2009	Sabangau (Borneo)	Rehabilitants in Borneo	Russon et al. 2009				
C	Nail cleaning	Use small stick to clean under finger nail	T	B Ora	unk	van Schaik et al. 2009	Ketambe (Sumatra)	Rehabilitants in Borneo	Russon et al. 2009				
C	Poultice use	Chewing leaves and applying resulting poultice to wound	T	B Ora	unk	van Schaik et al. 2009	Sabangau (Borneo)	Rehabilitants in Borneo	Russon et al. 2009				
C	Pout	Sender protrudes its lips forming a round ‘trumpet’-like shape	G	B Ora	2	Cartmill & Byrne, 2010	Twycross Zoo (UK)	Leipzig Zoo (Germany), Zürich Zoo (Switzerland)	Liebal et al. 2006				
B	Tandem walk	Subject positions arm over the body of the recipient and both walk forward while maintaining position	G	B Ora	2	Cartmill & Byrne, 2010	Twycross Zoo (UK)					chimp, bon, gor	c: Hobaiter & Byrne, 2011; K. Solocombe and K. Liebal (pers. comm.); b: Graham et al. 2016; g: Genty et al. 2009; S. Massi (pers. comm.)
B	Tongue out	Protrude tonge*	G	B Ora	2	Cartmill & Byrne, 2010	Twycross Zoo (UK)					gor	C. Hobaiter (pers. comm.)
C	Tooth pick	Use a small stick to clean teeth	T	B Ora	unk	van Schaik et al. 2009	Ketambe (Sumatra)	Suaq Balimbing (Sumatra)	Meulman PhD thesis	Rehabilitants in Borneo	Russon et al. 2009	capu, chimp	cap: Haslam & Falotico, 2015; c: Gruber et al. 2010

C	Tree hole tool use	Using (twig) tool to poke into tree holes to obtain social insects or their products	T	B Ora	>1	van Schaik et al. 2009	Suaq Balimbing (Sumatra)	Rehabilitants in Borneo	Russon et al. 2009	capu	Mannu & Ottoni, 2009
C	Nest smack	Call type made during nest making	V	B Ora	>1	Wich et al. 2012	Tuanan (Borneo)	Rehabilitants in Borneo, Suaq (Sumatra)	Russon et al. 2009; C. Schuppli (pers. comm.)		
C	Throat scrape	Call type made by mothers to call infants	V	B Ora	>1	Wich et al. 2012	Tuanan (Borneo)	Tanjung Puting and Rehabilitants in Borneo	Russon et al. 2009		
A	**Harmonic uuh**	**Call type made by mothers to call infants**	**V**	**S Ora**	**>1**	**Wich et al. 2012**	**Ketambe (Sumatra)**				
A	**Grinding**	**Loud grinding of the teeth**	**V**	**S Ora**	**>1**	**Hardus et al. 2009**	**Ketambe rehabilitans in Sumatra**				
B	Dug Hole drinking	Dig a hole on edge of stream or bay with hand, wait for it to fill with water and then drink it*	ER	W Gor	unk	Robbins et al. 2016	Bai Hokou (Central African Republic)			chimp, orang	c: Nishida et al. 1999; o: Russon et al. 2009
B	Lap cover	Covering lap with vegetation during resting*	T	M Gor	unk	Robbins et al. 2016	Karisoke (Rwanda)			bon, orang	b: Hohmann & Fruth, 2003; o: Russon et al. 2009
A	**Mouth washing**	**Taking water into mouth, then moving it**	**O**	**W Gor**	**unk**	**Robbins et al. 2016**	**Bai Hokou (Central African**				

