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Manipulation abilities among hominids: a multidisciplinary study with behavior, morphology and modelling

Ameline Bardo

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Mécanismes adaptatifs & évolution

UMR 7179, CNRS, MNHN / équipe FUNEVOL

Manipulation abilities among hominids: a multidisciplinary study with behavior, morphology and modelling

Par Ameline Bardo

Thèse de doctorat de Biologie interdisciplinaire

Dirigée par Emmanuelle Pouydebat

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Table of contents

RÉSUMÉ	11
CHAPTER 1 - GENERAL INTRODUCTION	13
CHAPTER 2 - DO BIMANUAL COORDINATION, TOOL USE AND BODY POSTURE CONTRIBUTE EQUALLY TO HAND PREFERENCES IN BONOBOBOS?	23
1. Introduction.....	26
2. Material and Methods.....	29
3. Results	33
4. Discussion	38
5. Conclusion	46
CHAPTER 3 - BEHAVIORAL AND FUNCTIONAL STRATEGIES DURING TOOL USE TASKS IN BONOBOBOS	49
1. Introduction.....	52
2. Material and Methods.....	54
3. Results	59
4. Discussion	73
5. Conclusion	81
CHAPTER 4 - ARE HUMANS UNIQUE? ARE GORILLAS AND/OR ORANGUTANS UNIQUE? WHAT MANUAL SPECIFICITIES EXIST FOR EACH SPECIES?	83
1. Introduction.....	85
2. Material and Methods.....	87
3. Results	94
4. Discussion	106
5. Conclusion	111

CHAPTER 5 - MORPHOLOGICAL VARIABILITY OF THE TRAPEZIOMETACARPAL COMPLEX AMONG HOMINIDS AND FUNCTIONAL INVOLVEMENT	115
1. Introduction.....	118
2. Material and Methods.....	121
3. Results	128
4. Discussion	137
5. Conclusion	144
CHAPTER 6 - BIOMECHANICAL ANALYSES OF THE CONSEQUENCES OF DIFFERENT HAND MORPHOMETRIC ON TOOL GRASP ABILITIES USING MUSCULO-SKELETAL SIMULATION: A PRELIMINARY STUDY.....	149
1. Introduction.....	152
2. Material and Methods.....	154
3. Results	159
4. Discussion	168
5. Conclusion	172
CHAPTER 7 – GENERAL DISCUSSION, CONCLUSION & PERSPECTIVES	175
1. General discussion.....	177
2. Conclusion	187
REFERENCES	191
ANNEXES	217
ABSTRACT.....	268

RÉSUMÉ

Au sein du règne animal, les humains sont considérés comme possédant des capacités manuelles uniques. Cependant, nous ne savons toujours pas quelles sont les réelles capacités manuelles des primates, ni comment elles ont évolué. Les humains sont-ils réellement uniques ? Cette thèse vise à étudier les capacités de manipulation chez des Hominidés en lien avec l'anatomie et la fonction de leur main, en utilisant une approche interdisciplinaire combinant différentes approches : comportementale, morphologique, fonctionnelle et biomécanique. Pour quantifier les stratégies comportementales et les capacités de manipulation chez des Hominidés, j'ai mené une étude éthologique sur différents grands singes captifs et sur les humains au cours d'une même tâche complexe d'utilisation d'outils. J'ai utilisé des approches comparatives de morphométrie géométrique 3D sur le complexe trapézio-métacarpien combiné avec un modèle musculo-squelettique pour mieux interpréter les résultats comportementaux et pour tester le lien entre la morphométrie de la main et les contraintes biomécaniques durant l'utilisation d'outils chez les Hominidés. Les résultats de cette thèse montrent que les grands singes manifestent des capacités dynamiques de manipulation, mais que chaque espèce a ses propres spécificités. Plus de capacités dynamiques complexes, comme les mouvements intra-manuels, sont observés pour les bonobos et les gorilles que pour les orangs-outans. Les différents modes de vie des espèces peuvent expliquer cette variabilité. En outre, au cours de la tâche complexe d'utilisation d'outils, les humains montrent une meilleure performance que les grands singes et montrent des spécificités. Cette nouvelle approche intégrative montre clairement aussi que les différentes capacités de manipulation des Hominidés ne peuvent pas seulement être une conséquence des différentes morphologies de l'articulation trapézio-métacarpienne, mais aussi des différentes contraintes mécaniques liées à la morphométrie globale de la main. Ces résultats mettent en évidence la difficulté de déduire les capacités manuelles d'espèces fossiles à partir de certaines informations provenant de la forme de l'os, sans tenir compte de la morphométrie globale de la main et de son lien possible avec les contraintes biomécaniques. Cette thèse fournit de nouvelles informations sur les capacités manuelles des Hominidés, sur les différentes contraintes entourant ces capacités, et de nouvelles informations afin de mieux comprendre l'évolution des capacités manuelles chez les primates.

Chapter 1 – General introduction

General introduction

We use our hands daily in diverse activities without really realizing the complexity of our actions in terms of grasping and manipulative abilities. Our hands are complex tools which allow us to interact with our environment for essential behaviors such as feeding, and also during creative activities such as painting. Since at least Darwin (1871), there has been a great interest in the evolution of the human hand and manipulative abilities. The twentieth century has been prolific in that field, especially on the anatomy and evolution of the primate hand thanks to two researchers: Frederick Wood Jones and John Russell Napier (e.g. Wood Jones, 1916, 1942; Napier, 1960, 1993; see Lemelin and Schmitt, 2016). This early research led to numerous other studies that have suggested a variety of hypotheses on the origins and evolution of grasping.

The main hypothesis suggests that grasping abilities in primates have emerged in the earliest primates from selection for effective navigation on fine branches in an arboreal niche (Cartmill, 1974, Bloch and Boyer, 2002) and that the manual abilities would have coevolved with bipedalism, tool-making and use (Figure 1), brain enlargement and laterality, and/or language in humans (Wilson, 1998). Humans are supposed to possess more complex manual abilities than non-human primates. Their manipulative skills are traditionally linked to specific morphological features, such as a long, mobile and powerful thumb, that are considered to be linked to stone tool-making (Napier, 1960; Marzke, 1997, Susman, 1998; Tocheri, 2008, Kivell, 2015). Humans differ from non-human primates and their extant relatives firstly by the fact that their hands do not have the double role for manipulative behavior and for locomotion (Napier, 1993). Indeed, non-human primates use their hand during different activities directly related with their environment, such as locomotion, foraging, manipulation of objects and interaction with conspecifics (Fragaszy, 1998). Secondly, humans appear to be the only species capable of applying large forces with a single hand when using precision grip involving the tips or pads of the fingers (Marzke, 1997, 2009; Marzke et al., 1992). This could be related to 1) their long thumb relative to the length of their fingers (Marzke and Marzke, 2000; Marzke, 2013), 2) their well-developed thumb muscles (Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012), and 3) the large range of movements at the first carpometacarpal joint (called also trapeziometacarpal joint) and

metacarpophalangeal joints (Taylor and Schwarz, 1955; Napier, 1962; Marzke, 1992, 1997; Marzke et al., 1998; Tocheri et al., 2008).

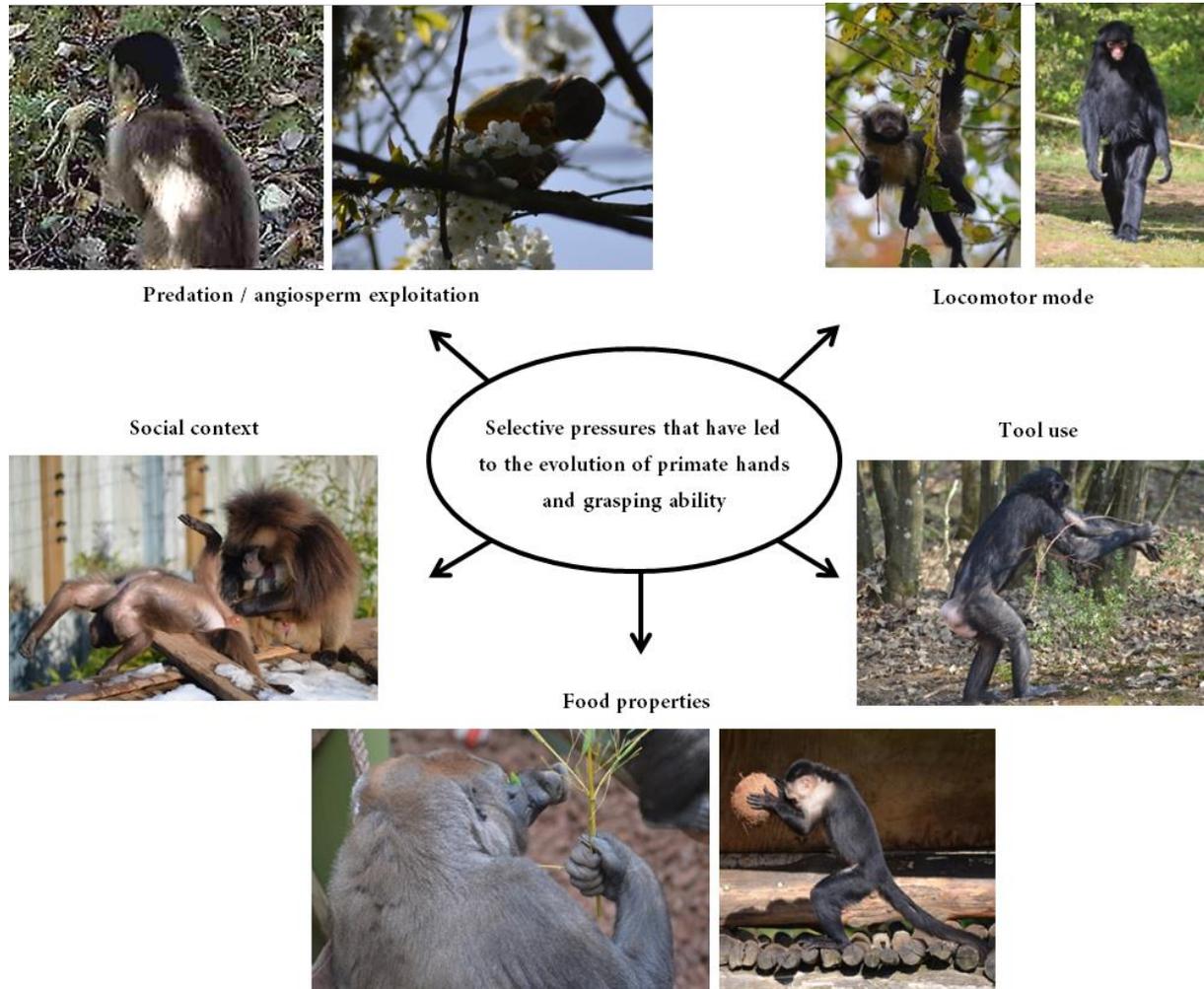


Figure 1. Pictures of different species of non-human primates during different behavioral activity contexts that have led to the evolution of primate hands and grasping ability. From left to right these pictures show: predation of a frog by *Sapajus xanthosternos* and angiosperm exploitation in tree by *Saimiri boliviensis peruviansis*; arboreal locomotion by *Sapajus xanthosternos* and terrestrial bipedalism by *Ateles paniscus*; grooming by *Theropithecus gelada*; tool use to recover a caterpillar by *Pan paniscus*; bimanual coordination to feed on leaves by *Gorilla gorilla gorilla* and coconut cracking by *Cebus capucinus*. Pictures ©A. Bardo and ©E. Pouydebat.

In this context, it has long been considered that humans have unique manual abilities in the animal kingdom. However, are humans really unique? It appears that there are similarities in manipulative abilities between humans and non-humans primates.

Firstly, other primates such as great apes and capuchins, when grasping static food, use various grasping postures, sometimes comparable to those used by humans, including the precision grip involving the tips of the thumb and index finger (Christel, 1993; Jones-Engels and Bard, 1996; Marzke and Wullstein, 1996; Christel et al., 1998; Byrne et al., 2001; Pouydebat et al., 2009, 2011). In addition, during captive experiments, an orangutan and a bonobo were able to make stone flakes, even though they do not possess a long thumb or other “tool-making” morphological features (Wright, 1972; Schick and Toth, 1993; Schick et al., 1999). Moreover, some tool-making features have been shown in non-human primates (e.g. Susman, 1998) and also in early fossil hominins (Almécija et al., 2010) who lived before the appearance of stone tools in the archeological record. Thus, it appears necessary to better understand the real manipulative abilities of non-human primates and to connect these abilities with specific morphological features.

Secondly, we know that the human population is predominantly right-handed (i.e., ~90%) (Annett, 1985; Perelle and Ehrman, 1994), which would correspond to a left hemisphere specialization for manual control (e.g., Broca, 1877; Annett, 1972). This phenomenon is thought to have played a prominent role in lateralization of human language (e.g., Warren, 1980; Ettlinger, 1988; Corballis, 1998; Crow, 2004) and the emergence of other cognitive functions such as tool use (e.g., Kimura, 1979; Gibson and Ingold, 1993; Preston, 1998), manual gestures (Kimura, 1973a; Hopkins and Leavens, 1998; Rizzolatti and Arbib, 1998; Corballis, 2003; Pollick and de Waal, 2007), and throwing (Calvin, 1983; Hopkins et al., 1993, 2005b; Colell et al., 1995). Non-human primates also show hand preferences (e.g. Hopkins et al., 2011; for a review, see Papademetriou et al., 2005) but such a bias of 90% for the right hand has never been observed in any other species of primate (Vallortigara and Rogers, 2005). Thus, the origin of human hand preference remains unclear and is thought to be linked to the ability to execute complex tasks (Fagot and Vauclair, 1991; MacNeilage et al., 2009) and habitual bipedalism (Hopkins, 1993; Hopkins et al., 1993; Westergaard et al., 1998a; Chapelain et al., 2006; Westergaard et al., 1997). This led Kimura (1979) to suggest that both tool use (considered a complex task) and bipedalism contributed to the emergence of the lateralization of the brain, particularly the strong right hand preference in humans. However, it is unclear if the effects of task complexity and bipedalism are independent,

additive, or interactive. Finally, it remains unknown which of these two parameters, or both, induces a right or a left hand preference. A combined approach would help us to understand the respective implication of both parameters in the evolution of laterality and the emergence of the right hand bias in humans.

Thirdly, dynamic aspects of human manual function are well described (Exner, 1992; Santello et al., 1998; Braido and Zhang, 2004; Bullock and Dollars, 2011) and a detailed taxonomy of the various forms of in-hand movements is available (Elliot and Connolly, 1984). In-hand movements are defined as “coordinated movements of the digits to manipulate an object within the hand” (Elliot and Connolly, 1984: 284). However, though dynamic abilities are known in humans, our knowledge is lacking for non-human primates. Indeed, non-human primates manual abilities are mainly known from static grip posture studies, whereas studies on dynamic manual abilities are scarce (e.g. Byrne et al., 2001; Crast et al., 2009; Marzke et al., 2015). Crast and collaborators (2009) showed that captive chimpanzees (*Pan troglodytes*) use in-hand movements to reposition various objects in their hand. Moreover, among great apes, dynamic manual abilities were investigated mainly in chimpanzees (e.g. Boesch and Boesch, 1993; Marzke and Wullstein, 1996; Crast et al., 2009; Marzke et al., 2015), sparse studies focused on gorillas (*Gorilla sp.*) (e.g. Byrne et al., 2001) and data are lacking for bonobos (*Pan paniscus*) and orangutans (*Pongo sp.*). In addition, as manual abilities and function in primates are hypothesized to have coevolved with tool-making and use (e.g. Wilson, 1998), it appears necessary to explore tool manipulation in primates to understand the evolution of this behavior in relation to hand morphology. While wild chimpanzees and orangutans (*Pongo sp.*) use different tools in a variety of contexts (chimpanzees: Goodall, 1968; orangutans: van Schaik et al., 1996; Fox et al., 1999; Bentley-Condit and Smith, 2010; McGrew, 2010; Meulman and van Schaik, 2013), there are only two reported examples of tool use in wild gorillas for two individuals (*Gorilla gorilla sp.*: Breuer et al., 2005; Kinani and Zimmerman, 2014) and only few are reported in wild bonobos (*Pan paniscus*: Hohmann and Fruth, 2003). Thus, it seems important to explore tool manipulation in primates with a focus on less known species such as bonobos and gorillas. Great apes possess different hand morphology (Schultz, 1930) and they have different lifestyles, more terrestrial for gorillas, highly arboreal for orangutans and a mix of terrestriality and arboreality for *Pan* (bonobos and chimpanzees) (Fleagle, 1988). The exploration of the manual abilities of these species could help us to infer how our early ancestors may have balanced the functional requirements for both arboreal locomotion and tool-related behaviors.

In this context, it is not easy to recount the evolution of the manipulative abilities in primate taxa and we need to better understand the real manipulative abilities in extant primates, and to investigate hand anatomy and function in these species. Focusing on Hominids (*Homo*, *Pan* with chimpanzees and bonobos, gorillas, orangutans, and their extinct relatives; Diogo and Wood, 2012) seems important in order to understand the evolution of manipulative abilities in humans. Several methodological approaches are available to examine manipulative abilities in Hominids.

New methodologies, such as biomechanical studies, three-dimensional scanning and microtomography have allowed more informed inferences of manipulative abilities in early humans (Kivell, 2015). Feix et al. (2015) created a kinematic model of thumb and index precision grip and movement based on a broad sample of extant primates and fossil hominins, allowing showing the manipulation workspace for precision grip in relation to the bones of the hand. They showed that joint mobility and finger proportions are essential for determining the potential of precision grip and manipulation but also that having a long thumb or great joint mobility alone does not necessarily provide high dexterity. Moreover, they showed that *Australopithecus afarensis* and *Australopithecus sediba* could have the potential to use precision grip like modern humans. This result supported previous interpretations of increased dexterity in *Australopithecus* (e.g. Kivell et al., 2011) and recent archeological evidence of tool-related behavior before *Homo* (Harmand et al., 2015).

New three-dimensional scanning methodologies have provided more comprehensive functional analyses of bone morphology, by quantification of form that is not possible using traditional methods such as linear measurements (e.g. Tocheri, 2007; Tocheri et al., 2003, 2005; Marzke et al., 2010; Orr et al., 2010). This method was used for example by Tocheri and colleagues to quantify the carpal joints surfaces of hominins (Tocheri et al., 2003, 2005; Tocheri, 2007) and showed that the radial side of the wrist in later hominins (modern humans, Neandertals) is extremely unique in its placement of the bones at the base of the thumb compared to that of the apes and more primitive hominins. This result showed biomechanical advantages for load transmission in radio-ulnar direction of the wrist during powerful pollical grasping and thus during stone tool use and manufacture. Marzke and colleagues (2010) used a sophisticated mathematical modeling with a 3D approach to model the curvature of the trapeziometacarpal joint surface (between the carpal bone of the trapezium and the first metacarpal) among hominins and other primates. The trapeziometacarpal joint, which is saddle-shape, permits opposition of the thumb with other fingers (Napier, 1952,

1956). Marzke and colleagues (2010) showed that though apes and other catarrhines have a saddle-shape joint like humans, but non-human primates differ from humans in the degree of curvature of this joint. This feature seems to be derived for humans relative to apes and in *Australopithecus afarensis*, the saddle-shape of trapeziometacarpal joint surface is flatter in the dorsopalmar and radioulnar direction (Marzke et al., 2010). This hand morphology might facilitate forceful precision and power gripping during human's manipulative activities (Marzke et al., 2010). However, to understand the exact functional consequences of different carpal shapes and joint surfaces, we need to both work on functional and morphological data during various manual activities.

Finally, different hand grips in primates can be attributed, for example, to different hand morphologies (e.g. Marzke and Wullstein, 1996), different muscular anatomy (Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012) or social influences such as social learning (Whiten and Ham, 1992). Indeed, the hand of great apes compared to other primates has long and curved fingers and a proportionally short thumb that could limit the pad to pad contact in thumb opposition (e.g. Napier and Napier, 1967; Marzke and Wullstein, 1996). Additionally, the differences between humans and great apes could be due to the absence of several anatomical features. In fact, some human hand muscles such as the *flexor pollicis longus* and the *extensor pollicis brevis* which are related to the movement of the thumb are not present or not independent in the hands of great apes, except hylobatids (Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012). However, we don't really know the muscular constraints required to grasp an object for non-human primates because studies on their muscles activities are extremely scarce (e.g. macaques, Overduin et al., 2008) in contrast to the number of studies on humans (Vigouroux et al., 2011; Goislard de Monsabert et al., 2012). New methods such as modeling would be very useful to develop a musculoskeletal model based on ape morphological (e.g. size of the segments) and biomechanical data (e.g. force, kinematics, and muscle activities) as is available in humans (see Fernandez et al., 2016).

The scientific background on manipulative abilities in primates is rich. However, many questions are still unresolved. Developing new methodologies in an interdisciplinary framework by combining behavioral, morphological, functional and biomechanical approaches seems essential to answer many questions. This dissertation is developed in this context, and the principal research questions of this work can be summarized as followed:

What are the real manual abilities of Hominids?

Do humans really have unique manual abilities? And if yes, why?

Which morphological and mechanical parameters are associated with these manual abilities?

To answer these questions, I used an interdisciplinary approach combining ethology, functional morphology and modeling. I studied hand preference, performance, cognitive abilities and manual abilities. I specifically focused on dynamic manual abilities during complex tasks in bonobos (chapters 2 and 3) and humans, gorillas and orangutans (chapter 4), on the two bones at the base of the thumb (the trapezium and the first metacarpal) in Hominids by a three dimensional shape analysis (chapter 5), and on the influence of Hominids hand morphology on biomechanical constraints during the same grip techniques (chapter 6). Chapters 2 and 3 focused on bonobos (*Pan paniscus*) because they are closely related to humans with respect to phylogeny, sharing 98.4% of their coding DNA sequences (Wildman et al., 2003), and are often bipedal, like chimpanzees (*Pan troglodytes*; Doran, 1993; Videan and McGrew, 2001, 2002; D'Août et al., 2004), making them an excellent model. The general discussion of my doctoral dissertation combines all the results of these different questions and aims to draw the relationship between behavior, functional morphology, biomechanics, and ecology in primates (diet, locomotor modes) in order to discuss their implications on primate evolution.

Composition of this dissertation

This dissertation is organized in seven chapters including this general introduction followed by five chapters written as scientific articles, both published (chapters 2 and 3), one submitted (chapter 4), and two in preparation (chapters 5 and 6), and ends by the general discussion, conclusions, and perspectives for future investigations on this subject.

Chapter 2. Evolution of hand preference according to body posture and task complexity in bonobos (*Pan pansicus*).

Chapter 3. Behavioral and functional strategies during tool use tasks in bonobos.

Chapter 4. Are humans unique? Are gorillas and/or orangutans unique? What manual specificities exist for each species?

Chapter 5. Morphological variability of the trapeziometacarpal complex among Hominids and functional involvement.

Chapter 6. Biomechanical analyses of the consequences of different hand morphometric on tool grasp abilities using musculo-skeletal simulation: a preliminary study.

Chapter 7. General discussion, conclusion & perspectives.

In the annexes I have added the original published articles derived from my thesis work and for which I am the first author. In addition, in the annexes the different abstracts and posters I presented during several congress in the course of my PhD are listed.

Chapter 2 – Do bimanual coordination, tool use and body posture contribute equally to hand preferences in bonobos?

Do bimanual coordination, tool use and body posture contribute equally to hand preferences in bonobos?

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ABSTRACT

Approximately 90% of the human population is right-handed. The emergence of this hand preference in humans is thought to be linked to the ability to execute complex tasks and habitual bipedalism. In order to test these hypotheses, the present study explored, for the first time, hand preference in relation to both body posture (seated and bipedal) and task complexity (bimanual coordination and two tool use tasks of different complexity) in bonobos (*Pan paniscus*). Few studies have explored the effects of both posture and task complexity on handedness, and investigations with bonobos are scarce, particularly studies on tool use. Our study aims to overcome such a gap by addressing two main questions: 1) Does a bipedal posture increase the strength of hand preference and/or create a directional bias to the use of the right hand? 2) Independent of body posture, does task complexity increase the strength of the hand preference and/or create a directional bias to the use of the right hand? Our results show that independent of body posture, the more complex the task, the more lateralization occurred. Moreover, subjects tended to be right-handed for tasks involving tool use. However, posture had no significant effect on hand preference in the tasks tested here. Therefore, for a given task, bonobos were not more lateralized in a bipedal posture than in a seated one. Task complexity might thus have contributed more than bipedal posture to the emergence of human lateralization and the preponderance of right-handedness, although a larger sample size and more data are needed to be conclusive.

1. INTRODUCTION

Laterality, defined as the functional dominance of one side of the body relative to the other, has been studied primarily in humans (*Homo sapiens*). Broca (1877) studied the relationships between language disorders and brain damage, and was the first to reveal hemispheric functional specialization of the human brain. Moreover, the link between cortical asymmetry and manual asymmetry was established very early in humans (e.g., Broca, 1877; Annett, 1972) and has been confirmed in other vertebrates (Marchant and Steklis, 1986; Bradshaw, 1991; Hopkins and Morris, 1993; Bisazza et al., 1996).

The human population is predominantly (i.e., ~90%) right-handed (Annett, 1985; Perelle and Ehrman, 1994), which would correspond to a left hemisphere specialization for manual control. This phenomenon is thought to have played a prominent role in lateralization of human language (e.g., Warren, 1980; Ettliger, 1988; Corballis, 1998; Crow, 2004) and other cognitive functions such as tool use (e.g., Kimura, 1979; Gibson and Ingold, 1993; Preston, 1998), manual gestures (Kimura, 1973a; Hopkins and Leavens, 1998; Rizzolatti and Arbib, 1998; Corballis, 2003; Pollick and de Waal, 2007), and throwing (Calvin, 1983; Hopkins et al., 1993, 2005b; Colell et al., 1995). As nonhuman primates are genetically close to humans, they are often used as models to understand the origins of human brain asymmetry (MacNeilage et al., 1987; Fagot and Vauclair, 1991; McGrew and Marchant, 1997; Cashmore et al., 2008; for a review, see; Papademetriou et al., 2005). To date, such a bias of 90% for the right hand has never been observed in any other species of primate (Vallortigara and Rogers, 2005), and the origin of human hand preference remains unclear. However, several hypotheses have been proposed.

MacNeilage et al. (2009) suggested that early primates evolved in an ecological context where it was necessary to undertake more difficult and more elaborate tasks than, for example, simple grasping in order to find food, which led to a concomitant increase in hand preference. Fagot and Vauclair (1991), according to their ‘theory of the complexity of the task,’ proposed that hand preference would depend on the demands of the task. They defined complexity “in terms of the movement precision, relative to the spatiotemporal dimension of the task” and classified tasks according to two broad categories: “high-level” tasks and “low-level” tasks (Fagot and Vauclair, 1991:77, 80). High-level tasks are more complex than low-level tasks in terms of postural, perceptual, and cognitive demands. For nonhuman primates, high-level tasks increase the strength of laterality and induce a preference for the right or the

left hand (Fagot and Vauclair, 1991). A large number of studies in nonhuman primates also indicated that individuals were more strongly lateralized during a bimanual task considered as ‘complex’ than during a unimanual task considered as more ‘simple’ (gorilla: Byrne and Byrne, 1991; bonobo: Hopkins and de Waal, 1995; orangutan: Rogers and Kaplan, 1996; chimpanzee: Hopkins et al., 2007b; capuchin: Meunier and Vauclair, 2007). However, if the effect of the task on hand preference has been demonstrated in many studies, there is a lack of consensus around the definition of the complexity of the task. Indeed, each task has its own constraints, and each author identified various criteria depending on the task itself. This may be the reason why many definitions of task complexity are proposed in the literature. In addition, it is difficult to define exactly the various functional and cognitive requirements of a manual task, whereas it could help to define complexity and standardize the procedures and studies. We thus consider, in this study, the previous criteria mentioned in the literature, in addition to those we observed during the tasks in order to define complexity (see Methods). Complexity of the task was previously defined according to criteria such as: the use of one hand versus two hands in bimanual coordination (MacNeilage et al., 1987; Hopkins, 1995), the number of stages required to realize the task (Marchant and McGrew, 1991), the level of precision of the required motor acts (Healey et al., 1986; Morris et al., 1993), the use of visual guidance (MacNeilage et al., 1987; Fagot and Vauclair, 1988a,b) or tactile discrimination (Ettlinger, 1961), and, finally, any combination of these criteria (Fagot and Vauclair, 1991). Regarding the literature, tool use should be considered as a complex task since many of the criteria mentioned above are involved in tool use. Many definitions of tool use exist (reviewed in St. Amant and Horton, 2008), and here we use the widely accepted definition of Beck (1980:10): the use of an object to change “the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool.” If complex tasks increase laterality (Fagot and Vauclair, 1991), tool use tasks should induce a stronger hand preference than ‘simpler’ tasks, which has been already shown in apes (chimpanzees: Boesch, 1991; Sugiyama et al., 1993; orangutans: O'Malley and McGrew, 2006; gorillas: Pouydebat et al., 2010).

Another factor that might influence hand preference involves body posture. Bipedal or standing postures have been suggested to induce a stronger hand preference than other postures (e.g., chimpanzee and orangutan: Hopkins, 1993; bonobo: Hopkins et al., 1993). Moreover, a bipedal posture is also thought to influence the direction of laterality with a

preference for the right hand (e.g., chimpanzee and orangutan: Hopkins, 1993; bonobo: Hopkins et al., 1993; macaque: Westergaard et al., 1998a; Cercopithecus: Chapelain et al., 2006; capuchin: Westergaard et al., 1997). This led Kimura (1979) to suggest that both tool use and bipedalism contributed to the emergence of the lateralization of the brain, particularly the strong right hand preference in humans. This suggests the need to simultaneously evaluate the effects of tool use and bipedal posture on hand preference. To date, only two studies have examined hand preference when using tools in bipedal postures: one on chimpanzees (Braccini et al., 2010) and the other on capuchins (Westergaard et al., 1998b). In both species, authors showed that individuals were more lateralized while manipulating tools in a bipedal posture than in a quadrupedal one, with no significant group-level difference for hand preference. These results tend to validate the hypothesis linking the emergence of lateralization to tool use and bipedalism, but more investigations on other individuals of the same and other species are needed. Specifically, it remains unclear whether task complexity or bipedal posture has the greatest effect on laterality. Moreover, it is unclear if the effects of task complexity and bipedalism are independent, additive, or interactive. Finally, it remains unknown whether either parameter induces a right or a left hand preference. A combined approach would help us to understand the respective implication of both parameters in the evolution of laterality and the emergence of the right hand bias in humans.

Our main objective was to test the interaction between task complexity and body posture on hand preference simultaneously. To this end, we investigated the interaction of these two parameters in captive bonobos by quantifying, for the first time, hand preference in relation to both body posture (seated and bipedal) and task complexity: (i) bimanual coordination, (ii) food extraction with a tool, and (iii) food recovery in a maze with a tool through a wire netting. The last two tasks required the use of a tool that has never been tested in bonobos. We conducted this study on bonobos because they are, like chimpanzees (*Pan troglodytes*), close to humans with respect to phylogeny, sharing 98.4% of their coding DNA sequences (Wildman et al., 2003). However, behavioral data are scarce for bonobos, specifically concerning hand preference (around ten studies; e.g., Hopkins et al., 1993; De Vleeschouwer et al., 1995; Christel et al., 1998; Harrison and Nystrom, 2008; Chapelain et al., 2011), hand preference during tool use (Shafer, 1997; Harrison and Nystrom, 2008; Chapelain, 2010), and tool use in general (in the wild: Kano, 1982; Ingmanson, 1996; Hohmann and Fruth, 2003; in captivity: Jordan, 1982; Toth et al., 1993; Gold, 2002). Finally,

bonobos are often bipedal, similar to chimpanzees, making them an excellent model (Doran, 1993; Videan and McGrew, 2001, 2002; D'Août et al., 2004).

Based on this existing literature, we thus suggested two main hypotheses (H): H1) bipedal posture increases the strength of hand preference and generates a directional bias to the use of the right hand; and H2) the complexity of the task increases the strength of hand preference, and tool use creates a directional bias to the use of the right hand.

2. MATERIAL AND METHODS

2.1. Subjects

This study was conducted from 19 January to 27 April 2012 at the “Vallée des singes” (France, 86), on a small group of nine captive bonobos (five females and four males), ranging in age from 4 to 43 years (mean age of 15.88 years, SE= 4.12). One young female (4 years old) had not yet included tool use in her behavioral repertoire and she was not included in the analyses. The bonobos were housed in an indoor building consisting of a network of 8 cages from 30 to 98 m² with a height of up to 6 m (2 main large cages and 6 smaller cages). Animals had access to a large wooded outdoor island. Water was available *ad libitum* in their pens and the food used for our protocol was part of the daily diet. All subjects were tested within their social group, in cages not visible to the public. Before our study, this group received pipes and pierced logs that required tools to extract various foods on a weekly basis. Thus, the group was already used to, and experienced in, food extraction.

2.2. General Procedure

Hand preference was documented in three tasks differing by their complexity and for each task, in a seated posture and a bipedal posture. We considered individuals to be in a bipedal posture when they were upright, that is to say when the angle between the trunk and the thigh was greater than 90° with the knee extended (thigh-leg angle >90°). Only one task was imposed each day per session. A session lasted 30 min on average and lasted until the food was gone. Two cameras (Sanyo® Full HD) at 60 frames/second, one fixed and the other mobile, were used during the tests, thus optimizing the collection of data. The mobile camera was always filming the same cage, and the other camera was used to randomly film different

cages every day. A focal sampling method of 5 min of filming on average for one individual was conducted until the food was eaten. Video analysis was performed with Windows Media Player® using a focal sampling protocol (Altmann, 1974).

2.3. Experimental tasks

2.3.1. Task 1: Coordinated bimanual task

The first experiment was the “TUBE” task (Hopkins, 1995). In this task, the individual maintained a tube containing food with one hand, and reached inside the tube with one or more fingers of the other hand (the dominant hand). The tubes presented to the bonobos were made of PVC (30 cm long, 40 mm diameter, 155 g empty, 400 g full). They were filled with sticky food on the inside edge of both extremities. According to the literature, the complexity of this task resides in the fact that the tube requires coordinated bimanual hand movements with different roles for each hand (e.g. Byrne and Byrne, 1991; Byrne et al., 2001). Two criteria of success were observed for this task: individuals had to grab and hold the tube with one hand and then extract the food with the other hand. We provided fourteen tubes horizontally suspended by the center at a height necessitating a bipedal posture (Figure 1a) and fourteen tubes on the ground to induce a seated posture. Twenty-eight sessions were conducted with one session per day. On average, each subject was observed on 12.9 ± 1.2 days for the seated posture and 9.8 ± 1.4 days for the bipedal posture. The hand used to extract the food was noted with two different recording techniques: “frequencies” and “bouts”. For the frequencies, we counted each time the subject inserted one or more fingers into the tube and subsequently brought them to its mouth. This variable has been used in most other tube task studies (e.g. Hopkins, 1995; Hopkins et al., 2003; Meunier and Vauclair, 2007) and we used the same technique in order to favor comparisons. However, this method has been criticized as lacking data independence (Marchant and McGrew, 1991; Palmer, 2003). So, to ensure data independence, we also recorded bouts, corresponding to a series of identical actions, by recording only the first pattern of each sequence (e.g. Marchant and McGrew, 1991). A bout was considered completed each time the subject performed an action allowing a change of the dominant hand. Hand preference was analyzed for each individual with a minimum of ten bouts.

2.3.2. Task 2: The food extraction task

In this task, hand preference was studied during a manipulative task involving tool use for food extraction. The task was comparable to the “termite-fishing” task, well known in wild chimpanzees (Goodall, 1968) but still never observed in wild bonobos (McGrew et al., 2007). To accomplish this task, twelve logs (53.25 cm long; SE =2.90 cm and diameter 9.17 cm; SE=0.88 cm), pierced in their center, were hung vertically at different heights (6 logs hung low and 6 high) so that individuals could perform this task in seated and bipedal posture (Figure 1b) within each session. Sticky food was placed inside the holes. Branches (maximum length of 3 m) were provided to bonobos. The hand used to hold the branch was recorded each time a subject inserted a branch into a hole of a log, removed it from the hole, and brought it to its mouth with one hand. We considered this task more complex than the tube task because more criteria were required to succeed. Indeed, individuals had to use a tool with one hand to be able to extract the food and visual guidance was required to insert the tool into the holes. The other hand was placed on the log or on the mesh. As with the tube task, we used two recording techniques: “frequency” and “bouts”. Eleven test sessions were conducted with one session per day, and each subject was observed between five and nine days (mean = 6.875, SE = 0.58).

2.3.3. Task 3: The maze task

This experimental setup represents a new task, specifically created for this study. The subject needed to recover walnuts positioned on a wooden maze (Figure 1c) outside the cage (grid with a mesh size of 5x5 cm), with a stick. Nine mazes (45 cm wide by 60 cm long) differing in the shape, position, and size of the wooden obstacles (providing a different potential path of the walnut in each maze), were fixed outside the cages at different heights. In order to minimize as much as possible the social tensions in the group, the mazes were moved away from each other and the walnuts were placed in the mazes at the same moment. Four mazes were placed at 30 cm from the floor in the two main cages and five mazes at 60 cm height in the smaller cages so that individuals could choose to position themselves in a seated or bipedal posture. The walnuts were placed at the end of the maze (at 60 cm away from the individual). This task was considered the most complex one in this study because it required several steps to be performed. As in the food extraction task, individuals had to use a tool to succeed. However, the maze task requires the use of a tool to recover the walnut by facing

many obstacles: first, obstacles placed inside the maze in order to complicate the trajectory of the walnut and second, between the maze and the individual (wire netting). These obstacles involved several constraints in terms of forelimb coordination, body posture adjustments, manual skills and vision. The behavior studied was the hand holding the branch. Fifteen sessions (each session comprising between 2 and 8 walnuts by maze per day) were filmed. As for the two other tasks, we first planned to use “frequency” and “bouts” recording techniques, thinking that subjects would have alternated hand use or could leave their tool during the task. However, the individuals never changed hands nor left their tool during all the maze sessions and we have thus recorded frequencies only. The hand holding the branch when recovering the walnut was thus recorded. Each subject was observed between nine and fourteen days (mean = 11.85 and SE = 0.70) and only those who obtained a minimum of six successes for the maze were kept for the analyses. Among our nine subjects, a young male never succeeded to access the mazes and two other individuals (one male and one female) did not perform this task in a bipedal posture.



Figure 1. Pictures of the three tasks accomplished by bonobos: the tube task, with a tube hung horizontally (a), the extracting food task with tool, in a bipedal posture (b) and the maze task with a tool, in a seated posture (c).

2.4. Data analysis

The data obtained in this study were analyzed using the methods proposed by Hopkins (1999). For each subject the binomial z -scores were calculated based on frequency (Table 1) and bouts. The z -scores allowed us to categorize the bonobos individually as right-handed ($z \geq 1.96$), left-handed ($z \leq -1.96$), or without hand preference ($-1.96 < z < 1.96$). Next, the individual hand preference index (Handedness Index, denoted by HI) was calculated using the

formula: $HI = (R - L) / (R + L)$. HI varies from -1 to 1; negative values indicating a left-hand bias, and positive values indicating a right hand bias. Thanks to these individual HI, we evaluated hand preference at group level using a Wilcoxon signed-rank test for one sample. Finally, we calculated for each subject the absolute value of HI (denoted ABS-HI), which indicates the strength of hand preference. The stronger the laterality, the closer the ABS-HI is to 1. We evaluated if the hand preference based on z -score changed for each subject between the postures and tasks with a chi-square goodness of fit test (e.g. Bogart et al., 2012). For pairwise comparisons, we considered only the individuals who were represented in both compared tasks. We compared only tasks performed by a minimum of 6 individuals. All statistical tests were performed with the software R (R development Core Team 2013) (exact method) and were two-tailed with a level of significance set at $p < 0.05$.

3. RESULTS

3.1. Bouts versus frequency

Regarding the z -scores, we found differences between frequency and bout data for the tube task in bipedal posture where two bonobos previously classified as left-handed were classified with no preference (Table 1). To test data independence (Marchant and McGrew, 1991), we compared the HI values found between the two recording techniques (see Methods) for the two postures in the tube task and the food extraction task. For all conditions we found a significant positive correlation between HI measured with frequencies and HI measured using bouts (Spearman correlation, $N = 8$: tube task seated $r = 0.97$, $p < 0.001$; tube task bipedal $r = 0.95$, $p < 0.01$; food extraction task seated $r = 1$, $p < 0.01$; food extraction task bipedal $r = 1$, $p < 0.05$) indicating that these two approaches are similarly sensitive to individual hand preferences (Bogart et al., 2012; Hopkins, 2013). Thus, all analyses only used frequency data for determining individual hand preference as has been proposed in other studies (e.g. Bogart et al., 2012).

Table 1. Raw data and statistical results with frequencies, for the three tasks and the two postural conditions (seated and bipedal).^a

Individuals		Seated						Bipedal					
		Bout R/L	Freq R/L	HI	ABS-HI	Z	Category	Bout R/L	Freq R/L	HI	ABS-HI	Z	Category
Tube Task	Diwani	1/65	1/161	-0.988	0.988	-12.57	LH	1/26	4/57	-0.869	0.869	-6.786	LH
	Kirembo	51/2	132/4	0.941	0.941	10.976	RH	62/0	110/0	1	1	10.488	RH
	Daniela	46/8	185/24	0.77	0.77	11.137	RH	35/12	93/16	0.70	0.70	7.3753	RH
	Ukela	8/42	15/197	-0.858	0.858	-12.5	LH	3/7	4/22	-0.692	0.692	-3.5301	LH A
	Khaya	6/49	12/156	-0.857	0.857	-11.11	LH	6/16	14/35	-0.428	0.428	-3	LH
	Lingala	18/38	35/91	-0.444	0.444	-4.9889	LH	26/29	42/64	-0.207	0.207	-2.1368	LH A
	David	28/28	90/86	0.023	0.023	0.03015	A	7/3	12/5	0.412	0.412	1.6977	A
	Kelele	40/14	91/31	0.492	0.492	5.4321	RH	51/16	101/23	0.629	0.629	7.0046	RH
Means		55.5	163.88	-0.115	0.672			37.5	75.25	0.068	0.618		
<i>Standard error</i>		<i>1.647</i>	<i>12.309</i>	<i>0.276</i>	<i>0.116</i>			<i>8.161</i>	<i>14.868</i>	<i>0.249</i>	<i>0.091</i>		
Extracting Food Task	Diwani	70/0	129/0	1	1	11.3578	RH	23/0	25/0	1	1	5	RH
	Kirembo	68/0	86/0	1	1	9.2736	RH	27/0	33/0	1	1	5.7446	RH
	Daniela	54/13	69/28	0.423	0.423	4.1629	RH	37/18	59/22	0.457	0.457	4.1111	RH
	Ukela	0/38	3/67	-0.914	0.914	-7.6495	LH	0/12	0/20	-1	1	-4.4721	LH
	Khaya	57/0	101/0	1	1	10.05	RH	60/0	172/0	1	1	13.115	RH
	Lingala	70/0	163/0	1	1	12.767	RH	60/0	155/0	1	1	12.45	RH
	David	70/0	112/0	1	1	10.583	RH	21/0	26/0	1	1	5.099	RH
	Kelele	44/17	54/23	0.403	0.403	3.5328	RH	22/0	22/0	1	1	4.6904	RH
Means		62.625	104.38	0.614	0.842			35	66.75	0.719	0.932		
<i>Standard error</i>		<i>3.677</i>	<i>10.107</i>	<i>0.238</i>	<i>0.094</i>			<i>6.322</i>	<i>22.449</i>	<i>0.249</i>	<i>0.068</i>		
Maze Task	Diwani		35/0	1	1	5.916	RH		9/0	1	1	3	RH
	Kirembo		30/0	1	1	5.477	RH		33/0	1	1	5.745	RH
	Daniela		33/0	1	1	5.744	RH		26/0	1	1	5.099	RH
	Ukela		0/23	-1	1	-4.796	LH		0				
	Khaya		23/0	1	1	4.796	RH		21/0	1	1	4.582	RH
	Lingala		30/0	1	1	5.477	RH		33/0	1	1	5.744	RH
	David		18/0	1	1	4.242	RH		0				
	Means		27.429	0.714	1				20.333	1	1		
<i>Standard error</i>		<i>2.338</i>	<i>0.285</i>	<i>0</i>				<i>4.467</i>	<i>0</i>	<i>0</i>			

^a R = Number of right-hand responses. L = Number of left-hand responses. HI = Handedness Index. ABS-HI = Absolute value of HI. z = z-scores. Category (based on the z-scores): LH = left-handed individuals, RH = right-handed individuals, A = ambiguously-handed individuals and in italics the differences based on bout data.

3.2. Quantification of hand preference and influence of posture

3.2.1. Task 1: The coordinated bimanual task

Three bonobos were classified as right-handed, one was classified with no preference, and four were classified as left-handed for both postures. At the group level, we had no differences on the HI values for the seated posture (One-sample Wilcoxon signed-rank test; $N = 8$, $z = 15$, $p = 0.74$) and the bipedal one (One-sample Wilcoxon signed-rank test; $N = 8$, $z = 20$, $p = 0.84$), indicating individualistic hand preferences. A significant difference in the HI values was found between the seated and bipedal postures (Wilcoxon signed-rank test; $N = 8$, $z = 2$, $p = 0.02$) indicating a trend that bonobos were more lateralized in the seated posture over that of the bipedal posture. When we considered hand preferences based on z -scores for the two postures, a chi-square goodness of fit test revealed that the distribution of hand preference was random [$\chi^2(2, n = 8) = 0$, $p = 1$], indicating that there was no difference in the hand used between the postures. Concerning the ABS-HI values, no difference appeared between seated and bipedal postures, (Wilcoxon signed-rank test; $N = 8$, $z = 24$, $p = 0.46$), indicating that individuals were not more significantly strongly lateralized in seated than bipedal posture.

3.2.2. Task 2: The food extraction task

All the individuals were lateralized in the food extraction task for both postures. Seven bonobos were classified as right-handed and one as left-handed. At the group level, a preference for the right hand appeared for seated posture (One-sample Wilcoxon signed-rank test; $N = 8$, $z = 36$, $p < 0.01$) and in bipedal posture individual also seemed to have a preference for the right hand (One-sample Wilcoxon signed-rank test; $N = 8$, $z = 31$, $p = 0.05$). When we considered hand preferences based on z scores for the two posture, a chi-square goodness of fit test revealed that the distribution of hand preference was not random [$\chi^2(2, n = 8) = 10.75$, $p < 0.01$]. For both posture, there were significantly more right than left handed subject [$\chi^2(1, n = 8) = 4.5$, $p < 0.05$]. No significant difference on HI values (Wilcoxon signed-rank test; $N = 8$, $z = 2$, $p = 0.59$), nor on ABS-HI values (Wilcoxon signed-rank test; $N = 8$, $z = 0$, $p = 0.11$), was observed between bipedal and seated postures.

3.2.3. Task 3: The maze task

Individuals were exclusively right- or left-handed and they never changed hand between the nine different mazes suggesting that the manual preference was not affected by the structure of the mazes. Thus, we added the data of each maze to consider hand preference in the seated ($N = 7$) and the bipedal ($N = 5$) postures. Individuals never changed their body posture (from seated to quadrupedal and conversely) during the maze task. Considering hand preference, we showed that in the seated posture six bonobos demonstrated an exclusive use of the right hand and one individual an exclusive use of its left hand. Among the six right-handed individuals in seated posture, only five performed the task in bipedal posture and remained all right-handed in that case. At the group level, a preference for the right hand seemed to appear in seated posture (One-sample Wilcoxon signed-rank test; $N = 7$, $z = 24$, $p = 0.06$) and in bipedal one with only right-handed individuals. For both postures, the strength of lateralization was maximal for all the individuals ($ABS-HI = 1$).

3.3. Influence of the complexity of the task and body posture

In both seated (Figure 2a) and bipedal postures (Figure 2b), individuals classified as left handed or no preference during the tube task inverted to the right-hand during the food extraction and the maze task, except one. One individual remained left-handed throughout the study (Table 1).

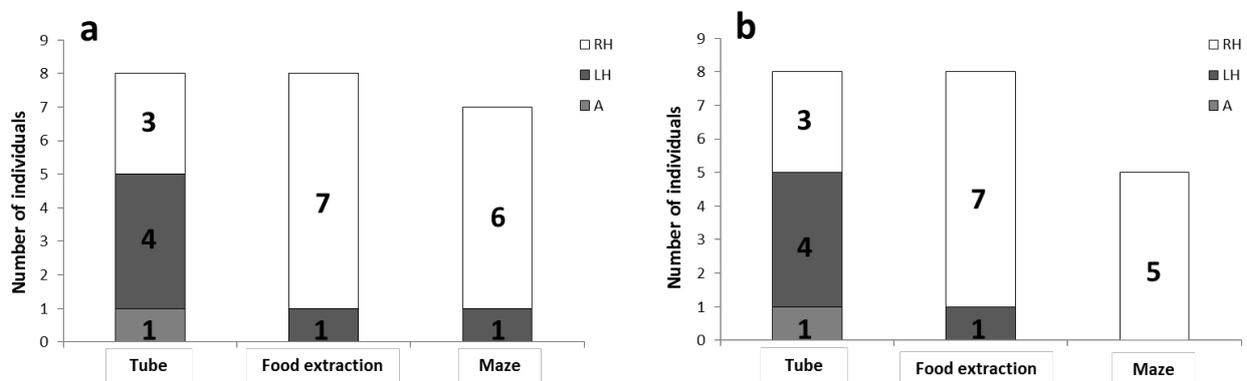


Figure 2. Number of right-handed (RH); left-handed (LH), and ambiguously-handed (A) subjects by task and by posture: seated (a) and bipedal (b), with frequencies data.

In the seated posture, the HI values were significantly higher for the maze task than during the tube task (Wilcoxon signed-rank test; $N = 7$, $z = 26$, $p < 0.05$) indicating a preference for the right hand during the maze task. Between the HI values of the tube task and the food extraction task we did not find differences in seated posture (Wilcoxon signed-rank test; $N = 8$, $z = 8$, $p = 0.19$) and in bipedal posture we observed a trend for a greater preference for the right hand during food extraction than for the tube task (Wilcoxon signed-rank test; $N = 8$, $z = 3$, $p = 0.06$). When we considered hand preferences categories for the three tasks in seated posture, a chi-square goodness of fit test revealed that the distribution of hand preference was random [$\chi^2(4, n = 7) = 7.2857$, $p = 0.12$], indicating that there was actually no difference in the actual hand used between tasks. When only the right-handed and left-handed categories are examined, we observed a trend for a preference for the right hand than left hand [$\chi^2(2, n = 7) = 5.4875$, $p = 0.06$]. Between the tube and food extraction tasks in bipedal posture, the distribution of hand preference was random [$\chi^2(2, n = 8) = 4.4$, $p = 0.11$], indicating that there was actually no difference in the actual hand used between the two tasks. Considering ABS-HI values, individuals were significantly more strongly lateralized in a seated posture during the maze task compared to the tube task (Wilcoxon signed-rank test; $N = 7$, $z = 0$, $p < 0.05$). Moreover, they were significantly more strongly lateralized in a bipedal posture during the food extraction task compared to the tube task (Wilcoxon signed-rank test; $N = 8$, $z = 2$, $p < 0.05$) (Figure 3).

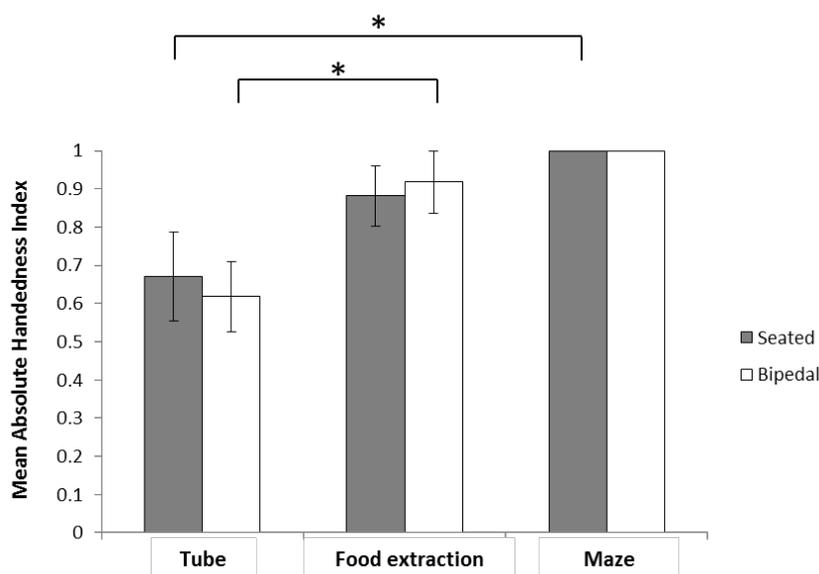


Figure 3. Mean absolute values of individual handedness index (ABS-HI), with frequencies, for the tube task ($N = 8$), the food extraction task ($N = 8$) and the maze task ($N = 7$ for the seated posture and $N = 5$ for the bipedal posture) depending on the posture. Bars = standard errors. * = $p < 0.05$.

4. DISCUSSION

This study is the first to simultaneously analyze the effect of both complexity and body posture on hand preference in bonobos. Our main result indicated that, independent of body posture, task complexity resulted in a greater lateralization for the two tool use tasks, with a tendency to preferentially use the right hand. In addition, one tool task was new and more complex than the other one, and specifically created for this study. Moreover, little research has been conducted on laterality in bonobos (with around 10 studies; e.g., Hopkins et al., 1993; De Vleeschouwer et al., 1995; Christel et al., 1998; Harrison and Nystrom, 2008; Chapelain et al., 2011), and very few studies have discussed the effects of both posture and complexity of a tool task on hand preference (e.g., Westergaard et al., 1998b; Braccini et al., 2010). As a result, this research is useful and compelling in spite of our small sample size. Indeed, even though we analyzed ‘only’ eight individuals, the large number of independent data points suggests robust results.