		back and forthwithin mouth before swallowing.					**Republic)**					
C	Nest reuse	Reusing actual nest	ER	W Gor	unk	Robbins et al. 2016	Moukabala (Gabon)	Kagwene (Cameroon)	(*Gorilla diehli*) Sunderland et al. 2009			
B	Shaking leaves	Shaking young tree leaves to clean off dirt*	T	W Gor	unk	Robbins et al. 2016	Moukabala (Gabon)				bon, chimp	b: M. Surbeck (pers. comm.); c: Nishida et al. 2010
A	**Tooth brushing**	**Rubbing fingers against teeth**	**O**	**W Gor**	**unk**	**Robbins et al. 2016**	**Bai Hokou (CAR)**					
C	Bite wrist + arm shake (=bite + arms shake on)	Biting wrist of one hand while shaking loosely the opposite arm (= biting other individual (usually its head) and shaking arms on the other's body)	G	W Gor	2(4)	Genty et al. 2009	Basel Zoo (Switzerland)	Bai Hokou (CAR), Mondika (CAR), Mongambe	S. Massi (pers. comm.)			
C	Lick hand	Licking palm of hand frantically and repetitively	G	W Gor	2	Genty et al. 2009	Basel Zoo (Switzerland)	Bai Hokou (CAR)	S. Massi (pers. comm.)			
C	Arm swing under with object (=arms swing with object)	Swinging arm back and forth from front of body to between legs while holding an	G	W Gor	4(3)	Genty et al. 2009	Basel Zoo (Switzerland)	Bai Hokou (CAR)	S. Massi (pers. comm.)		bon; chimp	b: Graham et al. 2016; M. Surbeck (pers. comm.); c: Hobaiter & Byrne, 2011

		object in hand (=swinging arms in front of body from one side to the other while holding object(s) in hand(s))										
C	Aimed throw	Animal throws sticks and branches at human observers and at conspecifics	T	Bon	unk	Hohmann & Fruth, 2003a,b in Pika et al. 2005	Lomako (DCR)	Wamba (DCR)	Graham PhD thesis		chimp, gor, orang	c: Hobaiter & Byrne, 2011; g: Genty et al. 2009; o: Knox et al. 2019
C	Arm up	One half bended arm is lifted, opening a sitting place at the performer’s side. A lateral embrace results when the partner accepts the offered place	G	Bon	5	de Waal, 1988 in Pika et al. 2005	San Diego Zoo (USA)	Wamba (DCR)	Graham et al. 2016		"arm raise": gor, orang. arm up: chimp	g: Genty et al. 2009; o: Cartmill & Byrne, 2010; c: de Waal, 1988
C	Branch clasp	When bon are grooming each other in trees, one or both individuals commonly hold onto branches	ER	Bon	>1	Hohmann & Frutz, 2003	Lomako (DCR)	LuiKotale (DCR)	M. Surbeck (pers. comm.)		chimp, orang (not when grooming)	K. Solocombe and C. Hobaiter (pers. comm.), Motes-Rodrigo (pers. obs.)

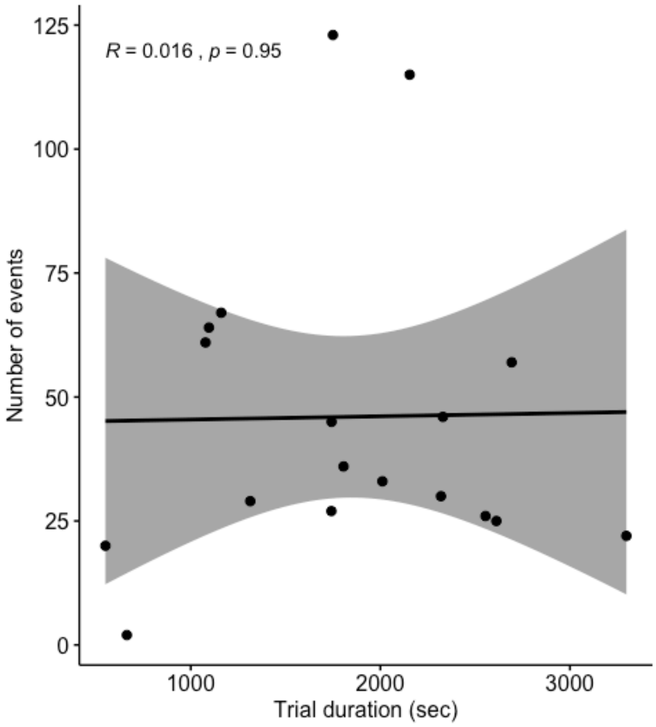
C	Branch din	When traveling on the ground, male bon often bend saplings or shrubs and then release them	ER	Bon	unk	Hohmann & Frutz, 2003	Lomako (DCR)	LuiKotale (DCR) and Kokolopori (DCR)	M. Surbeck (pers. comm.)		
B	Branch slap	Males and females slap noisily on either the branch supporting them or the tree's trunk	ER	Bon	>1	Hohmann & Frutz, 2003	Lomako (DCR)			gor, chimp	g: S. Massi (pers. comm.); c: Nishida et al. 2010 (maybe different)
B	Chest beat	Animal slaps repetitively on own chest with alternating open hands or knuckles	G	Bon	5	de Waal, 1988 in Pika et al. 2005	San Diego Zoo (USA)			gor, chimp	g: Genty et al. 2009; S. Massi (pers. comm.); c: van Lawick-Goodall, 1967, p. 128 sensu de Waal 1988; K. Liebal (pers. comm.)
C	Crouch	Quadrupedal posture with limbs flexed, hindquarters not turned towards another animal	O	Bon	unk	Kano, 1992, 1998 in Pika et al. 2005	Wamba (DCR)	LuiKotale (DCR) and Kokolopori (DCR)	M. Surbeck (pers. comm.)	chimp	K. Solocombe and K. Liebal (pers. comm.)
C	Duiker chase	Bonobos of both sexes occasionally lunge at a duiker (Cephalophus sp.)	ER	Bon	>1	Hohmann & Frutz, 2003	Lomako (DCR)	LuiKotale (DCR) and Kokolopori (DCR)	M. Surbeck (pers. comm.)	chimp	K. Solocombe (pers. comm.)
B	Fly whisk	Females	T	Bon	unk	Hohmann &	Lomako			chimp	Whiten et al.

		sometimes use small, leafy twigs to shoo away sweat bees from their genital swellings				Frutz, 2003	(DCR)					1999
C	Food rub	Take a fruit, hold it in the palm of one hand, and wipe the surface with the palm (or occasionally the back) of the other hand	FP	Bon	>1	Hohmann & Frutz, 2003	Lomako (DCR)	LuiKotale (DCR) and Kokolopori (DCR)	M. Surbeck (pers. comm)		gor	Neadle et al. 2017
A	**Fruit detachment with feet**	**Holding fast to a branch, she stepped on the fruit and pushed with her feet until the fruit became detached and dropped**	**FP**	**Bon**	**4**	**Hohmann & Frutz, 2003**	**Lomako (DCR)**					
B	Groom slap	A groomer may suddenly strike the groomee with a flat palm	G	Bon	>1	Hohmann & Frutz, 2003	Lomako (DCR)				"slap other": all great apes	see Hobaiter & Byrne, 2011 for references, S. Massi (pers. comm.)
C	Hand clasp	Groomers may lift a groomee's arm and hold the arm in this	G	Bon	>1	Hohmann & Frutz, 2003	Lomako (DCR)	LuiKotale (DCR)	M. Surbeck (pers. comm.)		chimp	McGrew & Tutin, 1978; K. Solocombe and K. Liebal (pers.

		position by clasping the hand of the groomee										comm.)
C	Hunch quadrupedal	Stand, walk, or run on all fours with rounded back and head pulled in between shoulders	O	Bon	unk	Nishida et al. 1999 in Pika et al. 2005	Wamba (DCR)?	San Diego Zoo (USA)	de Waal, 1988 (not reported in Wamba by Graham et al. 2016)			
B	Leaf clip	Ripping of leaves from ground vegetation or from trees	T/G	Bon	>1	Hohmann & Fruth, 2003	Lomako (DCR)				chimp	Nishida et al. 1999; K. Solocombe (pers. comm.)
C	Leaf-cover	Covers the ventrum of its body with several leafy twigs	T	Bon	>1	Hohmann & Frutz, 2003	Lomako (DCR)	LuiKotale (DCR)	M. Surbeck (pers. comm.)		gor, orang	g: Robbins et al. 2016; o: Russon et al. 2009
B	Leaf sponge	Individuals being groomed may lift an arm, probably to give better access to the groomer	T	Bon	unk	Hohmann & Frutz, 2003					chimp, orang	c: Whiten et al. 1999; o: Russon et al. 2009
C	Leaf strip	Individuals of both sexes tear leaves from saplings or branches	O	Bon	>1	Hohmann & Frutz, 2003	Lomako (DCR)	LuiKotale (DCR) and Kokolopori (DCR)	M. Surbeck (pers. comm. Might be slightly different)			
B	Lower head	Two animals face each other in social	G	Bon	unk	Nishida et al. 1999 in Pika et al.	Wamba (DCR)?				chimp, crested macaqu	c: Nishida et al. 1999; Hobaiter & Byrne, 2011