4.1. Contributions to the theory of task complexity

We observed a significant increase in the strength of laterality according to task complexity, with a stronger hand preference in both tasks involving tool use. Moreover, four bonobos who were left-handed or with no preference in the tube task were right-handed for both the food extraction task with a tool and the maze task. Our results were in agreement with our hypotheses, based on the task complexity hypothesis (Fagot and Vauclair, 1991) and the tool use hypothesis (Kimura, 1979; Frost, 1980). In the course of evolution, complex behaviors might have increased and demanded greater time and energy costs (Mutha et al., 2013). It has been hypothesized that these costs may have been counterbalanced by the hemispheric specialization that emerged to accommodate increasing motor complexity during hominoid evolution (Mutha et al., 2013). There are probably other correlations with hemispheric specialization, such as the evolution of the size of the brain in primates. The evolution of larger brain size in primates would be accompanied by diminished interhemispheric connectivity and augmented intrahemispheric connectivity that might accompany the emergence of cerebral lateralization (Rilling and Insel, 1999). Moreover, increased motor complexity might lead to larger, more gyrified brains, which would then lead to hemispheric specialization (e.g., Aboitiz et al., 1992; Rilling and Insel, 1999). Thus, complex behaviors such as tool use would be strongly lateralized and could be managed in a

specific hemisphere in bonobos such as the left hemisphere, as in humans (reviewed in Johnson-Frey, 2004) and chimpanzees (Hopkins et al., 2007a). The tool use tasks conducted in this study might demand higher and more costly cognitive abilities than the bimanual coordinated task, and, as such, might promote the specialization of a cerebral hemisphere—particularly the left hemisphere, which controls the right hand. This could explain why our bonobos tended to preferentially use their right hand during our tool use tasks.

Concerning the tube task in the seated posture, we observed individual preference but no bias at the group level, which contrasts with results obtained for the same task in other species (e.g., chimpanzees: Hopkins, 1995; Hopkins et al., 2003; orangutans: Hopkins et al., 2003; baboons: Vauclair et al., 2005) that showed a bias in hand preference at the group level. One explanation might be our small sample size compared with other studies (e.g., Hopkins, 1995 with 110 chimpanzees; Vauclair et al., 2005 with 104 baboons). However, our results converged with a similar study on bonobos (Chapelain et al., 2011), which showed no bias in hand preference at the group level with a sample of 77 bonobos but did show a pronounced individual hand preference. We have no explanation for this difference within this species (Chapelain et al., 2011). Studies on hand preference for bonobos are scarce (e.g., Hopkins et al., 1993; De Vleeschouwer et al., 1995; Christel et al., 1998; Harrison and Nystrom, 2008; Chapelain et al., 2011), and the ecology of bonobos in their natural environment is poorly known (e.g., McGrew et al., 2007). More studies should be conducted to explore if bonobos use bimanual coordination more or less than other species do both in captivity and in the wild. Subsequently one may try to better understand the potential role of bimanual coordination from an evolutionary point of view.

Concerning the tool use tasks tested in this study, our results showed that the hand preference of bonobos was very strong, and even exclusive (i.e., individuals always used the same hand), for the maze task. Thus, even though bonobos have not appeared to use tools to obtain food in their natural environment (Ingmanson, 1996), they successfully completed these tool use tasks in this study. Chapelain (2010) studied tool use with 19 bonobos in a task ('termite fishing') similar to our food extraction task, and she observed 11 individuals that were lateralized (four left-handed and seven right-handed). Harrison and Nystrom (2008) examined hand preference for tool use actions that occurred in the daily activities with 12 bonobos. They observed seven lateralized individuals (three left-handed, four right-handed). These results differ from ours, as all of our subjects were lateralized and we found one left-handed and six right-handed individuals for the food extraction task. This difference could be

explained by the fact that during observations in previous studies, many parameters might have affected hand preference. In fact, in both studies they quantified the hand preference without taking into account the potential influence of the body posture and the potential influence of the variability of the type of tool used, in spite of their potential complexity differences. Regarding the findings in wild chimpanzees for ‘termite fishing,’ a significant group level left bias was reported by Lonsdorf and Hopkins (2005) and recently by Bogart et al. (2012), who combined their data with those obtained by McGrew and Marchant (1992, 1996) and Lonsdorf and Hopkins (2005) and based on this combined data set showed a left-hand bias for wild chimpanzees. In captivity, the same left bias was found by Fletcher and Weghorst (2005), but no bias was detected in the study by Hopkins and Rabinowitz (1997). In wild chimpanzees, most individuals were lateralized and showed an almost exclusive use of one hand (Nishida and Hiraiwa, 1982; McGrew and Marchant, 1992, 1999; Marchant and McGrew, 1996; Lonsdorf and Hopkins, 2005; Bogart et al., 2012), which was more consistent with our results (all individuals lateralized and 66% exclusively lateralized). Finally, because ‘termite-fishing’ behavior has never been observed in wild bonobos (McGrew et al., 2007), comparison between natural and artificial habitat is still not possible for this task.

The results of the maze task must be considered as preliminary because we had only a limited number of individuals to compare (seated posture $n = 7$ and bipedal posture $n = 5$). Yet, for both seated and bipedal postures, all individuals showed a strong hand preference with a tendency for the use of the right hand. Moreover, in this novel task we observed an exclusive hand preference, whereas only 66% were exclusively lateralized for the food extraction task with a tool. One explanation might be the task novelty. Indeed, novel tasks are known to elicit higher hand preferences than highly familiar tasks (Fagot and Vauclair, 1991). In fact, bonobos were supplied weekly with pipes and pierced logs requiring tools to extract various foods, and thus all of them were already experienced in food extraction before our experiments. However, the maze task was novel for the bonobos we studied, which could explain the greater strength in hand preference compared with the familiar actions of food extraction. Moreover, we considered the maze task more complex (regarding the definitions of literature and the presence of more criteria) than the food extraction task, which could explain why we observed an exclusive hand preference for all individuals in the maze task.

Our results contribute additional reflections on hand preference and supplied task complexity data in bonobos. Indeed, the maze task was interesting in terms of complexity because it required several cognitive processes such as using a tool and moving around

obstacles to retrieve walnuts. Bonobos might be exclusively lateralized for this task because it demanded many abilities, which were managed by one hemisphere to optimize manipulation, and specifically by the left one linked to calculation abilities in humans (Popper et al., 1977). However, some authors inferred that there was likely to be right hemisphere specialization for trajectory perception in humans (Boulinguez et al., 2003). In addition, the right hemisphere seems to be used to process geometrical and global spatial cues in many species (humans: Wendt and Risberg, 1994; rats: Cowell et al., 1997; chicks: Tommasi and Vallortigara, 2004). Finally, some authors have suggested that preferred directions of arm movements are independent of visual perception of spatial directions (Dounskaia et al., 2014) and that hemispheric specialization emerged to accommodate increasing motor complexity during evolution in humans (Mutha et al., 2013). In particular, some studies suggested an enhanced role for the left hemisphere during the learning of new sequences and skills and that this specialization emerged from a left hemisphere specialization for predictive control (the ability to plan and coordinate motor actions; Mutha et al., 2012). This last idea is in agreement with our results, but neurological studies in primates during different manipulation tasks would be needed to better understand the hemispheric specialization for the hand preference.

4.2. Effect of posture on hand preference

Our results did not indicate posture (seated or bipedal) as an influencing factor on the direction of hand preference, nor on the strength of lateralization during the three tasks. Thus, our hypotheses that a bipedal posture should increase the strength of manual preference and generate a directional bias for the right hand were not supported by our data. According to these hypotheses, individuals in a bipedal posture should have been more strongly lateralized and should have had a directional bias in favor of the right hand. Other studies in bonobos showed an increase in the strength of hand preference and a right hand preference for a reaching task, when individuals shifted from a quadrupedal posture to a bipedal one (Hopkins et al., 1993). On the contrary, De Vleeschouwer et al. (1995) showed, in a group of five bonobos, a preference for using the left hand while the animals shifted from a seated to a bipedal posture. Still, most of these studies considered simple reaching tasks (Fagot and Vauclair, 1991). In our study we examined complex tasks for which individuals were already strongly lateralized in a seated posture, with a tendency to be right-handed. Thus, this could explain the lack of increase in right hand preference in a bipedal posture. However, as

previously discussed, because complexity differences elicited differences in direction and strength of hand preference, our results also suggest that the complexity of the task has a greater effect on hand preference than posture. This idea is supported by a study of capuchins involving a bimanual coordination similar to the tube task (vertically hung tubes) and taking into account the body posture (crouched and upright; Spinozzi et al., 1998). The results showed that individuals had no significant difference in either the direction of hand preference or in the strength of lateralization between the two postures. These results are in accordance with ours in that capuchins and bonobos were already lateralized in crouched and seated posture (respectively for the two species), and their hand preference and strength of laterality did not change when they performed the task in an upright posture. This suggests both that a bimanual coordinated task (that requires a precise bimanual coordination while manipulating a tube) is a high level, complex task (Fagot and Vauclair, 1991) and that bipedal posture might not provide any supplementary bias in laterality. However, the postural effect on bimanual coordination tasks should be studied in many other species of nonhuman primates to confirm this hypothesis.

Our study is the first one involving bipedal tool use in bonobos, and, to date, only two studies have been conducted on bipedal tool use in nonhuman primates: one in chimpanzees (Braccini et al., 2010) and the other in capuchins (Westergaard et al., 1998b). Our two tasks involving tool use showed no significant difference in direction of hand preference between a seated and a bipedal posture, which is in agreement with these two previous studies. However, these authors showed that chimpanzees and capuchins were more strongly lateralized when using tools in a bipedal posture, in contrast to our results showing that bonobos were strongly lateralized for both postures. This suggests three possible explanations: (1) our sample size was too small to show a significant effect of the posture, (2) the difference between laterality patterns found in other studies and our results could be due to an effect of the task (as suggested above), and (3) bonobos may be less sensitive to the effect of bipedalism compared with chimpanzees. Indeed, bonobos seem more adept at maintaining balance in a bipedal posture and might therefore be less susceptible to the effect thereof on hand preference than other species. For instance, Braccini et al. (2010:238) noted that: “the bipedal posture appeared to be difficult for the chimpanzee.” These authors noticed that in a bipedal posture the legs of chimpanzees were shaking and some individuals did not want to perform the task in this posture. We did not observe this phenomenon during our observations in bonobos. However, one can note that two individuals did not use a bipedal posture for the maze task

and one, the youngest subordinate male, never had access to mazes for the two postures. We could explain this observation by a problem of access opportunity related to the hierarchy. Indeed, the young subordinate male avoided the small cages that housed the mazes, most likely due to the higher amount of competition and his low ranking status. The second individual was the dominant female who only used the maze of the main cage that necessitated a seated posture. This could be explained by the fact that the dominant female often occupied the large cages in order to keep a close watch on group members. It would be interesting to conduct the maze task with isolated individuals, in the same cage, and/or by proposing only mazes necessitating bipedal posture in order to better understand the influence of comfort and hierarchy.

4.3. “Bouts” versus “Frequency”

Concerning the two different recording techniques (‘bouts’ versus ‘frequency’), our measurements for HI values were significantly and strongly correlated. Thus, using HI values based on frequency or bouts provided similar results in agreement with other studies (Westergaard and Suomi, 1996; Hopkins et al., 2001, 2004, 2005a; Palmer, 2002, 2003; Hopkins and Cantalupo, 2003; Bogart et al., 2012; Hopkins, 2013). However, regarding the z -scores, we found differences between frequency and bout data for the tube task in bipedal posture. In this case, the number of data points had an effect on our estimate of laterality. Some authors suggested that the use of frequencies may influence laterality estimates and may thus introduce sampling biases (McGrew and Marchant, 1997; Palmer, 2002, 2003; Hopkins and Cantalupo, 2003). However, in a recent article, Hopkins (2013) suggested that the use of the z -score with bout data might bias data towards the null hypothesis (no significant hand preference) because the z -score is sensitive to sample size and with bout data we typically have fewer numbers of right and left hand use for bouts than frequencies. Moreover, Hopkins (2013) suggested that there is no statistical justification for claims that the independence of data points introduces biases in the measurement of hand preference in nonhuman primates. Thus, as suggested by Hopkins (2013), it appears opportune to continue to record and report bouts and frequencies in behavioral asymmetry studies in order to resolve the disagreement about these two recording techniques.

4.4. Contributions to human evolution: link between hand preference, tool use, locomotion and language

Task complexity had a greater effect than posture on hand preference in our subjects. Our results have interesting implications for theories on the emergence of human lateralization in relation with tool use and bipedalism. Even if our data cannot by themselves explain the preponderance of right-handers in the human species, they support the tool use hypothesis (Kimura, 1979; Frost, 1980), which proposed that the preference for the right hand might have emerged in humans as an adaptation for complex tool use and manufacture.

Bonobos do not often use tools in the wild for feeding (Ingmanson, 1996), but in this study they used tools in this context with preferentially the right hand. Moreover, it seemed to require little effort for them to remain in a bipedal posture. Kimura (1979) suggested that tool use and bipedalism are linked to the emergence of the lateralization of the brain and particularly to the strong right hand preference in humans. In accordance with this hypothesis several studies suggested that hand preference in great apes might be linked to posture and/or tool use (Olson et al., 1990; Hopkins, 1993; Hopkins et al., 2007a; Cantalupo et al., 2008; Braccini et al., 2010). However, the bonobos we studied here often preferentially used the right hand in seated posture and bipedal posture did not have a supplementary effect on hand preference during tool use tasks. Moreover, several studies showed a preference for the right hand when individuals manipulated in bipedal postures but not in other postures such as seated or triped ones (e.g., chimpanzees and orangutans: Hopkins, 1993; bonobos: Hopkins et al., 1993; macaques: Westergaard et al., 1998a; *Cercopithecus*: Chapelain et al., 2006; capuchins: Westergaard et al., 1997). However, only one study directly examined bipedal tool use (Braccini et al., 2010) and did not report a preference for the right hand when chimpanzees used tools in this posture.

It is unlikely that bipedalism had such an important role in the elaboration of tool use and in the preponderance of the right hand preference in humans. Indeed, a recent neurological study conducted by Hashimoto et al. (2013:1) suggested “that adaptations underlying tool use evolved independently of those required for human bipedality.” Hand preference might be older than bipedalism in origin and rather linked to an arboreal lifestyle that requires complex body postures and manipulation. In fact, arboreal locomotion requires fine motor control, and the anatomical specializations of the forelimbs of arboreal species are probably associated with a well-developed grasping ability (Fabre et al., 2013). In addition,

there might have existed a link between the mode of locomotion and manipulative abilities, with a tendency for an exaptation of manipulation for arboreal species (Sustaita et al., 2013). In this context, the capacity to grasp has been proposed as a “critical adaptive innovation” for arboreal primates (Kivell et al., 2010:1549) and a “key feature” of primate evolution (Ravosa and Dagosto, 2007:18). An arboreal lifestyle could have led to the elaboration of manual skills and tool use in primates, and hand preference could have emerged from arboreal ancestors coming down to the ground to use tools like some apes today.

Finally, the present work shows that the link between bipedalism and hand preference is far from being established and that the link between bipedalism and the capacity to use and manufacture tools is far from being obvious. It thus remains to be demonstrated, and more studies are needed to explore the link between arboreal lifestyle and manual preference. In this framework, species such as gibbons, gorillas, orangutans, and bonobos are of particular interest.

Another factor often invoked in the emergence of the strong hand preference for the right hand in humans is language. A predominance of right hand use has been reported in gestures occurring while humans are talking (Kimura, 1973a,b), including the communication between deaf people (Grossi et al., 1996). These asymmetrical gestures reflect the dominance of the left hemisphere for the perception and production of speech (Knecht et al., 2000). Moreover, studies in humans showed that brain regions implicated in the perception and production of speech (Broca's area and Wernicke's area) were also implicated with tool use behavior (Hopkins et al., 2007b). Some authors suggest that the neuronal substrates of tool use may have served as a preadaptation for the evolution of language and speech in modern humans (e.g., Greenfield, 1991; Bradshaw and Rogers, 1993). Hopkins et al. (2007b) reported asymmetries in chimpanzees in the homologs to Broca's and Wernicke's areas associated with hand preference for tool use. Consequently, these authors suggested that control of complex motor tool use action may have served as a preadaptation for the emergence of neural capacities required for language in humans (Hopkins et al., 2007b). Our results in bonobos showed a tendency to preferentially use the right hand for tool use tasks, which reflects the dominance of the left hemisphere for these actions. Moreover, Kanzi, a bonobo, was thought to have rudimentary language comprehension skills comparable to a 2.5 year-old child and also displayed impressive symbolic communicative skills (e.g., Savage-Rumbaugh et al., 1977, 1985, 1986; Savage-Rumbaugh, 1987). So, it appears interesting to apply in bonobos the same neurological study of Hopkins et al. (2007b) to confirm the link between tool use

and language. This could bring us more information about the emergence of language regarding hypotheses that propose a relationship between language and hand preference (Hewes, 1973; Corballis, 2003; Vauclair, 2004), in that the emergence of right hand preference would be a preadaptation to language. However, more studies are needed to test the hypothesis that lateralization based on tool use preceded that for language (e.g., Steele and Uomini, 2009).

5. CONCLUSION

To conclude, although our sample size does not allow us to generalize at the group level, and even less at the population level, our large number of independent data points suggests robust results. It appears therefore essential to replicate our study in more groups of bonobos and to compare the maze task between different species of primates, including humans, in order to provide additional leads on the evolution of hand preference. Comparing this task among different primates would be of particular interest regarding the hypothesis proposing tool use as a selective pressure for hand preference (Kimura, 1979; Frost, 1980). It would also be essential to quantify hand preference in several primate species during natural activities varying in complexity in their natural habitat and on the ground, but also in trees.

SUMMARY OF THE CHAPTER 2

Title: Do bimanual coordination, tool use and body posture contribute equally to hand preferences in bonobos?

Questions: Does a bipedal posture increase the strength of hand preference and/or create a directional bias toward the use of the right hand? Independently of body posture, does task complexity increase the strength of the hand preference and/or create a directional bias toward the use of the right hand?

Model: Bonobos (*Pan paniscus*).

Method: Experimentation and ethological observation in Zoo (la Vallée des Singes).

Results: Independently of body posture, the more the task is complex, the more lateralization occurred, and individuals tended to be right-handed for tool use tasks.

Discussion: Task complexity might have contributed more than bipedal posture in the emergence of human lateralization and the preponderance of right-handedness. A larger sample size and more data from other species could be useful to reinforce this hypothesis. However, according to the great number of parameters involved in hand preference (e.g. task complexity, body posture, object position, object movement, social context, environment, etc.), a consensus seems impossible to find.

Perspectives: As task complexity and tool use appear as fundamental parameters in bonobos' hand specialization, we decided to quantify the functional and behavioral strategies used by this species during different tool use tasks varying in complexity. It is in this framework that we developed this objective in the chapter 3.

Chapter 3 – Behavioral and functional strategies during tool use tasks in bonobos

Behavioral and functional strategies during tool use tasks in bonobos

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ABSTRACT

Different primate species have developed extensive capacities for grasping and manipulating objects. However, the manual abilities of primates remain poorly known from a dynamic point of view. The aim of the present study was to quantify the functional and behavioral strategies used by captive bonobos (*Pan paniscus*) during tool use tasks. The study was conducted on eight captive bonobos which we observed during two tool use tasks: food extraction from a large piece of wood and food recovery from a maze. We focused on grasping postures, in-hand movements, the sequences of grasp postures used that have not been studied in bonobos, and the kind of tools selected. Bonobos used a great variety of grasping postures during both tool use tasks. They were capable of in-hand movement, demonstrated complex sequences of contacts, and showed more dynamic manipulation during the maze task than during the extraction task. They arrived on the location of the task with the tool already modified and used different kinds of tools according to the task. We also observed individual manual strategies. Bonobos were thus able to develop in-hand movements similar to humans and chimpanzees, demonstrated dynamic manipulation, and they responded to task constraints by selecting and modifying tools appropriately, usually before they started the tasks. These results show the necessity to quantify object manipulation in different species to better understand their real manual specificities, which is essential to reconstruct the evolution of primate manual abilities.

1. INTRODUCTION

A high degree of manual function and ability is thought to have been a crucial adaptation in primates and a primordial element in human evolution (Susman, 1994). All primates use their hands for feeding and moving, and during social interaction. In doing so, they show different types of grasping postures and hand movements according to the species (i.e. Fragarzy, 1998; Pouydebat et al., 2008, 2009; Reghem et al., 2013, 2014). In this context, the human hand is traditionally considered unique in the animal kingdom based on its functional characteristics involving the use of a variety of forceful precision grips, opposing the thumb with the pads of the fingers (Napier, 1960; Marzke, 1997; Susman, 1998; Tocheri et al., 2008). However, other primates such as great apes and capuchins use different grasping postures that are sometimes comparable to those used by humans, including the precision grip posture involving the tips of the thumb and index fingers (Christel, 1993; Jones-Engels and Bard, 1996; Marzke and Wullstein, 1996; Christel et al., 1998; Byrne et al., 2001; Pouydebat et al., 2009, 2011). Moreover, the real dynamic manual abilities of non-human primates are not sufficiently documented to be able to conclude that human hand abilities are unique. In this context, detailed studies of manual abilities in primates are essential in order to better understand the functional and behavioral strategies of each species in relation with its hand morphology and ecology. These kinds of data are also needed for assessing the evolution of grasping ability in primates more generally.

Several studies have described dynamic human hand movements (i.e. Elliot and Connolly, 1984; Exner, 1992; Santello et al., 1998; Braidó and Zhang, 2004; Bullock and Dollars, 2011) defined as “a form of precision handling in which an object is moved using the surface of the palm and the digits of one hand” (Craet et al., 2009: 274). Only a few studies have focused on non-human primates. Preliminary studies in chimpanzees (*Pan troglodytes*) showed the complexity of their dynamic manual abilities in captivity (Craet et al., 2009) and in the wild (Marzke et al., 2015). Moreover, in non-human primates, dynamic hand abilities have been investigated mainly in chimpanzees (i.e. Boesch and Boesch, 1993; Marzke and Wullstein, 1996; Craet et al., 2009; Marzke et al., 2015) and results for other great apes are lacking. Indeed, while wild chimpanzees and orangutans (*Pongo* sp.) use different tools in a variety of contexts (chimpanzees: Goodall, 1968; orangutans: van Schaik et al., 1996; Fox et al., 1999; Bentley-Condit and Smith, 2010; McGrew, 2010; Meulman and van Schaik, 2013), there are few reported examples of tool use in wild gorillas (*Gorilla gorilla* sp.; Breuer et al., 2005; Kinani and Zimmerman, 2014) and bonobos (*Pan paniscus*; Hohmann and Fruth,

2003). It appears thus necessary to explore the manual abilities during tool use in different non-human primates and to focus on lesser known species such as bonobos.

Termite fishing in wild bonobos has never been observed (McGrew et al., 2007), and there is only one report of “ant harvesting tools” discovered near termite mounds (Badrian et al., 1981: 179). Bonobos thus do not appear to use tools to manipulate food in their natural environment, but do use tools for social functions such as communication, play, cleaning, and protection from the rain (Ingmanson, 1996). The absence of extractive foraging in wild bonobos may be due to the small number of groups studied and/or the limited period of time dedicated to the observation (Gruber et al., 2010). This is supported by the fact that studies in captivity indicated that they use a variety of objects as tools for food acquisition (Visalberghi et al., 1995; Boose et al., 2013). Moreover, the ability to manufacture and use appropriate tools for food extraction has been demonstrated as well (Boose et al., 2013). In addition, bonobos have been shown to be able to produce stone tools in captivity (Toth et al., 1993; Schick et al., 1999; Roffman et al., 2012). Captive bonobos demonstrated the same capacity of understanding the properties of tools as other great apes do (Herrmann et al., 2008) and tool use in bonobos can be as complex as in chimpanzees (Takeshita et al., 1996; Gruber et al., 2010). Thus, the absence of habitual tool use in wild bonobos cannot be attributed to the lack of manual abilities (Takeshita et al., 1996). Moreover, manipulation abilities in bonobos have been investigated in detail during object grasping (Christel, 1993; Takeshita et al., 1996; Christel et al., 1998) but have never been examined during tool use behavior.

The aim of the present study was to quantify the functional and behavioral strategies used in captive bonobos during two different tool use tasks: a task of food extraction from a large piece of wood, and a task involving food recovery from a wooden maze (chapter 2). Our two tasks were defined as simple tool use actions following the definition that “simple tool use includes all instances where a single tool is used to perform all actions necessary to obtain the reward” (Boesch, 2013: 25). The food extraction task was comparable to the termite-fishing task recently described for captive bonobos (Boose et al., 2013). The mazes were different from those used in previous studies focusing on spatial memory (i.e. Paul et al., 2009), anxiety (i.e. Pinheiro et al., 2007) or virtual cognitive tasks (i.e. in macaque, Washburn and Astur, 2003). They were indeed not virtual but real and used to quantify the different strategies of manipulation in bonobos during tool use to recover food. Even if it is classified as a “simple” tool use task, we consider this task more complex than the food extraction task because it requires several steps (Parker and Gibson, 1977; Meulman and van Schaik, 2013).

Indeed, the maze task requires the use of a tool to reach and recover a walnut by facing many obstacles: first, obstacles placed inside the maze in order to complicate the path of the walnut, and second, wire netting placed between the maze and the subject. These obstacles involved several constraints in terms of forelimb coordination, body posture adjustments, manual abilities, and vision. We expected this variability of constraints between the two tasks to influence the functional and behavioral strategies. We focused on grasping postures, in-hand movements which have never before been studied in bonobos, sequences of postures used, and the kind of tools selected. As we only focused on the process that occurred at the task location, tool manufacture and modification processes are not documented here.

We hypothesized that (1) new types of grasping postures would be observed during tool use tasks compared to those previously observed during food grasping, (2) bonobos would use in-hand movements and complex sequences of postures during both tool use tasks, but possibly with a greater variability for the maze task, (3) following Boose and collaborators (2013), we also predicted that bonobos would use appropriate tools according to the task.

2. MATERIAL AND METHODS

2.1. Subjects and housing

The study was conducted from 1 February to 18 April 2012 at the “Vallée des singes” (France). A group of nine captive bonobos (five females and four males) from 4 to 43 years old (15.88 ± 4.12 years) was observed. According to the age classes of bonobos defined by Kano (1992), our group was composed of two adult females, two adult males, two adolescent females and two adolescent males. One juvenile female (4 years old), Nakala, had not yet included tool use in her behavioral repertoire and was excluded from the analyses. The bonobos were housed in an indoor building consisting of a network of eight cages from 30 to 98 m² with a height of 3 to 6 m (the two larger cages were visible to the public while the six smaller cages were not). Several climbing structures were present in each of the cages. This indoor building was connected to an outdoor island with grass and mature trees. However, bonobos could not access this island in February and March. They could go to the island in April, during the afternoon only. Water was available *ad libitum* in their pens and they were fed four times a day. The food used for our protocol was part of the daily diet. All subjects

were tested within their social group, in cages not visible to the public. Before our study, this group already had experience with food extraction tasks.

2.2. General Procedure

Tree branches of different lengths and shapes (maximum length of 3 m) were provided at the beginning of the experimental period, and were freely available to bonobos as raw material for potential tools. Thus, bonobos could manufacture and modify their tools freely. The tools manufactured by bonobos were not discarded during the experimental period and were left in the cages. One task was conducted per day in the morning and lasted until the food was consumed (around 30 minutes for both tasks). Two cameras (Sanyo® Xacti VPS-HD2000), one fixed and one mobile, were used during the experiments to optimize the recording and obtain detailed data of hand use. Videos were recorded at 60 frames/second. These recordings were conducted for the study on the hand preferences of bonobos (chapter 2), and in the present study we used the videos to quantify the tool use process.

2.3. Experimental tasks

2.3.1. Task 1: Food extraction.

Twelve logs (mean length = 53.25 ± 2.90 cm and mean diameter = 9.17 ± 0.88 cm) with ten holes (1.5 cm in diameter) drilled all around and over their entire length were hung vertically inside the cage (see Figure 4a). The logs were hung at different heights and were placed in every cage to avoid social tensions. Sticky food (fruit puree) was placed inside the holes. Subjects had to use a tool with one hand to be able to extract the food and visual guidance was required to insert the tool into the holes. The other hand was placed on the log or on the bars of the cage. Eleven test sessions were conducted with one session per day and each subject was observed between five and nine days (mean = 6.87 ± 0.58). The eight subjects performed the task. Some subjects were more rapid to extract food than others, or accessed the logs more easily, so we decided to use a focal sampling method of 2 minutes (defined here as a sequence). This method was used to ensure an approximately similar number of events between subjects. We decided to record data with the frequencies technique (i.e. Hopkins, 1995), in which each food extraction event is recorded, and not the bout technique in which

only the first pattern of a series of identical actions is recorded (i.e. Marchant and McGrew, 1991). Using the frequencies technique allowed us to not lose information on in-hand movements. Food extraction events were recorded if the bonobos were seated. One event was counted each time a subject inserted the tool into a hole, removed it from the hole, and brought it to its mouth with one hand (without bimanual coordination). The parameters observed during each event were the grasping posture, in-hand movements for repositioning the tool within one hand (surface of the palm and the fingers), tool selectivity with the types of tool used (length, diameter and shape). We recorded 564 events (mean = 70.5 ± 7.47 per subject) of extraction.

2.3.2. Task 2: The maze.

This task consisted of reaching walnuts positioned on a wooden maze (45 cm wide by 60 cm long) with a tool. The mazes were attached to the wire mesh of the cage (size = 5x5 cm), but hung outside the cage (see Figure 4b). To avoid competition and social tension, nine different mazes were placed simultaneously around the cages. These mazes differed in the shape, position, and size of the wooden obstacles. These differences provided different potential spatial adjustment of the walnuts inside each maze. In the study on the hand preferences of bonobos (chapter 2), we observed social pressure or competition during the maze task. Individuals preferred to visit mazes with simple spatial adjustment over more complex mazes. Thus, in this present study, we decided to focus on a specific maze (Figure 4b). This maze constituted a good compromise in term of complexity in order to observe a maximum of subjects. This was also a pragmatic choice as the structure of the building did not allow us to film all the mazes at the same time. The maze was positioned 30 cm from the ground in order to constrain bonobos to a seated posture. It was composed of 11 wooden obstacles of different shapes and sizes. The walnuts were placed at the end of the maze (60cm away from the subject). Among our eight subjects, a young male (Kelele) never succeeded to access the maze and one male (David) succeeded in reaching the maze only once, restricting the analysis to six subjects only. Three sessions per individual were recorded, one session corresponding to when a subject reached one walnut. On average 2.17 ± 0.31 days were necessary to get the data of one individual. A sequence began when a subject started to go through the maze with the walnut and ended when it could reach the walnut by hand. In addition to the different parameters observed for the food extraction task, during each session

we counted the number of hand movements used to reach the walnut (quantified by wrist movements), the number of touched wooden obstacles (placed inside the maze), and the time to reach the walnut and the number of position changes of the tool in the grid. We recorded an event each time a subject moved its fingers (i.e. displacements), stopped moving the tool for more than 20 s, and when a subject changed the position of the tool in the grid. Among all subjects and for all sessions, we recorded a total of 95 events.

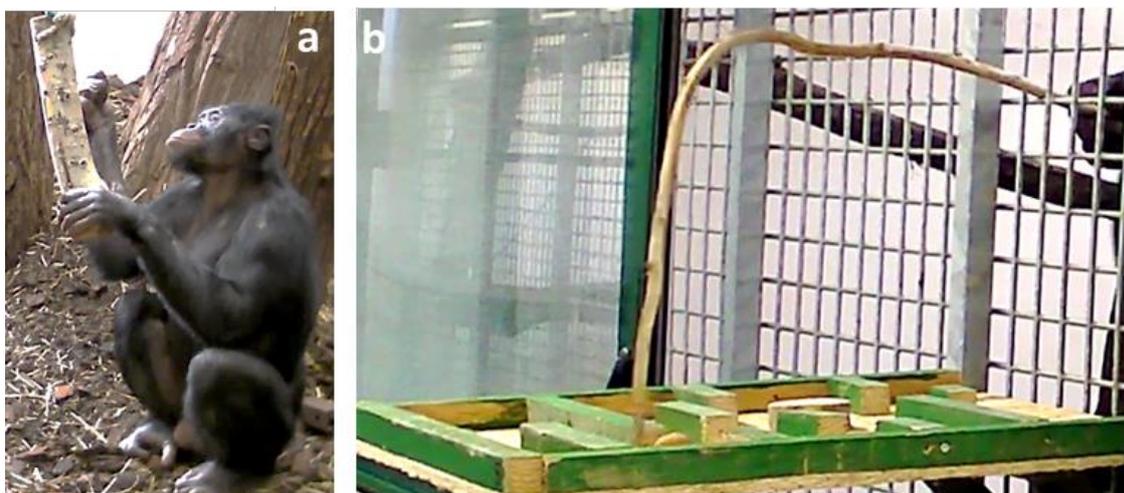


Figure 4. Testing situation: a) food extraction task and b) maze task. Subject in a) is holding the log with one hand and holding a stick in an extended transverse hook grasp with the other hand. The subject in b) is holding a curved tool with one hand with a thumb lateral grasp combined with a passive used of the palm.

2.4. Classification system

First, we characterized the strategies of tool grasping using a method recently implemented by Borel et al. (2016a). Each grasping posture was characterized by a combination of hand contact areas with the tool and defined following the anatomical terminology (see Figure 5). To name the grasping postures we used the Marzke's typology of grasp (Marzke and Wullstein, 1996; Marzke et al., 2015) and we divided the grasp types into five categories (Table 2):

- *Category 1*: contact between distal phalanges of the thumb and the index finger. This category corresponds to the category called “precision grip” in Jones-Engels and Bard (1996) and “Thumb-index grips” in Pouydebat et al. (2011).
- *Category 2*: contact between the distal phalanx of the thumb, the lateral side of the middle, proximal phalanxes of the index finger and the tool. This category included the grasping postures called “thumb lateral” in Pouydebat et al. (2011).

- *Category 3*: contact between one or several fingers, except the thumb, and the tool, called “without thumb” in Pouydebat et al. (2011).
- *Category 4*: contact involving palm, the thumb and one or several part of other fingers and the tool, involving the power grasping posture (Napier, 1956; Jones-Engels and Bard, 1996), and called “palm grips” in Pouydebat et al. (2011).
- *Category 5*: contact types which fell outside the above categories, involving the “hook grip” in Napier (1956) and called “other grips” in Jones-Engels and Bard (1996).

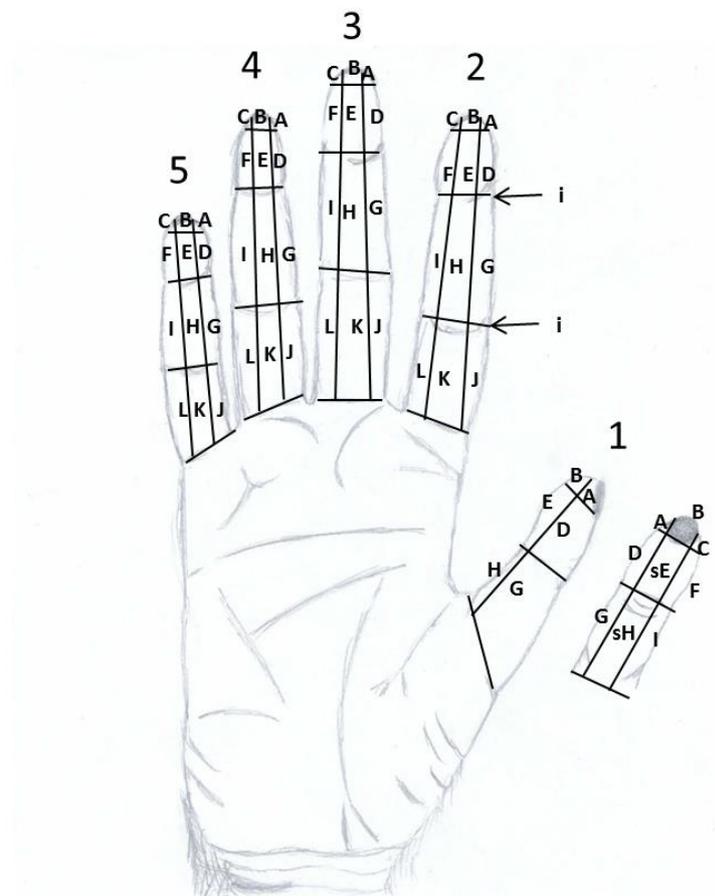


Figure 5. Right hand of a Bonobo with the code used for each contact area (adapted from Borel et al., 2016a) and with the right thumb in dorsal view. A contact area is indicated with the first letter of the hand (R for right or L for left), the number of the finger and the letter(s) of the contact area (i.e. R1E.2G). For dorsal contact we added the letter “s” before the letter of contact area (i.e. 2sH for the dorsal area of the middle phalanx of the index finger). For interphalangeal contacts, we added the letter “i” between the two letters of phalanx (i.e. 2DiG for contact with the distal interphalangeal joint of the index finger).

2.5. Data analysis

Video analysis was performed with VLC® media player using a focal sampling protocol (Altmann, 1974). For multiple comparisons, we used the Friedman chi-squared test and for pairwise comparisons the Wilcoxon signed-rank test, with continuity correction for the maze task as we analyzed a small sample ($N = 6$). We performed statistical tests in the software R (R development Core Team 2013). Tests were two-tailed with a significance level set at 0.05.

Time-based sequence analysis was used to quantify and visualize the combinations of the contact areas between hand and tool during tool use tasks. The combinations of the contact areas, with the time associated were exported to the software R (R development Core Team 2013) and Time-based sequence analysis were performed with the package TraMineR (Gabadinho et al., 2011) modified by Borel et al. (2016a).

In order to describe the strategies used during the maze task on all the sessions ($N = 18$), a Principal Component Analysis (PCA) was performed on six variables (P): the number of in-hand movements, the number of combinations of contacts areas, the number of hand movements used to reach the walnut, the number of touched wooden obstacles, the time to reach the walnut, the number of position changes of the tool in the grid. PCA was performed in R (R development Core Team 2013), with the raw data normalized for all the sessions of all subjects.

3. RESULTS

3.1. Grasping postures and combinations of contact areas

A total of 17 grasp types were observed during the two tasks with different variants for some grasp types (Table 2).

3.1.1. Task 1: Food extraction.

We recorded a total of 564 grasping events. Except for Khaya, who used only one grasp type, subjects used from two to eight grasp types (mean = 4.71 ± 0.75) (Table 3). Grasps for which bonobos used their thumbs and index fingers in varying combinations of contact areas (Figure 6) accounted for 50% of all events (282/564). Subjects used their full

palm passively (the tool was just in contact with the palm which didn't firmly grasp it) combined with a thumb lateral grasp in 6% of cases (34/564), and the distal palm in 3% (17/564) during extended transverse hook grasps and 4-jaw extended transverse hook grasps.

We recorded a total of 37 combinations of contacts areas (see Figure 5 for the method to quantify these combinations) and 81.1 % (N = 30/37) of these combinations were used by only one individual. Each subject used between one and 12 (mean = 6.38 ± 1.35) different combinations of contacts areas.

The four males used more combinations of contact areas (mean = 8.75 ± 1.88) and various grasp types (mean = 6 ± 0.91) than the four females (combinations, mean = 4 ± 1.08 ; grasping postures, mean = 2.5 ± 0.64).

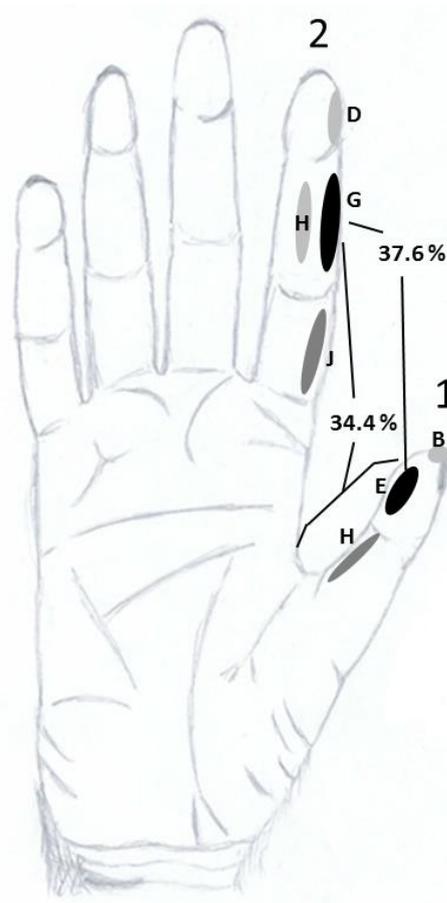


Figure 6. Combination of contact areas between the thumb and the index for the food extraction task, whether for the right or left hand. At the group level, the more the area is dark the more this area was used. For example, the two main combinations were 1E.2G and 1EH.2G, corresponding respectively to the Two-jaw chuck pad-to-side and the V pocket grasping postures.

Table 2. Variability of the grasping postures used to hold a tool during the two tasks and the number of events by task.

Category of grasping postures	Grasping postures name	Acronym	Description	Number of observations by task	
				Task 1	Task 2
Thumb-index grips	Two-jaw chuck ^a pad-to-pad side	2JCPS	Tool held between pad of the thumb and side of the pad of the index finger.	N = 8/564	-
	Two-jaw chuck thumb-to-index	2JC	Tool held between pad of the thumb and the ventral part of middle phalanx of the index finger.	N = 4/564	-
Thumb lateral	Two-jaw chuck tip-to-side	2JCTS	Tool held between tip of the thumb and the side of the index finger.	-	N = 2/95
	Two-jaw chuck pad-to-side ^b	2JCPS	Tool held between pad of the thumb and the side of the index finger.	N = 165/564	N = 9/95
	Two-jaw chuck proximal-to-side	2JCPrxS	Tool held between proximal phalanx of the thumb and the side of the index finger.	N = 2/564	-
Without thumb	Scissor hold ^c	SH	Tool held between fingers 2-3.	-	N = 2/95
	3-jaw chuck	3JC	Tool held by flexed fingers 2-3 and between the side of finger 4.	N = 48/564	-
				Tool held between flexed fingers 2-3 and the proximal phalanx of finger 5.	-
With palm	Thumb lateral with palm	P2JCPS	Tool held between thumb and index finger with passive contact of the palm with the tool.	N = 34/564	-
	Power grip	P	Tool held in opposition between the palm and flexed fingers with a possible pressure applied by the thumb.	-	N = 2/95
Other grips	V pocket ^c	VP	Tool held in web between full thumb and index finger, other fingers were flexed but not in contact with the tool.	N = 103/564	-
	3-jaw chuck with thumb	T3JC	Tool held between the middle phalanges of fingers 2-3 and with a pressure applied by the thumb.	N = 45/564	N = 2/95
			Tool held between the distal part of the thumb and the palmar aspect of the middle phalanx of fingers 2-3.	-	N = 4/95
			Tool held by flexed fingers 2-3 and with counter pressure applied by the thumb.	-	N = 4/95
Tool held by lateral and distal part of the thumb, flexed index, and lateral aspect of finger 3.			-	N = 9/95	

			Tool held by lateral and distal part of the thumb and between flexed fingers 2-3.	-	N = 1/95
<i>Hook grasping postures</i>	Transverse hook ^b	TH	Tool held by all fingers flexed at interphalangeal joints, the thumb may be adducted or opposed, and the distal part of the palm was not involved.	N = 90/564	N = 11/95
	4-jaw chuck transverse hook	4JCTH	Tool held by fingers 1-2 and 4-5 flexed at interphalangeal joints; finger 3 was straight, and the distal part of the palm was not involved.	N = 3/564	-
			Tool held by fingers 1-4 flexed at interphalangeal joints, and the distal part of the palm was not involved. Contact with any part of phalanx of fingers 1-3 and the side of the middle phalanx of finger 4	N = 45/564	-
	Extended transverse hook ^b	ETH	Tool held by all fingers flexed at all joints and the distal part of the palm was involved.	N = 8/564	N = 30/95
	4-jaw chuck extended transverse hook	4JCETH	Tool held by fingers 2-5 flexed at all joints, the thumb may be adducted or opposed, and the distal part of the palm was involved.	N = 9/564	-
	Diagonal hook ^b	DH	Tool held by decreasingly flexed distal fingers 5-1; the distal part of the palm was not involved.	-	N = 10/95
	Extended diagonal hook ^b	EDH	Tool held by decreasingly flexed full fingers 5-1; the distal part of the palm was involved.	-	N = 8/95

^a “X-jaw chuck” typology of Marzke and collaborators (Marzke and Wullstein, 1996; Marzke et al., 2015) refers to the number of fingers, X, that clamp an object. ^{b,c} The grasping postures are named and are described for chimpanzees in ^b Marzke and Wullstein (1996) and ^c in Marzke et al. (2015).

3.1.2. Task 2: Maze.

We recorded a total of 95 grasping events. Except for Khaya, who used only one type of grasp, subjects used from two to four grasp types (mean = 2.83 ± 0.54) during the total of the three sessions. During one session they used on average 1.28 ± 0.14 grasp types. Compared to the food extraction task, individuals during the maze task used more hook grasping postures (Table 2). Some postures were only used by one individual and very few individuals used more than one preferred grasp type (Table 4).

We recorded a total of 32 combinations of contact areas, and 31 combinations were used by only one subject, indicating strong intra-variability. Subjects used between three and nine different combinations of contact areas (mean = 5.5 ± 0.99).

The four females used on average more combinations of contact areas (mean = 6.5 ± 1.19) than the two males (see methods section for explanation about less males observed for this task) (mean = 3.5 ± 0.5) while both used similar number of grasp types (mean for females = 2.75 ± 0.75 ; mean for males = 3 ± 1).

Table 3. Percentages of grasping postures used for each subject during the food extraction task.^a

Grasping postures ^a	Daniela	Ukela	Kirembo	Diwani	David	Khaya	Lingala	Kelele
2JCPS	8	26	6	36	8		90	22
TH	21	69	1	1				55
T3JC			10			100		
VP	37				82		10	20
ETH			6	1	3			
3JC			31	24				
P2JCPS	34			15				
4JCTH			45	10				
2JCPPS		6			5			
2JCPrxS					1			2
4JCETH				10				
2J				2				
C								

^a 2JCPS = Two-jaw chuck pad-to-side; TH = Transverse hook; T3JC = 3-jaw chuck with thumb; VP = V pocket; ETH = Extended transverse hook; 3JC = 3-jaw chuck; P2JCPS = Thumb lateral with palm; 4JCTH = 4-jaw chuck transverse hook; 2JCPPS = Two-jaw chuck pad-to-pad side; 2JCPrxS = Two-jaw chuck proximal-to-side; 4JCETH = 4-jaw chuck extended transverse hook; 2JC = Two-jaw chuck thumb-to-index.

Table 4. Percentages of grasping postures used for each subject during the maze task.^a

Grasping postures ^a	Daniela	Ukela	Kirembo	Diwani	Khaya	Lingala
T3JC	11		22	67	100	
TH	3	26	44			
DH		35		33		
2JCPS		4				80
EDH		35				
ETH	81					
3JC			11			
2JCTS						20
SH			22			
P	5					

^a T3JC = 3-jaw chuck with thumb; TH = Transverse hook; DH = Diagonal hook; 2JCPS = Two-jaw chuck pad-to-side; EDH = Extended diagonal hook; ETH = Extended transverse hook; 3JC = 3-jaw chuck; 2JCTS = Two-jaw chuck tip-to-side; SH = Scissor hold; P = Power grip.

3.2. Dynamic tool manipulation: in-hand movements and sequences of contact areas

We quantified ten in-hand movements and combinations of in-hand movements in this research (defined in Table 5).

3.2.1. Task 1: Food extraction.

We observed in-hand movements only five times during the 564 grasping events. Three kinds of in-hand movements were observed: roll (ROL; used one time by Daniela), thumb extension and flexion (T.EF; used one time by Daniela and two times by Diwani) and extension and flexion of all fingers (EF; used one time by David).

During the sequences of extraction, we observed few changes of contact areas between the tool and the hand. Five subjects (four males and one female) changed their contact areas during two or three sequences of extraction (mean = 2.6 ± 0.63). The female (Daniela) just combined the palm with a thumb lateral grasp during two sequences (N total = 6). Males changed their combinations of contact areas between two and four times during one sequence (mean = 2.45 ± 0.21). They also changed the number of fingers placed on the tool, inducing more changes in grasp types than Daniela.

3.2.2. Task 2: Maze.

We recorded a total of 77 in-hand movements events classified in ten different types (as defined in Table 5). We did not observe statistically significant differences in the number of in-hand movements used between the three sessions (Friedman rank sum test, $Q = 9.5146$, $df = 5$, $P = 0.09$). Of the six subjects observed for this task, all used in-hand movements. Some movements were not used in every session or by every subject, and some movements were applied between two and five subjects (see Table 6). The in-hand movement applied most by all subjects except Kirembo, was thumb extension and flexion (T.EF) (Table 6). The two oldest females, Daniela and Ukela, used more in-hand movements during the three sessions as well as on average than other subjects (Table 6). Daniela used more different types of in-hand movements ($N = 8/10$) than other subjects. We also noticed that Lingala adjusted the tool in her hand using her lips and Ukela used a foot. This occurred only one time in one session for both subjects.

More changes of combinations of contact areas between hand and tool were observed during a single session for this task (Figure 7) than for food extraction. It was the two adult females which changed more often their combinations of contact areas (nine times for Ukela and six times for Daniela during the first session) (Figure 7). The other subjects changed between zero and two times during one session (Figure 7). Daniela put the most time to reach the walnut (152 s) and Kirembo the least amount of time (20 s) (Figure 7). Females got the walnut on average in 102.75 ± 10.80 s with 119.33 ± 14.04 s for adult females and 86.16 ± 14.37 s for adolescent females. Adult males took on average 70.5 ± 15.70 s.

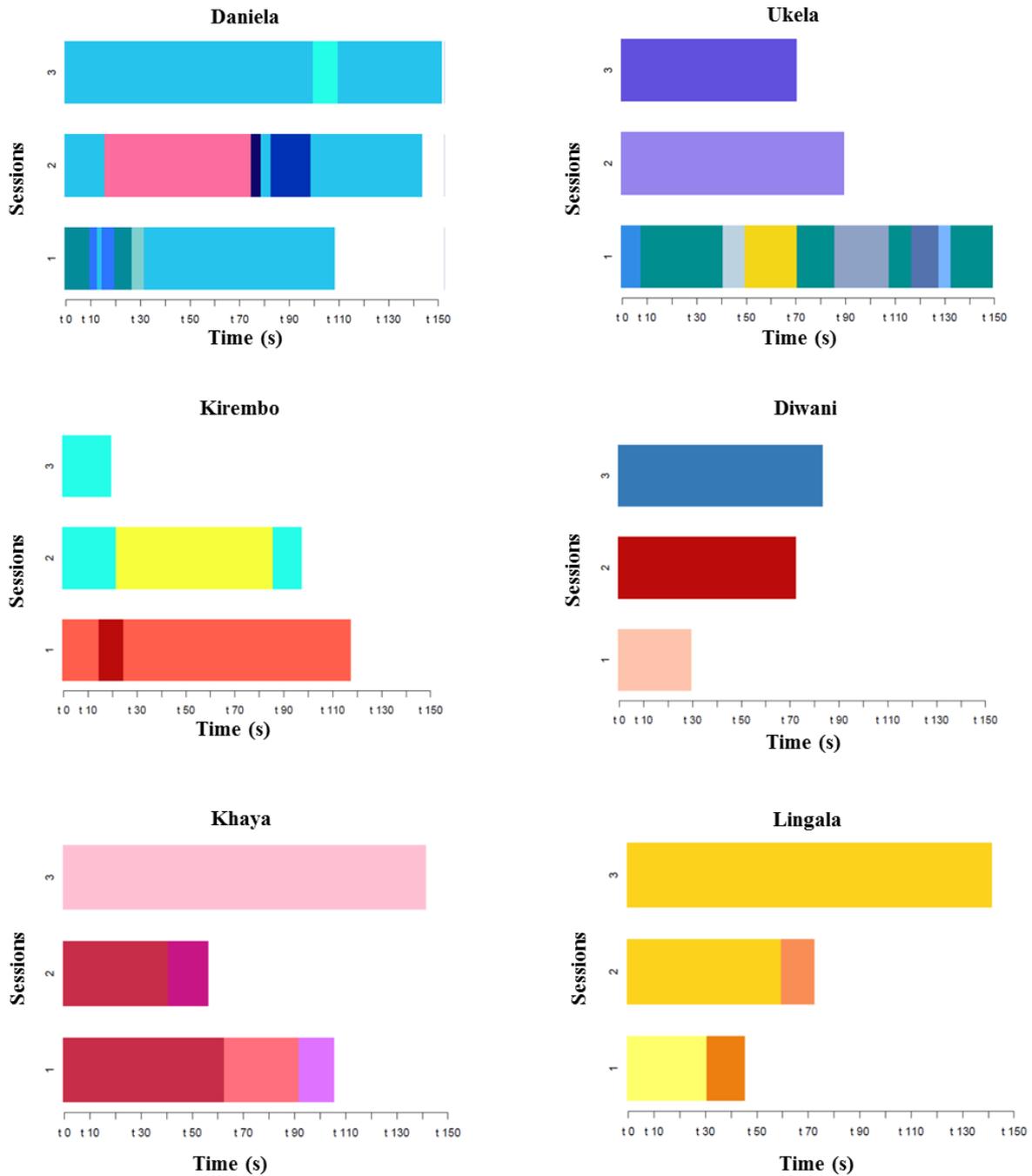


Figure 7. Sequences of combinations of contact areas used by each subject and by session for the maze task. Each color corresponds to a specific combination of contact areas (for example the blue in session three of Daniela corresponds to the combination R1E.2EHK.3EHK.4EHK.5EH).

Table 5. Definition of the different in-hand movements and their combinations to reposition the tool in the hand observed during the two tasks.^a

Type	Definition
Extension and Flexion (EF)	<i>Finger movements</i> Opening and closing all fingers (EF), moving away from midline of the hand and the tool slides along the fingers or palm.
Thumb adduction (TAD) ^a Thumb extension and flexion (T.EF)	<i>Thumb movement alone moves tool</i> Thumb moves toward midline of the hand.
Index abduction (IAB) ^a Index extension and flexion (I.EF)	<i>Index movement alone moves tool</i> Index moves away from midline of the hand.
Roll (ROL) ^a	<i>Tool held between two digits</i> Fingers move opposite to one another to twist or roll the tool along one axis.
Extension and Flexion of fingers and Thumb abduction/adduction (EF.TAB/EF.TAD)	<i>Combination of in-hand movements</i> Opening and closing fingers 2 to 5 and thumb moves away (TAB) or toward the midline of the hand (TAD).
Extension of all fingers, releases the tool and takes it later (E.REL)	Opening fingers moving away from the midline of the hand which releases and grasps the tool again.
Extension of all fingers and help of the second hand to repositioning tool (E.H)	Opening fingers moving away from midline of hand; the object slides along the fingers or palm and the second hand helps to repositioning the tool in the hand.