		grooming, and one partner flexes the neck to offer the top of head for grooming				2005					e, gibbons	and references within (present grooming); crm: K. Solocombe; gib: K. Liebal (pers. comm.)
C	Mock bite	Keep mouth wide open without the retraction of lips and press the teeth to the back, shoulder or other body part without biting	G	Bon	unk	Kano, 1992, 1998 in Pika et al. 2005	Wamba (DCR)	LuiKotale (DCR) and Kokolopori (DCR)	M. Surbeck (pers. comm.)		"bite": all great ape species; crested macaque	see Hobaiter & Byrne, 2011 for references; K. Liebal (pers. comm.); crm: K. Solocombe (pers. comm.)
B	Move hand and arm across body (3)	Move hand and arm across body*	G	Bon	unk	Savage & Bakeman, 1978 in Pika et al. 2005	Yerkes Primate Center (USA)				chimp	Roberts et al. 2014
C	Stick scratch	Break off a twig from a tree and use it to scratch her back	T	Bon	2	Hohmann & Frutz, 2003	Lomako (DCR)	Lola Ya Bonobo (DCR)	Gruber et al. 2010 ("self grooming using tools")		spider monkey orang	sm: Lindshield & Rodrigues, 2009; o: Russon et al. 2009
C	Stretch over	The arm is stretched and raised until about head level with the palm facing downward	G	Bon	unk	de Waal, 1988 in Pika et al. 2005	San Diego Zoo (USA)	Wamba (DCR)	Graham PhD thesis			
B	Teeth chatter	Rapidly grinding together the	G	Bon	3	Hohmann & Frutz, 2003	Lomako (DCR)				"teeth clacking":	K. Liebal (pers. comm.), Nishida et al. 2004

		upper and lower teeth rows									chimp	
C	Upside-down hanging	An individual hangs bottomup with hands grasping a branch and the legs, abducted at the hip, either slightly bent around the branch or hanging free with the knees touching the chest	O	Bon	5	Hohmann & Frutz, 2003	Lomako (DCR)	LuiKotale (DCR) and Kokolopori (DCR)	M. Surbeck (pers. comm.)			
B	Vegetation seat	Male and female bon sometimes bend small trees or shrubs to the ground and sit down on their leafy parts	tool	Bon	unk	Hohmann & Frutz, 2003	Lomako (DCR)				"seat sticks" chimp, gor, during nest building, orang	c: Hicks et al. 2019, C. Hobaiter (pers. comm.); g: S. Massi (pers. comm.); o: Russon et al. 2009



Chapter 4 Supplementary Figure 1: Pearson correlation between the number of events performed by the orangutans and the trial length.

Chapter 4 Supplementary Table 1: Individual flake exchanges during the two conditions and total number of exchanged flakes. In parenthesis is the proportion of flakes exchanged from those provided. "+2" indicates that the refitted flakes were also exchanged.

Individual	Familiarization	Trial 1	Trial 2	Trial 3	Trial 4	Total flakes exchanged
Loui	10 (100%)	6(100%)	6(100%)	6+2 (100%)	6+2 (100%)	38
Matthieu	10 (100%)	6(100%)	6+2 (100%)	6+2 (100%)	6+2 (100%)	40

Appendix: Building process of the artificial concrete hammers

(Pictures used with permission)

Plastic molds (bottom halves of milk bottles) of different sizes were used to shape the artificial concrete hammers. The bottom of the molds was covered with clay in order to give the hammers a rounded "potato-like" shape.

The hammers were built around metal structures with a central axis and several perpendicular nails branching out. In addition, and to strengthen the inside of the hammers, a metallic scaffold was built with metal wire.

After placing the metal structures inside the molds, these were filled with a concrete mix. The concrete mix normally used for construction is composed by 1 part of pure concrete and 4 parts of gravel or mixed concrete, sand and gravel. Here, to make the hammers as strong as possible we made a 1:2 mix of 1 part pure concrete and 2 parts mixed concrete, sand and gravel.
During the filling process, the molds were shook and hit against the floor to remove bubbles.

After filling the molds, the concrete was further mixed with a drill in order to remove the bubbles that could remain inside. Removing the bubbles was a necessary step as every bubble was a weak point where the hammer could fracture.

After removing the bubbles, the concrete was left to dry for 4 days in the sun.
After 4 days, the molds were cut off and the hammers were left to dry for one more week outdoors.