^a Named and defined in Crast et al., 2009.

Table 6. Details of in-hand movements used by session (S) by each subject and the mean number of in-hand movements (with standard errors) during one session by each subject. Table footnote: In-hand movements are described in table 2. EF = Extension and Flexion; TAD = Thumb adduction; T.EF = Thumb extension and flexion; IAB = Index abduction; I.EF = Index extension and flexion; ROL = Roll; EF.TAB = Extension and Flexion of fingers and Thumb abduction; EF.TAD = Extension and Flexion of fingers and Thumb adduction; E.REL = Extension of all fingers, releases the tool and takes it later; E.H = Extension of all fingers and help of the second hand to repositioning tool.

In-hand movements	Daniela				Ukela				Kirembo				Divani				Khaya				Lingala				
	S1	S2	S3	Mean and SE	S1	S2	S3	Mean and SE	S1	S2	S3	Mean and SE	S1	S2	S3	Mean and SE	S1	S2	S3	Mean and SE	S1	S2	S3	Mean and SE	
EF	4	8	8	6.67±1.33	9	5	3	5.67±1.76	2	0	0	0.67±0.67	-	-	-	-	-	-	-	-	-	-	-	-	-
TAD	1	0	0	0.33±0.33	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
T.EF	4	0	1	1.67±1.2	1	2	2	1.67±0.33	-	-	-	-	1	1	1	1±0	0	0	1	0.33±0.33	0	2	0	0.67±0.67	-
IAB	-	-	-	-	1	0	0	0.33±0.33	0	1	0	0.33±0.33	-	-	-	-	-	-	-	-	-	-	-	-	-
I.EF	0	0	1	0.33±0.33	-	-	-	-	-	-	-	-	-	-	-	-	1	1	3	1.67±0.67	-	-	-	-	-
ROL	0	2	0	0.67±0.67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EF.TAB	2	1	0	1±0.58	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EF.TAD	1	0	0	0.33±0.33	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E.REL	-	-	-	-	-	-	-	-	0	2	1	1±0.58	-	-	-	-	2	0	0	0.67±0.67	1	0	0	0.33±0.33	-
E.H	0	1	0	0.67±0.67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total	12	12	10	11.33±0.67	11	7	5	7.67±1.76	2	3	1	2±0.6	1	1	1	1±0	3	1	4	2.67±0.88	1	2	0	1±0.58	-

3.3. Tools selected

Subjects arrived on the location of the task with their tool already modified in 99.47 % of the cases for the food extraction task (N = 561/564) and in 83.33 % of the cases for the maze task (N = 15/18). For the six events of modifications, we observed five individuals who used two techniques. Four individuals grasped the tool with one hand and used their mouth to break the tool thereby shrinking it, and one individual for two events used both hands to break the tool and its mouth to peel bark.

As every tool was different, we classified the tools according to their length, shape, and diameter. Two types of tool shape were identified: curved (see Figure 4b) and straight. For the diameter, tools were classified in two categories: the fine tools with a diameter of less than 1 cm and the coarse tools with a diameter greater than 1 cm. The diameter of the tool did not seem to have a significant effect on the number of fingers used to grasp the tool (for tests with 2 to 5 fingers, Friedman rank sum tests, N = 8, P > 0.05).

3.3.1. Task 1: Food extraction.

Subjects used six tools lengths between 10 and 60 cm. No particular length was preferred (Friedman rank sum test, N = 8, $Q = 4.1528$, $df = 7$, P = 0.76). However, it seemed that they used more small tools (i.e. less or equal than 30 cm long; N = 439/564) than long tools (i.e. more than 30 cm; N = 125/564). They used significantly more straight tools (97.2 %; N = 548/564) than curved tools (2.8 %; N = 16/564) (Wilcoxon rank sum test with continuity correction, N = 8, $W = 0$, P < 0.001). We observed two types of tool tips, “brush tip” and “pointed tips”, which were significantly more used (73.05 %; N = 412/564) than straight tips (26.95 %; N = 152/564) (Wilcoxon rank sum test with continuity correction; N = 8, $W = 59$, P < 0.01). Considering the diameter of the tools, bonobos used significantly more fine tools (N = 527/564) than coarse tools (N = 37/564) (Wilcoxon signed rank test, N = 8, $W = 36$, $df = 7$, P < 0.01).

3.3.2. Task 2: Maze.

We recorded 18 tools differing by their shape, size, and diameter were used by the bonobos. Curved tools (see Figure 1b for an example of curved tool) were used in 66.7 % (N = 12/18) but were not used statistically significantly more than straight ones (33.3 %; N = 6/18)

(Wilcoxon rank sum test with continuity correction, $N = 6$, $W = 5$, $P = 0.28$). We observed that all subjects used curved tools and three individuals (Daniela, Ukela and Diwani) spontaneously chose this type of tool at the beginning (first session). More subjects used curved tools during the third session (Daniela, Ukela, Diwani, Kirembo, and Khaya). Daniela and her son Diwani used curved tools in each session while the others changed between sessions.

We observed two types of length, long tools (more than 60 cm long; 60 cm being the length of the maze) and short tools (less or equal than 60 cm long). Subjects used significantly more long tools (77.8 %; $N = 14/18$) than short tools (22.2 %; $N = 4/18$) (Wilcoxon signed rank-test with continuity correction, $N = 6$, $W = 0$, $P = 0.03$). We observed three types of tool tips; “pointed tips” (55.6 %; $N = 10/18$), “large tips” (22.2 %; $N = 4/18$), and “straight tips” (22.2 %; $N = 4/18$). No significant statistical differences between these three types of tips were noticed (Friedman rank sum test, $N = 6$, $Q = 0.3846$, $df = 5$, $P = 0.99$). Considering the diameter of the tools, they used significantly more coarse tools ($N = 16/18$) than fine tools ($N = 2/18$) (Wilcoxon signed rank test with continuity correction, $N = 6$, $W = 0$, $df = 5$, $P < 0.05$).

3.4. Principal component analysis for the maze task

For the three sessions, subjects needed an average of 35.28 ± 3.32 hand movements to get the walnut. They touched obstacles on average 6.17 ± 0.94 times. They changed the placement of tools in the grid on average 5.67 ± 1.82 times.

The three first axes of the PCA performed on the raw data explained 89 % of the total variance. The first axis (44 %) was determined by time needed to retrieve the walnut (loading = 0.49), the number of repositioning movements (loading = 0.47), the number of in-hand movements used (loading = 0.45), and the total number of hand movements used (loading = 0.35). The second axis (25 %) was explained by the total number of obstacles touched (loading = 0.81) and the number of repositioning movements (loading = 0.39). The third axis (20 %) was determined by the number of tool repositioning in the grid (loading = 0.74) and the total number of combinations of contact areas used (loading = 0.57). The PCA distinguished between the different strategies observed for each subject and for some subjects between them (Figure 8a,b,c). PC1 attempted to distinguish sessions within each subject. Sessions situated along the positive side of PC1 took more time, more repositioning movements, more in-hand movements and overall hand movements than sessions situated along the negative side of this axis (Figure 8a). These results indicated intra-individual

variation in the strategies used by each subject for these four parameters, except for Khaya and Daniela who seemed to be rather standardized in their strategies with less variation between sessions than other subjects. PC2 attempted to distinguish subjects by their strategies and the differences in the number of obstacles touched and the number of repositioning movements. Subjects situated along the negative side of PC2 touched more obstacles and repositioned their tool more than subjects situated along the positive side of this axis (Figure 8b). These results indicated inter-individual variation in the general strategies used, with specific strategies observed for the four adults with respect to the number of obstacles touched and the number of repositioning movements. Khaya and Lingala seemed not to use stable strategies and showed strong variability between sessions. PC3 attempted to distinguish sessions and subjects but mostly distinguished two sessions of Daniela from all the other sessions. Sessions of the subjects situated along the positive end of the axis were performed with more tool repositioning and fewer combinations of contacts used than sessions situated along the negative side of this axis (Figure 8c). We suggest that each individual can perform the task differently according to the grasp type that they use.

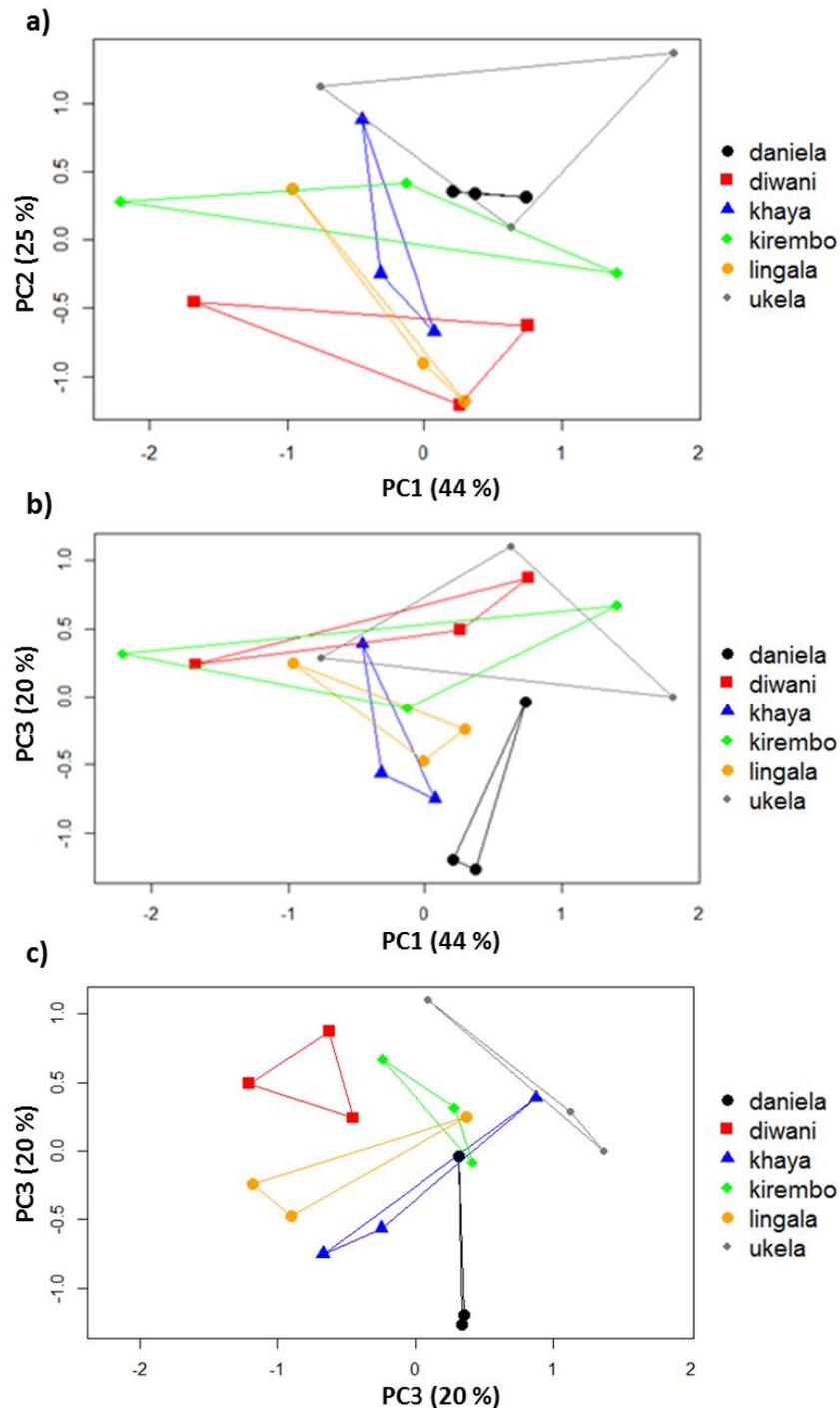


Figure 8. Results of the three first axes (PC1, PC2, PC3) of a principal component analysis performed on six variables, with all the data for all the sessions of all individuals. Polygons represent individuals and points sessions. PC1 distinguished sessions within each subject; sessions situated along the positive side of PC1 took more time, more repositioning movements, more in-hand movements and overall hand movements than sessions situated along the negative side of this axis. PC2 attempted to distinguish subjects based on their strategies; subjects situated along the negative side of PC2 touched more obstacles and repositioned their tool more than subjects situated along the positive side of this axis. PC3 also attempted to distinguish between subjects, but mainly separated two sessions of Daniela from all other sessions; sessions situated along the positive side repositioned their tool more and used fewer combinations of contact areas than subjects situated along the negative side of this axis.

4. DISCUSSION

Our study revealed three major findings regarding tool manipulation in bonobos. First, bonobos used a great variety of grasp types during tool use tasks. Second, bonobos used in-hand movement, demonstrated complex sequences of contacts, and showed more dynamic manipulation during the maze task than during the extraction task. Finally, they responded to task constraints by selecting and/or modifying tools appropriately, usually before they started the tasks. Ours results also indicated that bonobos showed individual manual strategies. These results make this study useful and compelling in spite of our small sample size and show new insights into both functional and behavioral manipulative abilities and possible morphological correlates with these abilities. The following discussion considers the implications of our findings with regard to the specific tasks of the bonobos, the individual differences observed, and the evolution of manual abilities in primates.

4.1. New grasping postures and functional links

In accordance with our first hypothesis, new grasp types in captive bonobos were observed. In previous studies, respectively four (Christel, 1993) and seven (Christel et al., 1998) variants of grasp types between thumb and index finger were observed. During the two tool tasks we also observed a grasp type between the thumb and index finger with nine variants but little implication of the tip of the thumb. The two-jaw chuck pad-to-side grasp type was the most observed in this group of captive bonobos during the food extraction task. This observation is consistent with previous research on herbaceous termite or ant fishing in chimpanzees (i.e. Marzke et al., 2015; Lesnik et al., 2015), and this grip was also used by wild chimpanzees for perforating the opening of a termite nest (Lesnik et al., 2015).

One variant of the 3-jaw chuck with thumb, where the tool was held between the middle phalanges of fingers 2-3 and with pressure applied by the thumb, was observed recently for the first time in wild chimpanzees (Lesnik et al., 2015). Lesnik and collaborators (2015) called this grasp type “interdigital brace” and in human studies it is defined as an inefficient variant of pencil grasp (Selin, 2003). These authors ranked this grip as being more powerful than the two-jaw chuck pad-to-side grasp type because “it is the bracing of the tool against the hand that gives the grip its greatest strength” (Lesnik et al., 2015: 256). In our

study, only one subject (Khaya) used this grasp all the time during the two tasks. Perhaps for bonobos this is not an efficient grasp type for these tasks.

All of the grasp types observed here were also reported in captive and wild chimpanzees for diverse activities such as tool use (Marzke and Wullstein, 1996; Jones-Engels and Bard, 1996; Pouydebat et al., 2011; Lesnik et al., 2015; Marzke et al., 2015). Similar to these previous studies, we observed different grasp types and a tendency to use different grasp types according to the demand of the task. More hook grasp types were observed during the maze task than for extraction. Hook grasps were used by wild chimpanzees during feeding (Marzke et al., 2015) or tool use (Lesnik et al., 2015), and also gorillas during feeding (i.e. Byrne, 1994). It appears that this grasp type with the fingers flexed around the tool applies more force, increasing the force exerted on the tool allowing to push the walnut more efficiently. We suggest that hook grasps might be more efficient than grasp types between the thumb and index finger for the maze task and subjects that used more power than precision succeeded in the maze task more often. Moreover, grasp types between the thumb and the index finger, including the two-jaw chuck pad-to-side grasp, may be more efficient for extraction. In fact, food extraction involved the extraction of food from a small hole with a relatively fine tool, which likely involves more precision during the manipulation. It also appeared that the V pocket grasp type, where the tool was held between the web of the thumb and index finger, was effective during food extraction. The use of the web between the full thumb and index finger could help to stabilize the tool during precise extraction. Moreover, some grasp types, like the scissor hold (tool grasp between fingers 2-3), were used less by bonobos during the maze task. This grip was completely absent during food extraction. Thus, grasp types differed according to the demand of the task.

4.2. Grasping postures and hand morphology

The reason for the rare use of the thumb's tip in bonobos performing the two tool use tasks could be due to the shape of the tool. The cylindrical tool needs to be firmly grasped between the fingers, and the distal parts of the fingers are rolled around the tool. It also could be explained by the fact that bonobos need, when the thumb is involved, all the phalanges and not only the distal one to firmly grasp the tool. Indeed, bonobos used the thumb to hold the tool in general in an opposed position to other fingers which maintained the tool in the hand. The use of the thumb in opposition to other fingers in chimpanzees was explained by the

transverse portion of the intrinsic thumb adductor muscle which was well-developed compared to humans (Marzke et al., 1999).

The reason for the rare use of the thumb in bonobos performing the maze task could also be due to the absence of several anatomical features. It appears that some human hand muscles are not present in the hands of great apes (Diogo and Wood, 2011; Diogo et al., 2012). Especially two thumb muscles, the *flexor pollicis longus* and *extensor pollicis brevis* which are related to the movement of the thumb and probably important in human tool manipulation (Diogo et al., 2012). These two muscles are only rarely present in great apes (as hylobatids) (Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012). As the maze required forceful grips from the fingers on the tool to retrieve the walnut, we suggest that the absence of these muscles in the hand of bonobos may prevent them to use the tip of the thumb during grasps which involve strong force. Grasping an object indeed necessitates complex muscular coordination and requires high intensities of muscle forces up to 2 times the force exerted on the object in humans (Vigouroux et al., 2011; Goislard de Monsabert et al., 2012). Investigating this coordination and quantifying muscle activities in apes would be of great interest to explore the relationship between hand morphology and hand activities. However, due to the high level of implantation complexity and ethical implications for primates, studies reporting muscles activities during grasping actions in non-human primates are extremely scarce (i.e. Overduin et al., 2008). In the framework of this study; we thus can expect that the morphometry of the bonobo's hand, such as short size of their thumb compared to their long fingers, involves different biomechanical constraints during grasping actions. For example, a smaller thumb would generate different finger joint angle, corresponding to different moment arms and probably would engage different joint and muscle loadings. Consequently the rare use of the thumb for the bonobo could be the results of a choice based on biomechanical loadings, which cannot be balanced by their musculature when grasping with the thumb. Nevertheless, the mechanics of the hand of great apes is poorly understood compared to humans (e.g. for review: Taylor and Schwarz, 1955; e.g. for exhaustive information: Connolly, 1998; Jones and Lederman, 2006) and only the development of a musculoskeletal model based on ape morphological (i.e. size of the segments) and biomechanical data (i.e. force, kinematics, muscle activities) may be appropriate to test this hypothesis.

4.3. Dynamic tool manipulation

With regard to our second hypothesis, our observations showed that bonobos did indeed use in-hand movements to reposition the tool. These manual abilities suggest that bonobos have the level of neuromotor control with the neuromuscular and morphological requirements necessary for complex fingers manipulation. These results confirm the recent study in captive chimpanzees (Craet et al., 2009), that showed their abilities to use complex in-hand movements, suggesting that this dynamic ability is not unique to human hands and could be present at least in the last common ancestor of Hominini.

Bonobos used more in-hand movements during the maze task than during food extraction. This result could be explained by the task itself. In fact, the extraction task did not require complex manipulation in contrast to the maze task which involved many obstacles such as the wire netting between the subject and the maze and the obstacles inside the maze. This task involved repositioning and a dynamic manipulation with more changes of the combinations of contact areas compared to the food extraction task. No movements of the objects between the thumb and fingertips were observed during Mahale chimpanzees feeding (Marzke et al., 2015), but they were observed in an experimental context (Craet et al., 2009). Marzke and collaborators (2015) showed that in-hand movements can be observed during tool-making and tool use behaviors at other chimpanzee sites. According to the taxonomy of Elliot and Connely (1984), bonobos here used more in-hand movements classified as “simple synergies”, where the tool was moved by flexing and extending the fingers without changing its orientation. In the study of Craet et al. (2009), chimpanzees showed complex in-hand movements classified as “sequential patterns” (Elliot and Connely, 1984), involving coordination of fingers in a characteristic sequence of movements. This difference could be explained by the tasks differing between our study and the study of Craet et al. (2009) where chimpanzees needed to grasp and insert the adequate small objects in the corresponding shaped cutouts. Thus, tasks necessitating tool or complex object manipulation and repositioning can require more dynamic strategies inside the hand itself according to the number of steps needed to perform the task. However, in-hand movements performed by chimpanzees (Craet et al., 2009) and in our study by bonobos involved the use of the palm whereas humans executed sequential movements without using the palm but the fingertips instead (Elliot and Connely, 1984). This suggests that the different neuromuscular anatomy and the morphometry of the hand between humans and great apes could involve different in-hand movements. However, more studies are needed to conclude this and a comparison

between humans and great apes during the same activities is especially needed to better understand the mechanisms of their hands.

It appeared difficult to quantify the manipulation with a common method to compare species. The method of time based sequence analysis of contacts areas (Borel et al., 2016a) that we used in our study does not imply direct contact with the observed individuals or the use of markers. Therefore, even if based on video analysis and including few limitations (see Borel et al. 2016a for complete discussion about advantages and limitations) it is a good compromise to obtain comparable data between different species. It allowed us to describe in detail the grasp types variability. It also provided a dynamic view of the manipulation strategies and thus allowed not only recording the number of occurrences of grasp types but also quantifying their duration of use. It has been possible to show that some grasp types were used longer than others. Individual differences were also examined and quantified with this method. This kind of method is a relevant approach to compare tasks and species in future studies, and to investigate more thoroughly inter and intra-individual variability.

4.4. Individual strategies

We observed different functional and behavioral strategies between the subjects and stronger differences between subjects during the maze task. These differences may be explained by morphological and/or behavioral effects. There may be other explanations and with other groups of bonobos there may not be any differences. Despite our small sample size, inter-individual variability is an important point to investigate.

A possible hypothesis for these individual preferences is that some subjects may have more experience in tool use and as such they would have developed an individual technique. For example, some individuals showed less grasp variability. We observed that these individuals, such as Daniela, had more access to the enrichments and thus more time to practice. Individuals in this captive group of eight bonobos could thus develop different grasp types and techniques according to: 1) the time spent obtaining food and 2) their experience in food extraction with tools before the onset of the study. Daniela seemed to be standardized in her strategies (i.e. time to retrieve the walnut, number of in-hand movements). Daniela was the oldest individual in this group and the dominant one. Could we expect bonobos to use different strategies according to the hierarchical rank or the age? We could not discuss this

point in the present study because of our small sample but we suggest one hypothesis that could be interesting to test in future studies. Indeed, Daniela could have developed a stable strategy according to her social status as she had more time to perform the task and because nobody took her place. The males and adolescent females, might have suffered from a lack of time to practice constraining them to use different strategies to reach the walnut as fast as possible before adult females took their place. We clearly need to work on a large sample of different group of bonobos to test this hypothesis.

One subject (Khaya) used only one grasp type during the two tasks: the 3-jaw chuck with thumb. This grasp type is typical of human pencil grasping and this female was raised by humans. We wonder if the use of this grasp type by Khaya was facilitated by this human proximity. However, this grasp type is also used by wild chimpanzees during termite nest perforation (Lesnik et al., 2015), without the proximity of humans. It would be interesting to study the acquisition and the development of these preferred grasp types in bonobos to investigate the presence of 1) a non-social process, 2) a social influence, or 3) social learning (see Whiten and Ham, 1992).

It could also be relevant to compare the maze task results of bonobos with other species to test if the strong individual preference for specific grasp types is particular to bonobos. Variability in the grasp types used by chimpanzees during a food task (Lesnik et al., 2015) or during different food manipulation tasks (Marzke et al., 2015) has been observed but individual preferences were not investigated. Moreover, in chimpanzees dominant males may show more specialization in their manual abilities than females. To investigate this, it would be interesting to observe the manual abilities in chimpanzees of both sexes.

4.5. Selectivity of tools already modified

Bonobos responded to task constraints by selecting and modifying tools appropriately, usually before they started the tasks. When we observed tool manufacture, bonobos used the same specific behaviors as other captive bonobos (Boose et al., 2013) and as wild chimpanzees (McGrew et al., 1979): detachment of raw material, side-branch removal, bark peeling. In our study, bonobos accomplished these steps by using one hand and the mouth or both hands. They used appropriate tools according to the task, in agreement with another study in captive bonobos (Boose et al., 2013). The tips of tools were modified especially for

the food extraction with “brush” and “pointed” tips like in wild chimpanzees in the Goulougo Triangle who modify herb stems to fashion a brush tip for termite fishing (Sanz et al., 2009). For the maze, bonobos used more curved tools than straight tools, and some subjects did so from the beginning of the task. This point is interesting in regard to anticipation and planning of the task by bonobos. This point has only been investigated to a limited extent study for bonobos (Bräuer and Call, 2015) compared to, for example, chimpanzees and orangutans (i.e. Osvath and Osvath, 2008). The fact that this group of bonobos had already experimented with tool manufacture and use in the context of their various enrichments may have impacted this. Alternatively, they may have immediately understood the future needs of the task. Boose and collaborators (2013) showed that bonobos rapidly became proficient in manufacturing tools and extracting bait from an artificial termite mound. Consequently, we could suppose that the group we studied was habituated to tool use and anticipated the choice of the tool according to the demands of the task. However, it may be a strategic choice to arrive directly with the tool already modified as we observed social pressure in this group. Thus, having a tool already modified could be a strategy developed by the males to save time before arriving on site. In females the strategy may be to take the modified tool of the males, which we observed in some cases. In this context, males may have selected more appropriate tools than females. To test this, it would, however, be necessary to analyze a large sample of bonobos.

4.6. Implications for the evolution of the human hand morphology

Our results indicated well developed manual abilities during tool use and manipulation in bonobos and a strong inter-individual variability in the functional strategies used. As bonobos have a different hand morphology than humans, including a shorter thumb and different muscles like chimpanzees (Marzke et al., 1999; Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012), our results may be interesting in regards to the evolution of manual abilities in primates in association with different locomotor modes.

Our findings in bonobos showed well developed abilities for tool manipulation with a wide variety of grasp types and in-hand movements. For our two tasks, bonobos also used one hand preferentially (chapter 2) and they used forceful grasp types with individual preferences. Hook grasps with an opposed thumb were particularly important during tool manipulation. Moreover, bonobos used the two-jaw chuck pad-to-side more often during food extraction.

This point is interesting in connection with the use of this grasp for the flake tool-using behavior which involved higher forces on the human thumb than tool-making behavior (Williams et al., 2012). Marzke (1983: 197) proposed that “this grip could have been exploited in the manipulation of small stone flakes and wood probes, and in the controlled manipulation of stone missiles”. Moreover, a bonobo named Kanzi removed flakes from stone cores with a hammer stone using a one hand technique (Schick and Toth, 1993) and created and selected appropriate flakes according to the task (Schick et al., 1999). These results could imply that a common ancestor to bonobos and humans with similar hand morphology to bonobos may have had similar functional capabilities. However, some authors consider the human hand more primitive than that of extant apes which have high levels of hand disparity explained by different evolutionary processes (Almecija et al., 2015). Thus, the bonobo hand could be more derived. In this context bonobos are interesting because they use different locomotion modes such as knuckle-walking and bipedalism and use both terrestrial and arboreal substrates (see D’Août et al., 2004 for a review). Thus, they appear adapted for arboreal behavior and terrestrial locomotion. Our results showed a variety of grasp types and in-hand movements in bonobos which could be linked to these types of locomotion (Christel et al., 1998). According to Almecija and collaborators (2015) the morphology of the hand of bonobos may have evolved in conjunction with their different mode of locomotion, as extant apes. This hypothesis was consistent with Rolian and collaborators (2010) which suggested that the evolution of the human hand is not linked to an adaptation for tool use or any other function, but rather that the hominin hand and feet coevolved. They suggested that the evolution of long robust big toes and short lateral toes for bipedalism led to changes in hominin fingers that may have facilitated the emergence of stone tool technology (Rolian et al., 2010).

No fossils of the last common ancestor of humans and apes have been discovered yet and the evolution of the human hand during the emergence of manual abilities to produce stone tool remains debated. Recent archeological and paleoanthropological discoveries showed that the earliest evidence of intentional stone tool production at 3.3 Ma (Harmand et al., 2015) predated the appearance of the genus *Homo* by at least 0.5 Ma (Skinner et al., 2015b), and that intensified manual manipulation could be linked to an arboreal lifestyle (Kivell et al., 2011; Kivell et al., 2015; Skinner et al., 2015a). These discoveries allow us to suggest that arboreal species could have the potential to produce and to use stone tools. Finally, following the studies conducted on Kanzi, who is able to manufacture and use various

stone tools (Schick and Toth, 1993; Schick et al., 1999), the first tool maker could have been a bonobo.

Finally, bonobos do not appear to have one specific technique to perform a given task but show individual preferences. These individual differences could be due to inter-individual morphological variability in bonobo hands. This strong variability quantified only in one small group of bonobos points out the extreme difficulty to infer the manual abilities of fossilized hand skeletons.

5. CONCLUSION

Our results provide evidence that food retrieval from a maze is associated with a more dynamic manipulation compared to a food extraction task. The dynamic manipulation of tools could be an important factor in the evolution of morpho-functional abilities of the human hand. However, as suggested by Weiss (2012) and Marzke (2013), human hand morphology may not have directly evolved by natural selection in relation to tool use. Our results show the importance of quantifying dynamic object manipulation in different species for new and complex tasks, and with new methods to better understand the manual specificities of each species, essential for a better reconstruction of the evolution of primate manual ability. It is also important to investigate hand function and mechanics in this context. The next step focusing on manual abilities through an integrative approach involving biomechanics, comparative anatomy and ethology is essential. Finally, our study suggests that inter-individual and intra-individual variability, and sex or gender differences need to be explored further.

SUMMARY OF THE CHAPTER 3

Title: Behavioral and functional strategies during two tool use tasks in bonobos.

Question: Do the functional and behavioral strategies used by bonobos vary according to the complexity of two different tool use tasks? Does a more complex task induce a more complex manipulation?

Model: Bonobos (*Pan paniscus*).

Method: Experimentation and ethological observation in Zoo (le Vallée des Singes).

Results: Bonobos were able to develop in-hand movements similar to humans and chimpanzees. They demonstrated dynamic manipulation, and they responded to task constraints by selecting and modifying tools appropriately, usually before they started the tasks. More complex manipulation was observed for the more complex task (the maze task) and bonobos demonstrate individual strategies.

Discussion: More complex tool manipulation might have contributed more than simple tool manipulation to the emergence of the high manipulative abilities in humans. In order to better understand manipulative abilities of individuals and various species, we thus need to develop procedures and experiments necessitating complex manipulation. In addition, we need to compare the manipulative abilities of humans and great apes during the same complex task to conclude on the specificity (or not) of humans abilities.

Perspectives: It would be very interesting to compare other great ape species, including humans during the maze task (which required dynamic manipulation for bonobos), and in the same conditions. Such an approach would provide a comparative functional analysis of the manual abilities in great apes and humans, allowing us to test if humans are really unique. This objective concerns the chapter 4.

Chapter 4 – Are humans unique? Are gorillas and/or orangutans unique? What manual specificities exist for each species?

Are humans unique? Are gorillas and/or orangutans unique? What manual specificities exist for each species?

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ABSTRACT

Humans are known to possess more complex manual abilities than non-human primates. Though many other primates need their hands for locomotion, they still show some manual abilities that are comparable to humans. However, the dynamic manipulative skills of primates have not been fully explored, especially during the same task. To fill this gap, we investigated performance indicators (e.g. duration of the task, number of wrist movements use etc.) linked to manipulative abilities of humans in the most terrestrial great apes (gorillas, *Gorilla gorilla*) and arboreal great apes (orangutans, *Pongo* sp.) during the same tool use task. The results clearly show that humans perform better than gorillas and orangutans, with performance linked to in-hand movements and specific grip types. Only humans use bimanual grip type, pad-to-pad precision grip and in hand-movements involving fingertips. Gorillas and orangutans use more power grips and gorillas develop more in-hand manipulation than orangutans showing more mouth manipulation. Finally, orangutans show more intra-species variability in the grip techniques. Human specificities quantified here could be explained by morphological and/or neuromuscular coordination differences relative to gorillas and orangutans. However, humans may have no “unique” manual abilities and non-humans primate species may not need to use these abilities to succeed at the task. Differences between these great apes could be explained by their different lifestyles (the most terrestrial of great apes versus the most arboreal).

1. INTRODUCTION

Since at least Darwin (1871), the evolution of human manipulative abilities has been of great interest and is hypothesized to have coevolved with bipedalism, tool-making and use, brain enlargement and laterality, and/or language in humans (Wilson, 1998). Human manipulative skills are traditionally linked to specific morphological features, such as a long, mobile and powerful thumb, that are considered to be associated with stone tool-making (Napier, 1960; Marzke, 1997, Susman, 1998; Tocheri, 2008). However, other primates, such as great apes and capuchin monkeys, use various manipulative postures that are comparable to those use by humans, including the precision grips (Christel, 1993; Jones-Engels and Bard, 1996; Marzke and Wullstein, 1996; Christel et al., 1998; Byrne et al., 2001; Pouydebat et al., 2009, 2011). In addition, in captive experiments, an orangutan and a bonobo are able to make stone flakes, even though they do not possess a long thumb or other “tool-making” morphological features (Wright, 1972; Schick and Toth, 1993; Schick et al., 1999). The manipulative abilities of some primates (primarily, great apes, capuchin and macaques) have been studied for decades and compared directly with simple human simple tasks (e.g. Christel, 1993; Pouydebat et al., 2009, 2011). However, as far as we know, no captive experiments compare their manual abilities during the same complex tool use task. Thus, the questions about human specificities and how manipulation abilities evolved in hominids are still unresolved. Do humans show real specific tool manipulation abilities compared to other hominids?

In humans, dynamic aspects of manual function are described (Exner, 1992; Santello et al., 1998; Braidó and Zhang, 2004; Bullock and Dollars, 2011) and a detailed taxonomy of the various forms of in-hand movements is available (Elliot and Connolly, 1984). In contrast, studies on dynamic manual abilities are scarce and were investigated mainly in chimpanzees (Boesch and Boesch, 1993; Marzke and Wullstein, 1996; Crast et al., 2009; Marzke et al., 2015), few in gorillas (*Gorilla sp.*) (Byrne et al., 2001) and bonobos (*Pan paniscus*) (Bardo et al., 2016), and are lacking for orangutans (*Pongo sp.*). Yet, studying the evolution of manual abilities in gorillas and orangutans is very important because they show highly manipulative abilities to process food in the wild (e.g. orangutans: van Schaik et al., 1996; Russon, 1998; gorillas: Byrne and Byrne, 1991; Byrne et al., 2001), have different lifestyles (arboreal for orangutans and terrestrial for gorillas) and differ in hand morphology (Shultz, 1930). Finally, it appears important to compare dynamic manual abilities between humans and great apes to better understand the conditions and restrictions underlying the occurrence of complex

manipulative abilities and the potential factors which could have made humans the most eminent tool using primates.

The present study aims to test if humans are unique among primates and possess manual specificities and to also to determine if manual specificities exist among great apes specificities. In this study, we quantify for the first time, the performance, grip techniques and dynamic manipulative abilities of humans in comparison with the most terrestrial and arboreal great apes (gorillas, *Gorilla gorilla*, and orangutans, *Pongo* sp., respectively) during the same tool use tasks and conditions (i.e. the maze task used also in chapter 3). To quantify manual ability in humans, some studies measure performance according to the time needed to complete the test or the movement time (Sollerman and Ejeskar, 1995; Turgeon et al., 1999; Aaron and Jansen, 2003; Schoneveld et al., 2009). For non-human primates, performance is also measured by the latency to use the preferred and the non-preferred hand during tasks (Fragaszy and Mitchell, 1990) or the time needed according to a minimum of trials to respond correctly to a task (Albiach-Serrano et al., 2012). In the present study we investigate the performance of each individual by quantifying the time necessary to complete the maze task adding many other motors skill parameters such as the number of wrist movements used to reach the walnut, the number of touch obstacles and the number of times the tool is repositioned in the grid.

2. MATERIAL AND METHODS

2.1. Subjects

Thirty-three subjects participated in the present study between 2014 and 2015: 20 *Homo sapiens*, 6 gorillas (*Gorilla gorilla*) and 7 orangutans (4 *Pongo Pygmaeus* and 3 *Pongo abelii*) (Table 7). The gorilla group consisted of 5 males (mean age = 18.6 years old, age range: 10-31 years) and 1 female (31 years old); the orangutan group consisted of 3 males (mean age = 16.3 years old, age range: 12-20 years) and 4 females (mean age = 20.5 years old, age range: 9-38 years). Non-human subjects were housed in different zoos (Table 7) and they were presented with the maze task for the first time, as were humans. The groups of great apes were housed in indoor and outdoor enclosures with regular feedings, daily enrichment and water *ad lib*. The study was conducted in the main cage in the indoor enclosure and subjects

spontaneously participated. Humans were tested with the presence of one observer in a closed room at the National Museum of Natural History in Paris (France).

2.2. Apparatus and procedure

The maze task consisted in reaching, with a tool, walnuts positioned on a wooden maze (45 cm wide by 60 cm long). The mazes were attached outside the cage on the wire mesh (size = 5x5 cm). The mazes were the same for all the species and were composed of 10 wooden obstacles of different shapes and sizes (Figure 9ab). The walnuts were placed at the end of the maze (60cm away from the subject). To avoid competition and social tension we placed the same number of mazes as the number of tested subjects around the cages simultaneously. For humans, the maze was placed on a table at 70 cm from the ground, and with a piece of wire mesh (100x100 cm) placed in front of the maze (Figure 9b). For great apes, the mazes were positioned between 40 and 60 cm from the ground. The position of the maze was related to the size of each individual in order to give them the possibility to use a seated posture for each session (Figure 9a). For humans, a chair (45 cm height) was positioned just in front of the maze. The only instruction for humans was to reach the walnut placed at the end of the maze imperatively through the wire netting.

Six sessions per individual were recorded, one session corresponding to one walnut reached. The aim was to capture the variation among species and individuals. Two days were necessary to get the data of one individual, 3 sessions per day and per individual. A sequence began when a subject started to put the tool through the wire mesh and ended when he/she could reach the walnut.

We provided standardized tools made of bamboo branches for all species to reduce their size effect on manual techniques used. Nine tools were provided for humans, with 3 lengths (1m, 60 cm and 45 cm) and 3 diameters (0.5 cm, 1 cm and 1.5 cm). For apes, 6 tools were provided per maze with 2 lengths (75 cm and 60 cm) and 3 diameters as humans. Fewer tools were provided to gorillas and orangutans for safety reasons and so the lengths were adapted to the lengths of tools for humans. We also provided additional tools of smaller length for humans because we expected that they would not be able to break the tools if necessary.

One fixed camera (CANON 600D©) was used during experiments for humans. For great apes, one camera (SONY Handycam HDR-CX240) was placed in front of each maze. Videos were recorded at 50 frames/second. At the end of experimentation, we asked the human subjects which hand they used more in their daily activities and 70 % considered themselves right-handed, 15 % left-handed and 15 % ambidextrous (they used their right hand as much as their left hand).

Table 7. Details individuals tested.

Species	Subject	Sex	Age (years)	Observation locations (France)
<i>Homo sapiens</i>	10 individuals	M	Age range 22-41 (mean =28)	National Museum of Natural History in Paris
<i>Homo sapiens</i>	10 individuals	F	Age range 22-30 (mean=26)	National Museum of Natural History in Paris
<i>Gorilla gorilla</i>	Ya Kwenza	M	30	Zoo of Amnéville
<i>Gorilla gorilla</i>	Meru	M	11	Zoo of Amnéville
<i>Gorilla gorilla</i>	Lengai	M	11	Zoo of Amnéville
<i>Gorilla gorilla</i>	Yaounde	M	31	Zoo of La Vallée des Singes
<i>Gorilla gorilla</i>	Sango	M	10	Zoo of La Vallée des Singes
<i>Gorilla gorilla</i>	Moseka	F	31	Zoo of La Vallée des Singes
<i>Pongo pygmaeus</i>	Sandai	M	20	Zoo of La Palmyre
<i>Pongo pygmaeus</i>	Tiba	F	38	Zoo of La Palmyre
<i>Pongo pygmaeus</i>	Theodora	F	26	Zoo of La Ménagerie du jardin des plantes à Paris
<i>Pongo pygmaeus</i>	Tamou	F	9	Zoo of La Ménagerie du jardin des plantes à Paris
<i>Pongo abelii</i>	Ludi	M	17	Zoo of Amnéville
<i>Pongo abelii</i>	Kawan	M	12	Zoo of Amnéville
<i>Pongo abelii</i>	Putri	F	9	Zoo of Amnéville

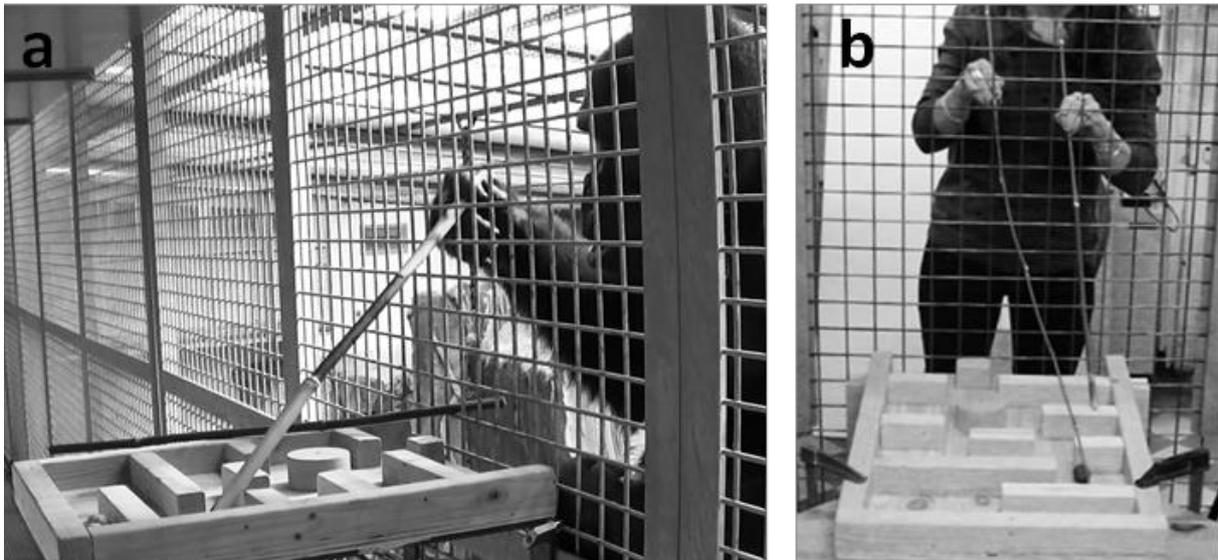


Figure 9. Testing situation of the maze task. In a) gorilla seated and b) human in bipedal posture. The maze was setup with obstacles inside and was the same for all species. In a) the gorilla used a unimanual grip type with an interdigital 2/3 brace grasp, and in b) the human used an asymmetric bimanual grip type with two tools held by a dynamic tripod grasp with both hands (See Methods and Table 8) .

2.3. Data scoring and classification system

During each session we quantified the different body postures used and body repositioning of individuals. For all sessions, humans used exclusively a bipedal posture and gorillas used exclusively a seated posture. For orangutans we observed that during one session they changed their body posture 2.98 times (± 0.93). Both species seemed to spend more time to perform the task in seated posture (45.6 % of the time) and hanging on the wire netting (40.9 % of the time) than in bipedal posture (13.5 % of the time), but without significant differences ($N = 7$, $Q = 2$, $df = 6$, $P > 0.05$). Thus, we decided to not take into account the different body postures in the orangutan analyses.

To investigate performance for the maze task, for each session and individual, we counted: the number of wrist movements used to reach the walnut (quantified by wrist movements), the number of touched wooden obstacles (placed inside the maze), the time span necessary duration (in seconds) to reach the walnut and the number of position changes of the tool in the grid. We considered that an obstacle was touched when the walnut was stopped and thus when the obstacle stopped the advancement of the walnut in the maze. We considered that touching an obstacle was due to a lack of control of the movement and thus this parameter allowed us to quantify the control of the movement.

The different grip types used to hold and use the tool were quantified and classified in 6 categories: unimanual grip involved one hand; symmetrical bimanual grip involved both hands simultaneously on one tool; asymmetrical bimanual grip involved both hands simultaneously on two tools (see for example Figure 9b); mouth grip; foot grip; and finally other grip with combinations of two grips (e.g. one feet and one hand). When they used one hand we quantified which hand (left or right) and during bimanual grip types we considered the dominant hand (M1). This hand was defined as the hand that directed movements of the tool and walnut during symmetrical bimanual grip or the hand that directed movements of the walnut during asymmetrical bimanual grip. The second hand (M2), considered and defined as the support hand, during symmetrical bimanual grip helped to stabilize the tool and during asymmetrical bimanual grip the second hand on the second tool helped maneuver the walnut in the maze.

To quantify the grasping postures we used the same method used in chapter 3 (Borel et al., 2016a) with the quantification of grasping postures by a combination of hand contact areas with the tool, defined following the anatomical terminology (Figure 10). To name the grasping postures we used existing typology for humans and great apes (see Table 8 footnote) and we divided the grasp types into five categories as in chapter 3:

- *Category 1*: the tool was held between the flexor aspect of the distal phalanges of the fingers and the opposing thumb. This category corresponds to the category called “precision grip” in Napier (1956).
- *Category 2*: the tool was held between the distal phalanx of the thumb, the lateral side of the middle, proximal phalanxes of the index finger and the tool. This category included the grasping postures called “thumb lateral” in Pouydebat et al. (2011).
- *Category 3*: contact between one or several fingers, except the thumb, and the tool, called “without thumb” in Pouydebat et al. (2011).
- *Category 4*: contact involving palm, the thumb and one or several part of other fingers and the tool, involving the power grasping posture (Napier, 1956; Jones-Engels and Bard, 1996), and called “palm grips” in Pouydebat et al. (2011).
- *Category 5*: contact types which fell outside the above categories, involving the “hook grip” in Napier (1956) and called “other grips” in Jones-Engels and Bard (1996).

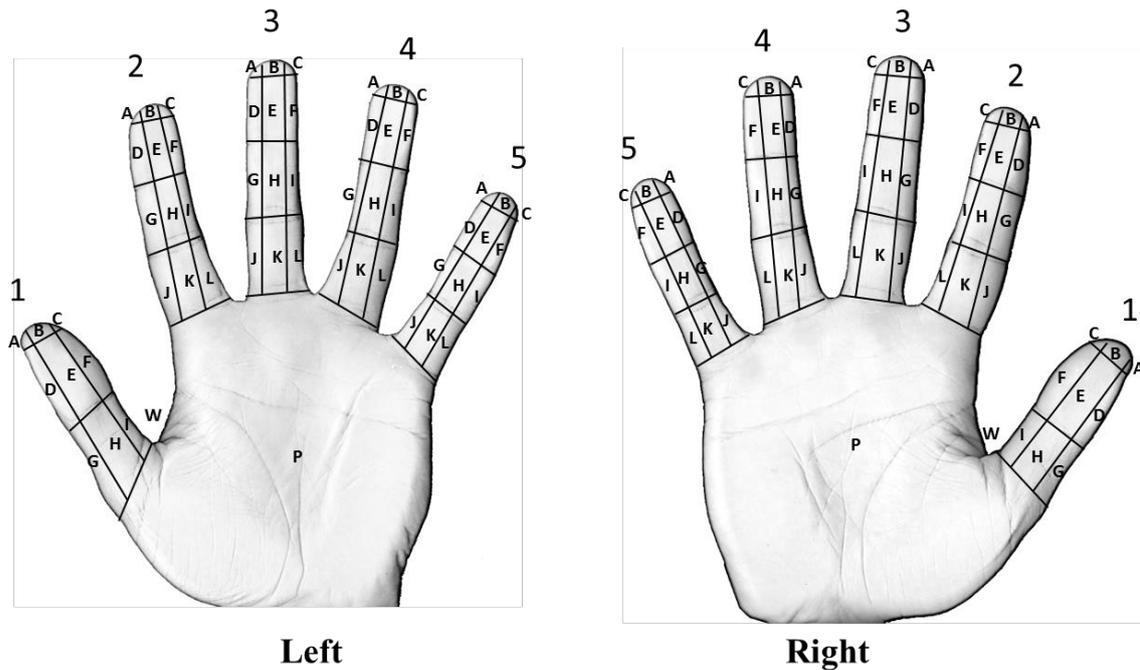


Figure 10. Code used for each contact area of the right and left hand. A contact area is indicated with the first letter of the hand (R for right or L for left), the number of the finger and the letter(s) of the contact area (i.e. R1E.R2G). Letter “P” was for palm and “W” for the web between full thumb and index finger.

We quantified the techniques used to reposition the tool in (i.e. in-hand movements) or with one hand or with the mouth. In-hand movements were characterized by finger movements that involved tool movement on the surface of the palm and the fingers. They were classified according to the Elliot and Connolly’s (1984) classification system and the adaptation of this classification by Crast et al. (2009) for chimpanzees. We classified in-hand movements in two categories, simple movements and complex movements: 1) simple movements involving one finger (“simple synergies”, Elliot and Connolly, 1984) or two fingers (“reciprocal synergies”, Elliot and Connolly, 1984) moving in opposite directions simultaneously; 2) complex movements involving sequential grasp and regrasp with independent co-ordination of fingers (Crast et al., 2009). Secondly, we quantified tool repositioning performed without in-hand movements but the help of the other hand (that didn’t hold the tool), the mouth and/or the feet.

2.4. Video Coding and Reliability Assessment

Videos were played with VLC media player and analyzed using a focal sampling protocol (Altmann, 1974). We recorded events each time a subject moved his fingers (e.g. displacements), stopped moving the tool for more than 20 s, and when a subject changed the position of the tool in the grid. We took into account the time for each event. We started to record data when the tool was within the wire mesh. For all subjects and for all sessions, we recorded 1158 events; 502 events for humans; 268 events for gorillas; 388 events for orangutans. The duration (in seconds) was used as a measure to quantify body postures, grip types, hand preference and grasping postures. Occurrences were the unit for the other observed parameters (i.e. number of in-hand movements, number of obstacles touched etc.).

Twenty percent of sessions were also coded by a second observer to assess inter-observer reliability, which was excellent for all the parameters quantified (Pearson's correlation coefficient = 0.98, $N = 660$) and good for the combinations of contact areas (Cohen's kappa $\kappa = 0.63$, $N = 216$). Therefore, only the data from the first observer were used for analysis.

2.5. Data analysis

The percentage of use of each body posture, grip type, hand preference and grasping posture was calculated relative to the total duration of the experiment for each individual. For the other parameters we worked on mean values for each individual. Because some of our data did not meet the normality and homogeneity assumptions for parametric tests, we used nonparametric statistics. The comparisons between species were performed by using Mann-Whitney test (U) for 2 species and for the three species by using Kruskal-Wallis rank sum tests (H) and if the tests were significant we used Dunn's-tests for multiple comparisons of independent samples (Z). The comparison between individuals of each species were performed by using Friedman rank sum tests (Q) and, if the tests were significant, we performed pairwise comparisons using the Wilcoxon signed rank test (W) with continuity correction. Tests were two-tailed with a significance level set at 0.05. Bonferroni correction was applied in the case of multiple comparisons (corrected P values are marked as P'). We performed statistical tests in the software R (R Core Team 2016). Time-based sequence analysis was used to quantify and visualize the combinations of the contact areas between

hand and tool during tool use tasks. The combinations of the contact areas with the associated time was exported to the software R (R development Core Team 2016) and time-based sequence analysis were performed with the package TraMineR (Gabadinho et al., 2011) adapted by Borel et al. (2016a).

In order to describe the techniques used by the individuals ($N = 33$) during the maze task and to characterize their performance, a Principal Component Analysis (PCA) was performed on six variables: the four performance parameters (duration of the task, number of wrist movements, number of touched obstacles, number of repositionings of the tool in the grid) and two dynamic in-hand parameters (number of in-hand movements and the number of combinations of contacts areas). PCA was performed in R (R Core Team 2016), with the mean data normed for all the sessions of all subjects. Multivariate Analyses Of Variance (MANOVA Pillai's trace multivariate test) (Pillai, 1985) were performed to compare the performance and the in-hand parameters according to the species, sex, grip types used and preferred grasping postures used.

3. RESULTS

3.1. Performance

We find significant differences between humans and great apes according to the performance parameters (Table S1). Gorillas and orangutans take more time to reach the walnut than humans (respectively, $Z = 3.592$, $N = 26$, $P' < 0.001$; $Z = 3.953$, $N = 27$, $P' < 0.001$). Gorillas and orangutans use more wrist movements than humans (respectively, $Z = 3.557$, $N = 26$, $P' = 0.001$; $Z = 3.989$, $N = 27$, $P' < 0.001$). Gorillas and orangutans touch more obstacles than humans (respectively, $Z = 4.214$, $N = 26$, $P' < 0.001$; $Z = 3.215$, $N = 27$, $P' < 0.01$). Gorillas and orangutans change more the position of the tool in the grid than humans (respectively, $Z = 3.131$, $N = 26$, $P' < 0.01$; $Z = 3.908$, $N = 27$, $P' < 0.001$).

3.2. Hand preference

For all species taken into account, we do not observe a preferred hand use ($W = 342$, $N = 33$, $P > 0.05$). Twelve humans used exclusively the right hand and two used exclusively the left hand (on 20 individuals). No directional hand preference was observed for the group of

gorillas ($W = 7, N = 6, P > 0.05$): four used exclusively the left hand and two used exclusively the right hand. For orangutans we did not observe a preferred hand ($W = 7, N = 7, P > 0.05$). Five individuals were ambidextrous but two individuals (Putri and Kawan) used exclusively the left hand.

3.3. Grip types

Gorillas used only unimanual grip to hold the tool during the task whereas orangutans used six grip types and humans three. Unimanual grip had the greatest duration of use but there were difference in the relative duration of unimanual group among the four species ($H = 19.032, N = 33, df = 2, P < 0.001$). Gorillas and orangutans used more unimanual grip than humans ($Z = 3.962, N = 26, P' < 0.001$; $Z = 2.738, N = 27, P' < 0.05$, respectively). Humans used unimanual grip 46.9 % of the time and two types of bimanual grip (symmetrical bimanual grip was used 46.2 % of the time and asymmetrical bimanual grip was used 6.9 % of the time). No particular grip was preferred in the group ($Q = 5.0586, N = 20, df = 19, P > 0.05$) but inter-individuals differences were found. Four subjects used only one grip technique; one in unimanual and three in symmetrical bimanual grip. Orangutans used unimanual grip 90.6 % of the time and inter-individual differences were found for the other grip types. Mouth grip was used 7.7 % of the time, other grip types, such as mouth with one foot, were used 0.1 % of the time by one individual, and symmetrical bimanual grip type was used 0.3 % of the time by 2 individuals and foot grip type was used 1.3 % of the time by 2 individuals.

3.4. Grasping postures

Table 8 defines all the grasping postures observed for all species classified in the five categories (see Material and Methods), with the percent mean duration of each grasping posture used by each species. A Pearson's Chi-squared test revealed that the species and their preferred postures were not used randomly [$\chi^2 (24, N = 33) = 52.145, P < 0.001$], indicating that each species used a preferred type of grasping posture.

Concerning the unimanual grips, the first category corresponding to "Precision grips" was not used by gorillas and was more used by humans than orangutans ($U = 109, N = 27, P <$

0.01) (Figure 11). The second category, “Thumb lateral”, was not used by gorillas and we did not observe differences between humans and orangutans ($U = 69$, $N = 27$, $P > 0.05$). The third category, “Without thumb”, was not used by humans and we did not observe differences between gorillas and orangutans ($U = 18$, $N = 13$, $P > 0.05$). For the fourth category, “Palm grips”, differences between species were observed ($H = 11.793$, $N = 30$, $df = 2$, $P < 0.01$), gorillas and orangutans used more palm grips than humans (respectively, $Z = 2.431$, $N = 26$, $P' < 0.05$; $Z = 3.002$, $N = 27$, $P' < 0.01$). For the fifth category, “Other grips”, differences between species were observed ($H = 8.127$, $N = 30$, $df = 2$, $P < 0.05$). Gorillas used more grasping postures classified as “other grip” than humans ($Z = 2.72$, $N = 23$, $P' < 0.05$) (Figure 11).

We recorded ten grasping postures used by humans (mean by individual = 2.65 ± 0.4) without preference within the group ($Q = 13.299$, $N = 10$, $df = 16$, $P > 0.05$). Inter-individual differences were observed in the preference for certain grasping variants. Humans seemed to use more “Lateral tripod grasp” (34.7 %), “Four finger fingers grasp” (30.5 %) and “Dynamic tripod grip” (13.8 %) as main grasping postures (Table 8). We recorded eight grasping postures used by gorillas (mean = 3.16 ± 0.9) without preferences ($Q = 6.8041$, $N = 8$, $df = 5$, $P > 0.05$). Gorillas seemed to use mainly interdigital finger brace grasping postures, with “Interdigital 2/3 brace” used 33.6 %, “Interdigital 3/4 brace” used 28.2 % and “Power grip” used 19.6 % of the time (Table 8). We recorded 16 grasping postures for orangutans (mean individual = 6.14 ± 1.3). Inter-individual differences were observed in the preference for certain grasping variants but they seemed to use mainly “Power grip” (33.4 %) and “V pocket” (33.7 %) (Table 8).

Concerning the bimanual grips, for humans no difference of grasping posture use categories were observed between the dominant hand and the support hand for the two grip types (for both grip types $P > 0.05$). We only observed the use of grasping postures in the “Without thumb” category during symmetrical bimanual grip type by the support hand (Table 8). During asymmetrical bimanual grip type, humans seemed to use more “Precision grip” categories with the dominant hand than with the support hand but no significant difference was found ($W = 25$, $N = 7$, $P = 0.07$) (Table 8).

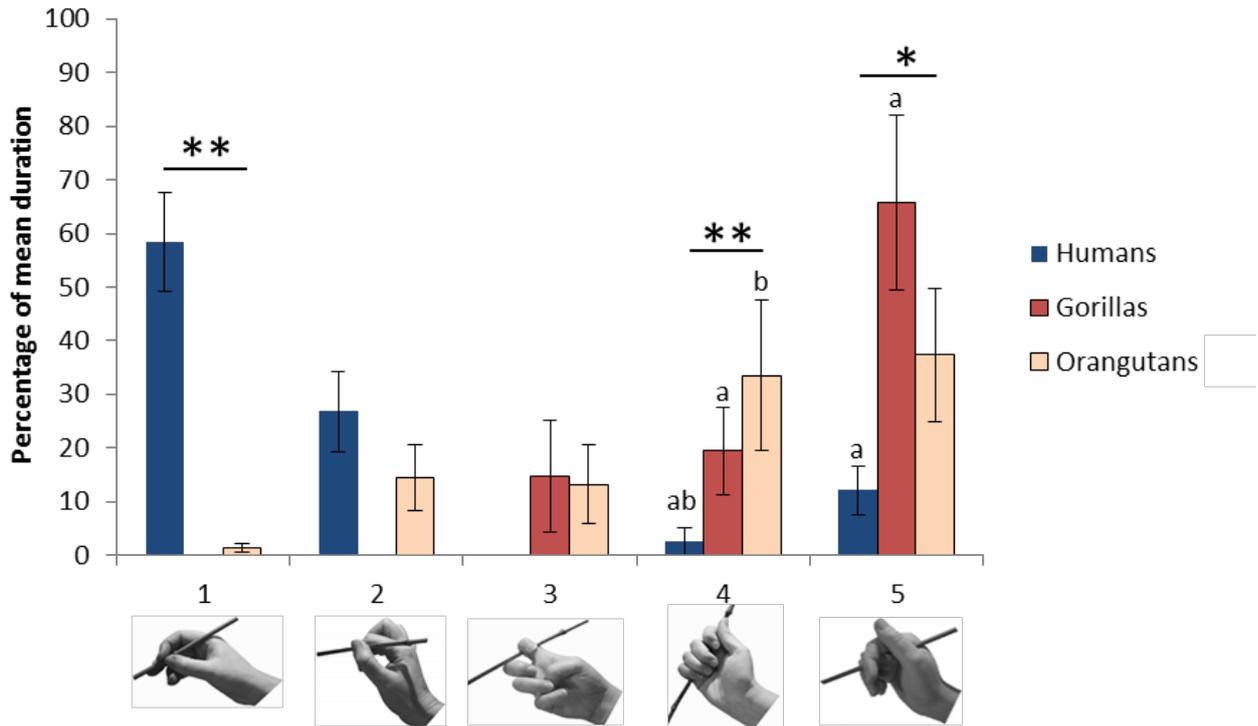


Table 8. Variability of the grasping postures used to hold a tool and the percentage of used by species. Illustrations examples of the grasping postures were realized with a human hand and so the position of the fingers could be changed according to the morphometric of the hand of the species. Humans used more “precisions grips”, gorillas used more “other grips”, and Sumatran orangutans used more “power grips” whereas Bornean orangutans used different types of grips.

Category of grasping postures	Name	Description	Humans					Gorillas	Orangutans	Illustrations
			Unimanual	Bimanual symmetric		Bimanual asymmetric				
				M1	M2	M1	M2			
<i>Precision grips</i>	Two-jaw chuck tip-to-tip ^a	Tool held between the tip of the thumb and the tip of index finger.	-	0.1	1.3	-	-	-	-	
	Two-jaw chuck pad-to-pad	Tool held between the pad of the thumb and the pad of index finger.	-	-	0.4	-	-	-	-	
	Two-jaw chuck pad-to-pad side	Tool held between the pad of the thumb and the side of the pad of index finger.	-	-	-	-	-	-	1.4	
	Dynamic tripod grip ^b	Tool stabilizes against radial side of third finger by thumb pulp with index pulp on top of the tool.	13.8	7.6	23.4	32	24	-	-	
	Four fingers grasp ^c	Tool held between the pad of the thumb and the pad of other fingers except fifth finger.	30.5	33.5	14.8	44.9	31.8	-	-	
	Five fingers grasp ^c	Tool held between the pad of the thumb and the pad of other fingers.	0.1	3.3	15.2	1	1.4	-	-	
<i>Thumb lateral</i>	Two-jaw chuck tip-to-side	Tool held between tip of the thumb and side of the pad of the index finger.	-	-	1	-	-	-	3.2	
	Two-jaw chuck pad-to-side ^a	Tool held between pad of the thumb and side of the pad of the index finger.	-	-	-	-	-	-	11.1	
	Lateral tripod grasp ^d	Tool stabilize against radial side of third finger with index pulp on top of the tool, and thumb adducted and braced over or under anywhere along lateral side of index finger.	34.7	30.4	4.4	11.9	14.8	-	-	
	Lateral four fingers grasp	Tool stabilize against radial side of index finger with index pulp on top of the tool and between tip or pad of third and fourth fingers with thumb adducted and braced over or under anywhere along lateral side of index finger.	-	-	1.1	-	-	-	-	

	Lateral five fingers grasp	Tool stabilize against radial side of index finger with index pulp on top of the tool and between tip or pad of the other fingers with thumb adducted and braced over or under anywhere along lateral side of index finger.	-	-	5.7	-	11	-	-	
	Cross thumb grasp ^e	Tool held against index finger with thumb crossed over object toward index finger, fingers fisted loosely into palm.	-	-	1.3	-	-	-	-	
<i>Without thumb</i>	Scissor hold ^f	Tool held between two fingers, excluding thumb.	-	-	-	-	-	1.2	2	
	Fingers hook ^a	Tool is enclosed by 1, 2 or 3 flexed fingers.	-	-	-	-	-	-	0.1	
	Transverse hook ^a	Tool held by all fingers flexed at interphalangeal joints, the thumb may be adducted or opposed, and the distal part of the palm was not involved.	-	-	-	-	-	1.7	0.4	
	Diagonal hook ^a	Tool held by decreasingly flexed distal fingers 5-1; the distal part of the palm was not involved.	-	-	-	-	-	-	0.1	
	Interdigital 2/3 finger hook	Tool held by flexed index and exits the hand between the proximal or middle phalanges of the index and third fingers.	-	-	-	-	-	0.5	2	
	Interdigital 3/4 finger hook	Tool held by flexed third finger and exits the hand between the proximal or middle phalanges of the third and fourth fingers.	-	-	-	-	-	-	0.4	
	Interdigital 3/4 fingers hook	Tool held by flexed third and fourth fingers and exits the hand between the proximal or middle phalanges of the third and fourth fingers.	-	-	-	-	-	10.7	8.2	
	Interdigital 4/5 finger hook	Tool held by flexed fourth finger and exits the hand between the proximal or middle phalanges of the fourth and fifth fingers.	-	-	-	-	-	-	0.1	
	Interdigital 4/5 fingers hook	Tool held by flexed third and fourth fingers and exits the hand between the proximal or middle phalanges of the fourth and fifth fingers.	-	-	-	-	-	4.3	-	

	Medial phalanges fingers support	Areas of the fingers, without thumb, just posed on the tool but do not hold it.	-	-	4	-	-	-	-	
	Fingers tips support		-	-	11.7	-	-	-	-	
<i>Palm grips</i>	Thumb lateral with passive palm	Tool held between thumb and index finger with passive contact of the palm with the tool.	-	-	-	-	-	-	0.2	
	Power grip	Tool held in opposition between the palm and flexed fingers with a possible pressure applied by the thumb.	4.8	5.7	10.8	8.9	12	19.8	33.4	
	Brush grasp	All the fingers are gathered along the tool with the object end against the palm.	-	2.8	-	-	-	-	-	
<i>Other grips</i>	Thumb wrap ^g	The thumb and the index cross over the tool.	0.6	1	-	1.4	-	-	-	
	V pocket ^f	Tool held in web between full thumb and index finger, other fingers were flexed but not in contact with the tool.	-	-	-	-	-	-	33.8	
	Interdigital 2/3 brace ^h	Tool is bracing in the webbing of the thumb, weaving under the index finger and exist the hand between fingers 2 and 3.	3.8	3.6	2.6	-	-	33.6	2.3	
	Interdigital 3/4 brace ^h	Tool is bracing in the webbing of the thumb, weaving under the second and third fingers and exist the hand between fingers 3 and 4.	-	0.8	2	-	-	28.2	1.3	
	Index grip ^f	Tool hooked by the index fingers and held by the thumb and the third fingers against the fourth and fifth fingers pad.	0.5	5.1	0.3	-	-	-	-	
	Index tripod grip	Tool stabilize against radial side of third finger by thumb pulp and hooked by index finger.	7.3	6.1	-	-	5	-	-	
	Transversal tripod grasp	Tool held between flexed index and third finger and pad of adducted thumb.	3.9	-	-	-	-	-	-	

Table footnote: ^{a-h} Named and described in ^a Marzke and Wullstein, 1996; ^b Wynn-Parry, 1966; ^c Schneck and Henderson, 1990; ^d Schneck, 1987, as cited in Schneck and Henderson, 1990; ^e Gesell, 1940, as cited in Schneck and Henderson, 1990; ^f Marzke et al., 2015; ^g Benbow, 1997; ^h Lesnik et al., 2015.

3.5. Tool repositioning

We recorded four distinct techniques used to move and reposition the tool in the hand with differences between species (Figure 12). The hand that did not hold the tool, was used by all the species, without species differences in mean events ($H = 0.1811$, $N = 33$, $df = 2$, $P > 0.05$). The mouth was used by gorillas and orangutans and the foot was only used by orangutans. Orangutans used more their mouth than gorillas ($U = 37$, $N = 13$, $P < 0.05$). In-hand movements were mainly recorded in humans and gorillas, without species differences in events ($W = 76.5$, $N = 26$, $P > 0.05$) (Figure 12 and Table 9). Just one Sumatran orangutan (Kawan) was observed to use in-hand movements. We recorded 11 types of in-hand movements for humans, 3 types for gorillas and 2 for orangutans. Also, these types of movements were not used by each individual or during each session (see in Table 9 the mean percentages and standard errors). Humans used simple and complex movements involving fingertips whereas gorillas and orangutans used only simple movements with simple synergies involving the palm (Table 9).

Gorillas and orangutans did not show a significant preferred strategy for repositioning the tool in their hand ($P > 0.05$) but orangutans seemed to reposition the mouth more often at 83 %. We observed no difference in humans in the number of in-hand movements used in the dominant hand regardless of grip type used (unimanual, symmetrical bimanual or asymmetrical bimanual) ($Q = 26.708$, $N = 3$, $df = 19$, $P > 0.05$). During asymmetrical bimanual grip in humans, there was no difference in the number of in-hand movements in hands ($W = 27$, $N = 7$, $P > 0.05$).

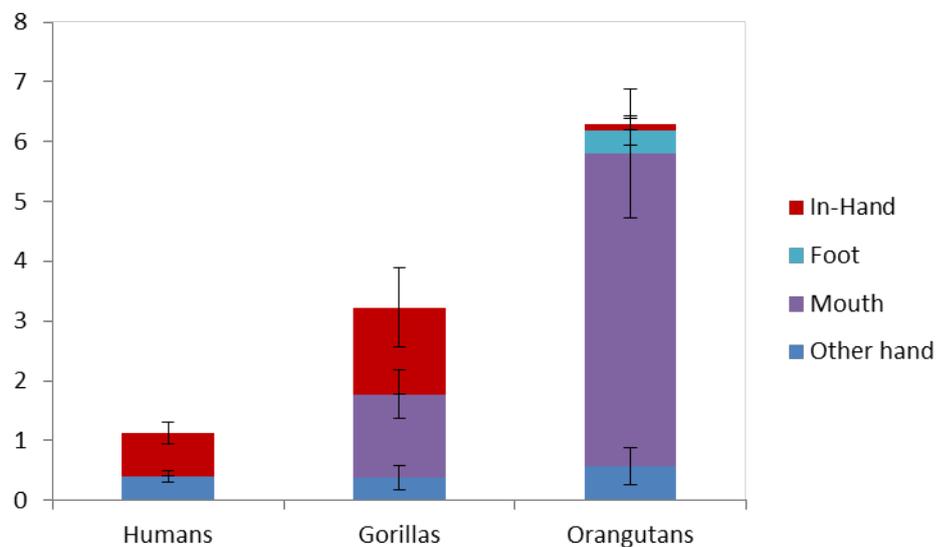


Figure 12. Techniques used to move and reposition tool in hand by each species.

Table 9. Description of the in-hand movements observed and number of individuals who used each kind of movement (N). For humans, M1 corresponds to the dominant hand during unimanual grip type and during asymmetrical bimanual grip type, and M2 corresponds to the support hand during asymmetrical bimanual grip type. Humans used simple and complex movements whereas gorillas and one orangutan, used only simple movements.

Category	Type	Definition	Humans (N = 14/20)		Gorillas (N = 5/6)	Orangutans (N = 1/7)
			M1	M2		
SIMPLE MOVEMENTS						
<i>Simple synergies</i> ^b	Thumb extension and Flexion	Extension of the thumb that already touched the tool which slides on/in finger or palm and flexion of the thumb to stop the tool sliding.	N = 1	N = 1	N = 2	N = 1
	Index extension and Flexion	Extension and flexion of the index finger to hook and to stabilize the tool (mostly used during interdigital 2/3 brace). The thumb could move but did not touch and move the tool.	N = 1	-	N = 5	-
	Thumb adduction ^a	Thumb moved toward midline of the hand and moved the tool that it already touched.	N = 3	N = 1	-	-
	Thumb abduction ^a	Thumb moved away from midline of the hand and moved the tool that it already touched.	N = 2	N = 1	-	-
	Index and thumb extension and flexion ^b	Simultaneous extension and flexion of the thumb and the index, the tool moved in a linear direction while the palm and fingers grasped it again.	-	N = 1	N = 3	N = 1
<i>Reciprocal synergies</i> ^b	Roll ^a	Fingers move opposite to one another to twist or roll the tool along one axis.	N = 4	-	-	-
	Thumb push ^a	Fingers grasp the tool and thumb extended and abducted to push out the tool from the palm.	N = 1	N = 1	-	-
COMPLEX MOVEMENTS						
	Rock ^b	Tool held transversally in the fingers and rocked. Thumb and third fingers tend to be stationary and flexion of the fourth and fifth fingers is accompanied by extension of the index (passive movement caused mechanically).	N = 1	-	-	-
	Linear step ^b	The fingers "walking" linearly on the tool with adduction and abduction of the thumb.	N = 9	N = 4	-	-
	Interdigital step ^b	The tool held with dynamic tripod grasp and was turned between index and third fingers to again grasp transversally with the extension of the index.	N = 2	-	-	-
	Complex shift ^c	"Walking" movement of the fingers on the tool used to reposition it. The tool moved in a linear direction. The thumb and the index finger moved simultaneously by extension and flexion.	N = 3	-	-	-

Footnotes: ^{a-c} In-hand movements describe in: ^a Crast et al., 2009; ^b Elliot and Connolly, 1984; ^c Pont et al., 2009. See these references for more functional details and illustrations of these in-hand movements.

3.6. Sequences of contact areas

Orangutans changed their contact area combinations a mean of 3.8 times (± 0.7) per session, while gorillas changed 2.9 times (± 0.6) per session, and humans change 2.3 times (± 0.1) per session (see Figure 13 for visualization examples). We observed no significant differences in mean number of contact area combinations used between species ($H = 3.0842$, $N = 33$, $df = 2$, $P > 0.05$).

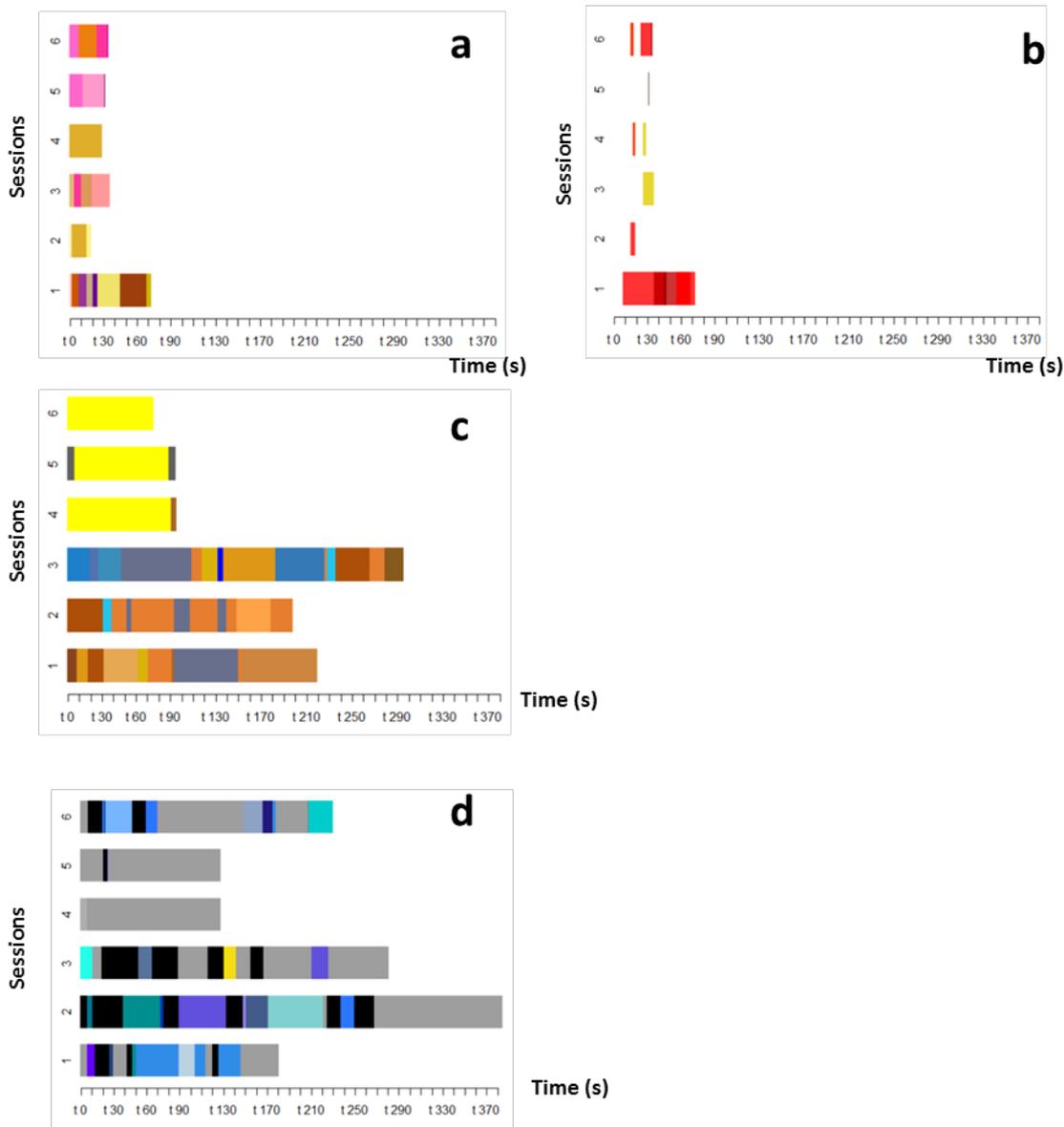


Figure 13. Examples contact area combination sequences for: a) human dominant hand, b) human support hand, c) gorilla, and d) orangutan. Each color corresponds to a specific contact area combination and black color corresponds to the use of the mouth. Categories of grasping postures are also presented by color categories: precision grips = pink, purple and red (both for bimanual symmetric grip type); thumb lateral = yellow; without thumb = blue; palm grips = grey; other grips = orange and brown. White = when the hand is not used.

3.7. Multivariate analysis on performance

The multivariate analysis showed significant differences of performance between species ($F(2, 30) = 1.2333, P < 0.001$); and between individuals according to the preferred grasping posture use ($F(8, 24) = 2.2727, P < 0.01$). No significant difference were observed between sex ($F(1, 31) = 0.2707, P > 0.05$) and grip type (unimanual, bimanual symmetric and asymmetric) ($F(2, 30) = 0.5288, P > 0.05$). The different performances between species could be explained by their different grasping postures.

The two first axes of the PCA explained 89 % of the total variance. The first axis (59 %) was mainly determined by the mean number of touched obstacles (loading = 0.90). The mean number of tool placement changes in the grid (loading = 0.26), the mean time spent recovering the walnut (loading = 0.25) and the mean number of hand movements used to push the walnut (loading = 0.17) also had an effect on PC1 (Figure 14). The second axis (30 %) was mainly determined by the mean number of in-hand movements used repositioning the tool in the hand (loading = 0.94) that was in opposition with four variables: the mean number of tool place changes in the grid (loading = - 0.20), the mean number of contact area changes between the hand and the tool (loading = - 0.16), the mean time spent recovering the walnut (loading = - 0.20) and the mean number of hand movements used to push the walnut (loading = - 0.11). The PCA distinguished the different performance and techniques used by humans and great apes (PC1) and between a few of the human, gorilla, and orangutan subjects (PC2) (Figure 14). Orangutans and gorillas were situated along the positive side of PC1 and, on average, touched more wooden obstacles, changed the place of the tool in the grid more often, spent more time recovering the walnut and using more number hand movements to recover the walnut than humans situated along the negative side of this axis (Figure 14). This result indicates better performance for humans with the use of grasping postures classified as precision grips: humans 1) control more their movements better than gorillas and orangutans, 2) reposition the tool in the grid less often, 3) spend less time to recovering the walnut, and 4) use fewer hand movements to recover the walnut. Some humans and gorillas situated along the positive side of PC2 used more in-hand movements on average than the other humans and gorillas. All orangutans situated along the negative side of PC2, changed the tool placement in the grid more often, changed their contact area combinations between the hand and the tool more often, spent more time recovering the walnut and used more numerous hand movements to push the walnut (Figure 14). The two gorillas which used more in-hand movements, and which appeared to outperform the other gorillas, were the two individuals who used the

interdigital 2/3 brace grasping posture the most, whereas the other individuals used the interdigital 3/4 brace grasping posture more often. No specific techniques were apparent among the humans, who used more in-hand movements and, for some individuals, also used precision grips.

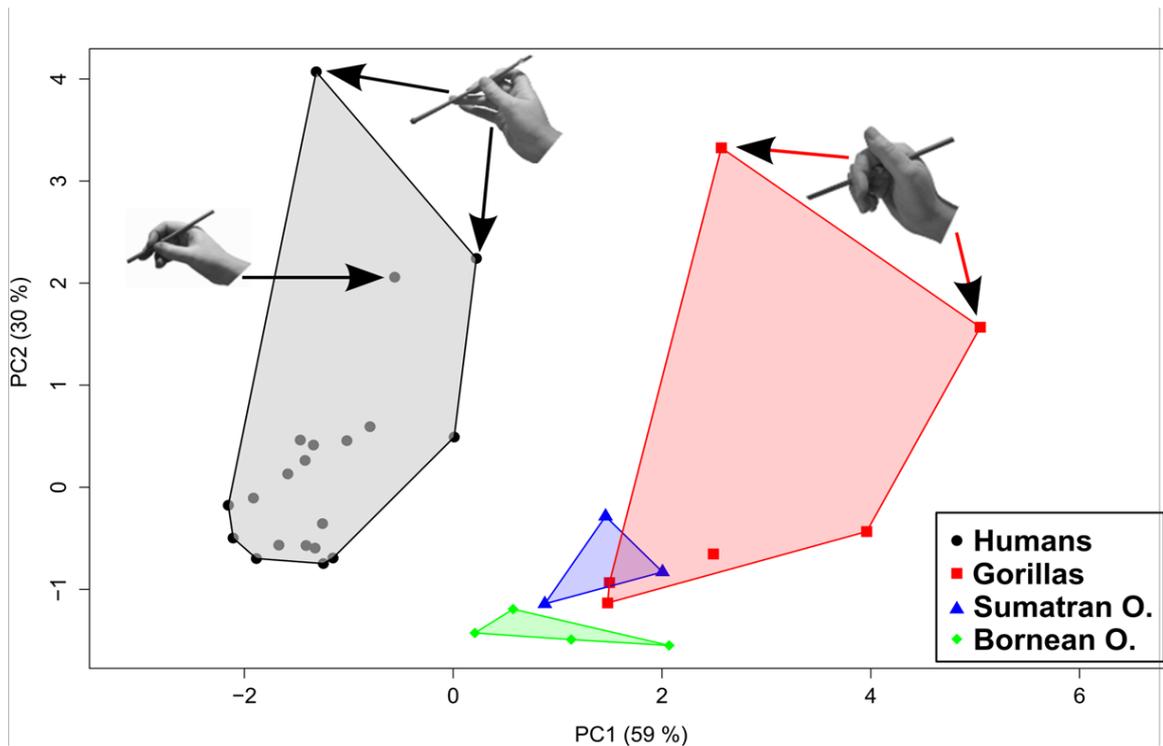


Figure 14. Principal Component Analysis performed on six variables (number of hand movements, number of touched wooden obstacles, time to reach the walnut, number of position changes of the tool in the grid, number of changes of combinations of contacts areas, number of in-hand movements use) for mean values of each individual. Polygons represent species and points individuals. Axis 1 distinguishes performance by humans from performance by gorillas and orangutans (both species). Axis 2 distinguishes performance used by some human and gorilla individuals from orangutans, based on their preferred grasp type: precision grips for humans (four finger grasp and dynamic tripod) and interdigital 2/3 brace for gorillas (see Table 8 for description).

4. DISCUSSION

In the present study, the same complex tool use task was tested on three species of hominids to compare their performances and manipulative techniques and to test if humans are unique. The results clearly show that humans perform better than gorillas and orangutans, with performance linked to in-hand movements and specific grip types. Only humans use bimanual grip type, pad-to-pad precision grip and in hand-movements involving fingertips. Gorillas and orangutans use more power grips and gorillas develop more in-hand manipulation than orangutans showing more mouth manipulation. Finally, orangutans show more intra-species variability in the grip techniques. Differences between humans, gorillas, and orangutans quantified here could be explained by morphological and/or neuromuscular coordination specificities. However, humans may have no “unique” manual abilities and non-human primate species may not need to use these abilities to succeed the task.

4.1. Performance

Our results show that performance differs according to species and the preferred grasping postures use by each individual. For task duration, which has been previously considered as an important measure of performance (Sollerman and Ejeskar, 1995; Schoneveld et al., 2009; Albiach-Serrano et al., 2012), we show that humans reach the walnut faster than gorillas and orangutans. Humans may possess greater motor skills than gorillas and orangutans in order to perform the task more rapidly. Moreover, for gorillas and orangutans, social pressure may have influenced task duration. Indeed, they perform the task in their social group and even if there is the same number of mazes as there are individuals, high ranked individuals often try to steal the walnut of the subordinate individual, which requires them to perform the task faster. It would be ideal to study individuals in isolated conditions, but such a procedure was not allowed. In addition, to test the effect of social rank on manipulative abilities would be of great interest on a large sample.

Considering the other parameters, humans also perform better than gorillas and orangutans, use less wrist movements to reach the walnut, touch fewer obstacles, and change the position of the tool in the grid less often. These results could demonstrate a lack of efficiency and precision of wrist movements for both great apes. Moreover, the precision grips used by humans could represent a good compromise between the mobility allowed by these grips for

the object grasp and the relative stability produced by the pulp surfaces of the fingers (Marzke, 1997). In addition, we found no significant differences in the performance between unimanual and bimanual grip types. We can wonder why humans use such complex manipulation involving coordination between both upper limbs without any benefit. Are humans more used to bimanual strategies conditioned from their childhood than non-human primates? It would be interesting to study a greater sample of humans to test the influence of unimanual and bimanual grip types on their performance during different manual activities. Finally, some individuals among humans and gorillas perform better than others, use more in-hand movements, change the place of the tool in the grid less often, change their contact area combinations between the hand and the tool less often, perform the task more rapidly and use fewer wrist movements to push the walnut. Thus, the use of in-hand movements could involve better manipulative control with less repositioning of the tool in the grid, and allowing faster task performance. Finally, the interdigital 2/3 brace grasping posture used by the best performing gorillas could allow more in-hand movement compared to the other grasping postures.

4.2. Specific techniques according to species

The different techniques observed between species could be due to many factors. The complexity of the maze task requires complex coordination of motor demands which could be expressed differently between species according to their motor skills and their morphology (Wainwright et al., 2008). The ability to perform many two-handed tasks routinely exists for both humans (Corbetta and Thelen, 1996) and great apes (e.g. chimpanzees: Marzke et al., 2015; gorillas: Byrne et al., 2001; orangutans: Peters and Rogers, 2008). In the present study, bimanual coordination grips were employed half of the time, only by humans. These bimanual coordination grips increase the complexity of manipulation (MacNeilage et al., 1987; Hopkins, 1995; Heldstab et al., 2016). Humans displayed symmetrical bimanual coordination, where both hands grasp the same tool, and also asymmetrical bimanual coordination where each hand grasped separate tools. Asymmetrical bimanual coordination appears to be a more difficult task and requires eye coordination with both distant hands. Symmetrical bimanual coordination was only observed one time by two orangutans. This result could be explained by the fact that one hand is most of the time hanging from the wiring. It is also showed that wild orangutans use unimanual feeding more than feeding involving two limbs (hand-hand or

hand-foot) (Peters and Rogers, 2008). Considering orangutans, they use specific grip types including the mouth and the foot probably due to their high arboreal lifestyle. Orangutans showed a strong preference for oral tool use over manual tool use in a previous study (O'Malley and McGrew, 2000), however, in the present study oral tool use occurred less than 10 % of the time. This result could be due to the cage wiring used in the current study which is not similar to the arboreal substrate where orangutans use tools in the wild. As orangutans are able to adopt many body postures (Thorpe and Crompton, 2006), the prevalence of non-oral manipulation could be linked to the task itself requiring both force and precision that the mouth may not provide. Gorillas use exclusively unimanual grip types, which is consistent with recent reports on tool use in wild gorillas (Breuer et al., 2005; Kinami et al., 2015). Extensive, but time consuming, studies in the wild could help improve our knowledge about interactions between environment, body posture, natural tasks and grasping techniques.

4.3. Grasping postures and in-hand movements

We already know that great apes can use precision grips (Christel, 1993; Jones-Engels and Bard, 1996; Marzke and Wullstein, 1996; Christel et al., 1998; Byrne et al., 2001; Pouydebat et al., 2009, 2011) and in-hand movements (Craet et al., 2009; Bardo et al., 2016) like humans. The human subjects in this study used pad-to-pad precision grip and in-hand movements with fingertips, while gorillas and orangutans used more grasping postures in which the tool is blocked into the hand (e.g. power grip) and in-hand movements which engage the palm. These differences between humans and great apes could be explained by the different neuromuscular anatomy and hand morphology. Indeed, gorillas (and gibbons) have the highest thumb-forefinger index among hominoids, while orangutans have the lowest (Shultz, 1930). Thus, gorillas could involve their thumb more than orangutans during in-hand movements, which is consistent with our results. Moreover, the differences between humans and great apes could be due to the absence of several anatomical features. It appears that some human hand muscles, such as *flexor pollicis longus* and *extensor pollicis brevis* which are related to the movement of the thumb, are not present in the hands of great apes, except hylobatids (Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012). Moreover, in contrast to humans (Vigouroux et al., 2011; Goislard de Monsabert et al., 2012), the muscle activities and muscular coordination required to grasp an object for great apes are not known. According to extremely scarce studies on muscles activities (Overduin et al., 2008) and our

results, we can expect that the morphometric of humans', gorillas' and orangutans' hand involves different biomechanical constraints during grasping actions. For example, a smaller thumb would generate a different finger joint angle, corresponding to different moment arms and probably would engage different joint and muscle loadings. Consequently, the rare use of fingertips for both great apes could be the result of a choice based on biomechanical loadings, which cannot be balanced by their musculature when grasping with the thumb. It would be very useful to develop a musculoskeletal model based on ape morphological (e.g. size of the segments) and biomechanical data (e.g. force, kinematics, muscle activities) as in humans (see Fernandez et al., 2016).

4.4. Hand preference

The tool use hypothesis (Kimura, 1979; Frost, 1980) suggests a strong bias for the right hand during tool use tasks. Other studies suggest an enhanced role for the left hemisphere during the learning of new sequences and skills and that this specialization emerged from a left hemisphere specialization for predictive control (the ability to plan and coordinate motor actions; Mutha et al., 2012). Our small sample size did not allow us to validate these hypotheses but we can mention that only humans were right handed in this study. Hand preferences varied across individuals for gorillas (4 left handed and 2 right handed) and orangutans (2 left handed and five ambidextrous). Directional hand preference during tool use was found previously, with a left-hand preference for wild chimpanzees (during termite fishing, Lonsdorf and Hopkins, 2005; Bogart et al., 2012), and captive gorillas (Pouydebat et al., 2010), a right-hand preference for captive bonobos (chapter 3), and no group-level bias for the right or the left hand for captives orangutans (O'Malley and McGrew, 2006). As arboreal apes, orangutans may be predicted to exhibit different patterns of manual lateralization than more terrestrial species, specifically a left-hand preference for manual actions while the other hand is used for support (MacNeilage et al. 1987). However, as in O'Malley and McGrew (2006) we not find directional bias in hand preference for orangutans. Thus, according to the variability of the results in the literature, we expect that plasticity of the brain and hemisphere specialization is underestimated. In addition, it is really difficult to conclude about hand preference and tool use because of the many parameters that can influence the hand preference (e.g. body posture, experience, properties of the object grasped, grasping techniques). Finally, it would be interesting to compare right-handed and

left-handed humans in order to understand the potential links between hand-preference, grasping posture and performance.

4.5. Specifics techniques according to individuals

Inter-individual variability is present in humans, high for orangutans and low for gorillas. Because the tasks in this study were not habitual, individuals adapted their techniques according to their individual experiences which may be different from one another. Indeed, for example children learn the pencil grip to write between four and six years old and there is variation in the development of this grip (Schneck and Henderson, 1990). Moreover, some individuals are sportive and/or musicians, and previous studies show that these activities have an effect on fine motor abilities (e.g. for music Costa-Giomi 2005) and on prehensile capabilities (e.g. for sport Cutts & Bollen, 1993; Shea et al., 1992). In other words, learning and practicing some activities could influence manipulative abilities in human adults which could explain the different techniques used by humans.

Considering orangutans, we find that they show more inter-variability in their techniques than humans and gorillas. The fact that orangutans frequently change their body posture could generate changes in their grasping postures and also could generate more repositioning of the tool, especially with the mouth. Interestingly, despite our small sample size and even though it was not a focus of the study, we observed differences between Bornean orangutans and their Sumatran relatives. We know that Sumatran forests tend to be more productive and less seasonal than Bornean forests, and these differences could potentially have generated different behavioral responses such as foraging strategies and sociality (Wich, Utami-Atmoko et al., 2009; van Schaik, 2013). There is also a difference in general morphology between both orangutan species (Courtenay et al. 1988; Groves et al., 1992) and we do not know if their hand morphology differs. These differences between species could explain different manipulative abilities and should be explored in future studies.

Gorillas show less inter-individual variability in the techniques they use and seem to be more stable (i.e. technique use for a long time). This could be due to the fact that compared to orangutans, they are more terrestrial and are less constrained by high body posture variability. They may be free to develop specific manipulative abilities including tool use and complex bimanual coordination (e.g. Meulman et al., 2012). Strong inter-individual variability was also demonstrated in the techniques used by bonobos (chapter 3) which seems

to be intermediate between gorillas and orangutans. Thus, gorillas, with their more terrestrial lifestyle, could have developed different motor skills and more specific techniques than arboreal species such as orangutans and these specific techniques could be shared among individuals. Cognitive and manual abilities of gorillas are poorly known and should be explored because they display high manipulative ability in the wild (Byrne et al., 2001) including tool use which was observed recently (Breuer et al., 2005; Kinami et al., 2015).

5. CONCLUSION

Our results indicate that all the species in this study are able to perform the task but with differences in performance and technique. Species could develop and adapt manual abilities according to the demands on their foraging niche. One study suggests that humans have the most complex foraging niche and so they have developed complex manual abilities, with the idea that the manipulation complexity would have coevolved with brain size and territoriality in primates (Heldstab et al., 2016). Though an analysis with a large sample size including many arboreal and terrestrial species would be necessary to test this hypothesis, our results are consistent with this previous study and with the hypothesis that territoriality facilitates the development of complex tool use (Meulman et al., 2012). Indeed, humans and gorillas show more complex manipulation skills during the maze task than orangutans, like the use of in-hand movements, a bias for a preferred hand, and more stable technique use (i.e. technique use for a long time). However, humans may have no “unique” manual abilities and non-humans primate species may not need to use the same manual abilities as humans during the maze task. Indeed, during the maze task one of the human specificities is bimanual coordination, which is a very high cost strategy. However, this strategy does not appear to outperform the other. So the lack of bimanual coordination in gorillas and orangutans could be the result of a choice based on the cost at the motor control level. In addition, great apes do not manufacture stone tools in the wild, but captive orangutans and bonobos are able to manufacture and use appropriate stone tools (Wright, 1972; Toth and Schick, 1993; Schick et al., 1999). Thus, orangutans and bonobos have the potential (e.g. functional, morphological, and cognitive) to manufacture stone tools but their environment may not demand the need to manufacture them. Finally, a very interesting point is the intra-species variability quantified and we need to explore the morphology of the primate hand to test whether this variability in manual activities could be explained by intra-specific morphological variability in bone shape.

SUPPLEMENTARY TABLE

Table S1. Statistical results from the comparison of performance parameters between species. Significant results are in red. We found differences between humans and the great ape species, but no differences between gorillas and orangutans.

	Duration to perform the task	Number of wrist movements	Number of touched obstacles	Number of repositioning of the tool in the grid
All species	$H = 22.958, N = 33, df = 2, P < 0.001$	$H = 23.006, N = 33, df = 2, P < 0.001$	$H = 22.837, N = 33, df = 2, P < 0.001$	$H = 20.306, N = 33, df = 2, P < 0.001$
Humans/Gorillas	$Z = 3.592, N = 26, P' < 0.001$	$Z = 3.557, N = 26, P' < 0.001$	$Z = 4.214, N = 26, P' < 0.001$	$Z = 3.131, N = 26, P' < 0.01$
Humans/Orangutans	$Z = 3.953, N = 27, P' < 0.001$	$Z = 3.989, N = 27, P' < 0.001$	$Z = 3.215, N = 27, P' < 0.01$	$Z = 3.908, N = 27, P' < 0.001$
Gorillas/Orangutans	$Z = 0.115, N = 13, P' > 0.05$	$Z = 0.173, N = 13, P' > 0.05$	$Z = 0.988, N = 13, P' > 0.05$	$Z = 0.465, N = 13, P' > 0.05$

SUMMARY OF THE CHAPTER 4

Title: Are humans unique? Are gorillas and/or orangutans unique? What manual specificities exist for each species?

Question: Do humans are more performant and show real specific tool manipulation abilities compared to other hominids? Do gorillas and orangutans demonstrate different strategies?

Model: Humans (*Homo sapiens*), gorillas (*Gorilla gorilla gorilla*), orangutans (*Pongo pygmaeus* and *Pongo abelii*).

Method: Experimentation and ethological observation in Zoos (Amnéville, Ménagerie du jardin des plantes in Paris, La Palmyre, la Vallée des Singes).

Results: Humans performed better than gorillas and orangutans, with performance linked to in-hand movements and specific grip types. Only humans used bimanual grip type, pad-to-pad precision grip and in hand-movements involving fingertips. Gorillas and orangutans used more power grips and gorillas developed more in-hand manipulation than orangutans showing more mouth manipulation. Finally, orangutans showed more intra-species variability in the grip techniques.

Discussion: Human specificities quantified here could be explained by morphological and/or neuromuscular as coordination specificities, as the differences quantified between gorillas and orangutans. However, humans may have no “unique” manual abilities and non-humans primate species may not need to use these abilities to succeed the task. Indeed, we can wonder why several humans chose a high cost strategy such as bimanual coordination which was not needed to succeed. Differences between these great apes could be explained by their different lifestyle (the most terrestrial of great apes versus the most arboreal).

Perspectives: It would be very useful to test the effect of morphological and biomechanical constraints on manipulative techniques used by humans and great apes during tool use. Such an approach could help to elucidate the links between the morphological parameters of the hand and the functional strategy quantified. Then, the next chapter (chapter 5) focuses on the morphological variability of the trapeziometacarpal complex among Hominids and its functional involvements, as this articulation appears important in human manipulative abilities. The consequences of different hand morphometric (humans and great apes) on tool grasp abilities are investigated in the chapter 6, using biomechanical analyses with musculo-skeletal simulation.

Chapter 5 – Morphological variability of the
trapeziometacarpal complex among hominids
and functional involvement

Morphological variability of the trapeziometacarpal complex among Hominids and functional involvement

Journal of Evolutionary Biology, in preparation.

ABSTRACT

In order to compare manual abilities of living primates and to interpret fossils, several studies focus on the trapeziometacarpal joint. However, comparisons and inferences remain difficult because of the shape of this joint, which is really difficult to analyze quantitatively. Moreover, no comparison takes into account the overall shape of the trapeziometacarpal complex (i.e. the overall trapezium and first metacarpal) and links shape variability with the observed manipulative abilities of living primates. The objective of this study is to (I) accurately describe the overall shape of the two bones of the trapeziometacarpal complex and quantify shape differences between various Hominids (modern humans and fossils, chimpanzees, bonobos, gorillas, orangutans), (II) describe and quantify shape co-variation between the trapezium and the first metacarpal, and (III) highlight the relevant shape data that could explain the manipulative abilities previously quantified. Using a 3D geometric morphometric surface analysis of the trapeziometacarpal complex, a multivariate analysis of shape variation of the trapezium clearly distinguishes *Homo* (modern and fossils) from great apes and, especially, *Pongo*. The analysis of the first metacarpal distinguishes *Homo* from *Pan* and *Pongo*. Shape co-variation are not only dominated by variations of joint surfaces and muscle attachments zones, but are driven by the overall shape variations of the two bones, indicating strong morphological relationships. Moreover, shape co-variation differs between species and appears to partially reflect the phylogeny with maybe some similar features between *Homo* and *Gorilla*. These differences between Hominids are certainly constrained or favored by various factors (e.g. lifestyle and manipulative abilities). Finally, the shape of the trapeziometacarpal complex seems to be linked to the manipulative abilities previously quantified, showing more thumb involvement in humans and African apes than in orangutans.

1. INTRODUCTION

The humans' manipulative skills are traditionally linked to specific morphological features that are considered to be associated with stone tool-making (Napier, 1960; Marzke, 1997; Susman, 1998; Tocheri et al., 2008). Some hand morphological features of primates were shown to affect their manual abilities, e.g. the size of the fingers, the width of the palm and the flexibility of the different articulations of the hands (Marzke et al., 1992). The shape of the trapeziometacarpal complex (TMC, consisting of the trapezium and the first metacarpal, see Figure 15) is considered important for human's manipulative activities since it appears to allow greater mobility of the carpometacarpal joint of the thumb in humans than in great apes (e.g. Marzke et al., 2010). Indeed, the specific saddle-shaped of the TMC joint permits opposition of the thumb with other fingers (Napier, 1952; 1956).

The TMC complex is studied in a clinical framework on humans (e.g. Napier, 1955; Cooney and Chao, 1977; Bettinger et al., 1999; Nanno et al., 2006) as well as in anthropology, with comparative studies in primates (e.g. Lewis, 1977; Rose, 1992; Tocheri et al., 2003, 2005; Marzke et al., 2010). Clinical studies provide very useful detailed information on the mechanics and the morphology of the human TMC complex. Morphological comparative analyses in primates allowed to better understand the relationships between manual abilities and particular lifestyles in primates. In addition, the inclusion of data regarding fossil taxa in these comparative analyses offered to interpret their potential manual abilities. Comparative studies with qualitative data showed differences in the shape of the TMC complex between humans and great apes related with hand functions, such as manipulation or locomotion for great apes (Lewis, 1977; Marzke, 1997). Quantitative studies on the primates' trapezium are more recent. These studies focus on the curvature of the TMC joint (Trinkaus, 1989; Marzke et al., 2010), the angles between the four joint surfaces of the trapezium (Tocheri et al., 2003), and the relative proportion of articular and non-articular surfaces on the trapezium (Tocheri et al., 2005). Marzke, Tocheri and colleagues (Tocheri et al., 2003, 2005; Marzke et al., 2010) use three-dimensional (3D) methods to analyze the complex shape of the carpal bones including the trapezium. Marzke and colleagues (2010), for example, use a mathematical modeling with a 3D approach to quantify the curvatures of the TMC joint surfaces among hominins and other primates. They quantify a difference in the degree of curvatures of these joints in primates. They conclude that the specific curvature of the TMC joint in humans, flatter than in non-human primates, may facilitate forceful precision and power grips during manipulative activities.

The morphology of the TMC appears a good indicator of manual abilities during locomotion and manipulation behaviors (e.g. Lewis, 1977; Rose, 1992; Tocheri et al., 2003, 2005; Marzke et al., 2010) but quantitative analyses mainly focus on the trapezium (Tocheri et al., 2003, 2005; Marzke et al., 2010). As far as we know, the quantification of the overall shape of the trapezium and of the first metacarpal were not investigated. Since the functional interaction between the trapezium and the first metacarpal determines the joint mobility, it appears important to study the shape variability of these two bones. Moreover, studying together these two bones can allow to describe the morpho-functional relationship between them. Shape co-variation of body parts (two bones) may result from a variety of factors: development, functional requirements, genetics, and evolutionary history (Cheverud, 1996; Klingenberg, 2008, 2009, 2010, 2014). The strength of shape co-variation can allow use to measure the intensity of the morphological and functional relationships between these two bones. Do different pattern of variation and co-variation exist between Hominids? What constraints could explain the differences, or not, between species? Moreover, it appears important to relate shape variability with behavioral data in order to better understand the relationships between form and function, and the evolutionary constraints applying on this complex that is so important for primates' manipulation abilities (e.g. Taylor and Schwarz, 1955; Marzke et al., 2010).

We previously found (chapters 2 and 3 of this dissertation), that humans and great apes show dynamic manual abilities during tool use behavior with the highest complexity for humans manipulations and the lowest for orangutans. We showed especially that humans use complex in-hand movements to reposition the tool during a complex tool use task, while bonobos and gorillas use simple in-hand movements with no rotation of the thumb and that orangutans do not even use in-hand movements. As we quantified these different manipulative abilities between species, we wonder if it could be related by an inter-species shape variability of the TMC complex across species. Will the pattern observed for shape variation is similar as for our behavioral data? And similar in the two bones? Finally, we would like to compare the shape co-variation of the two bones in extant species with that of extinct ones such as *Homo sapiens* ("Cro-Magnon") and *H. neanderthalensis* in order to discuss their potential manual abilities.

To deal with these questions, this study quantitatively analyze for the first time the overall morphology of the trapezium and of the first metacarpal together, and discusses the shape pattern in the light of the species manipulative abilities. Thus, the objective of this

study is to 1) accurately quantify the overall shape variability of the TMC complex in humans (modern and fossil) and great apes, using 3D geometric morphometrics, 2) quantify shape covariation between the two bones of this complex, and 3) find potential functional implications linked with our previously results regarding quantified manual abilities.

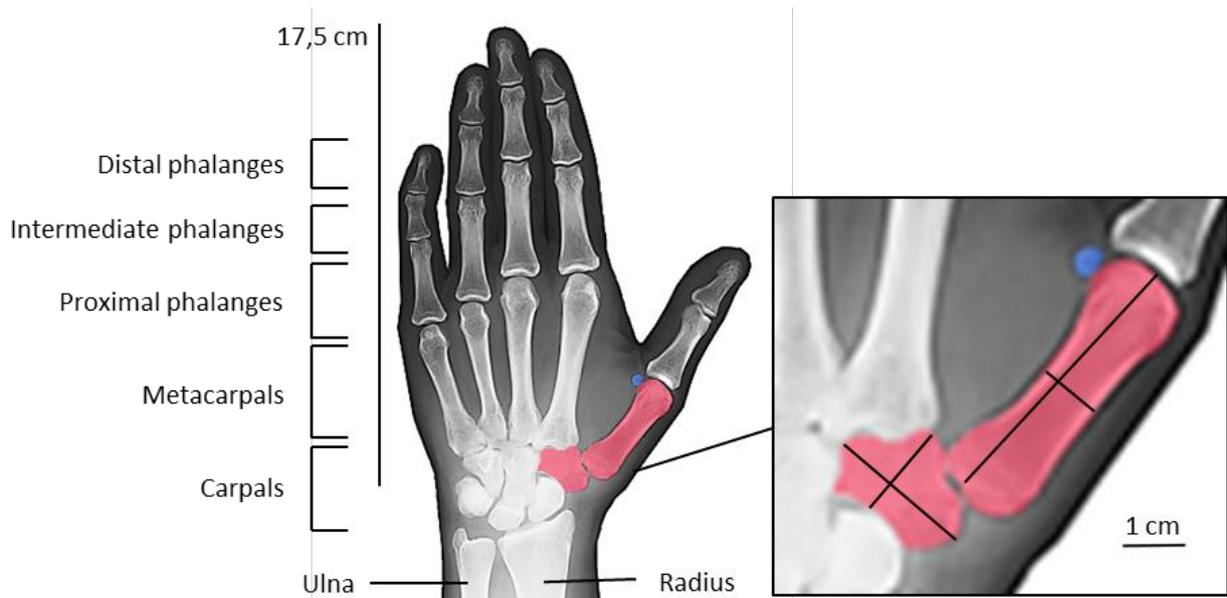


Figure 15. X-ray of a human left hand in dorsal view with the trapeziometacarpal complex (in red) connected by the trapezium and the first metacarpal at the base of the thumb, and with the common joint in saddle form. In blue is a sesamoid bone.

2. MATERIAL AND METHODS

2.1. Material

2.1.1. Anatomical descriptions

The TMC complex connects the trapezium and the first metacarpal. It is reinforced by sixteen ligaments (Bettinger et al., 1999), and presents insertions of tendons for intrinsic and extrinsic muscles of the hand (Taylor and Schwarz, 1955) (Figure 16). We describe the trapezium and the first metacarpal of humans, without detailing ligaments (for details see Bettinger et al., 1999), as a base to discuss our results. We followed the anatomical descriptions of Gray (1918), Lewis (1977), and Scheuer and Black (2000).

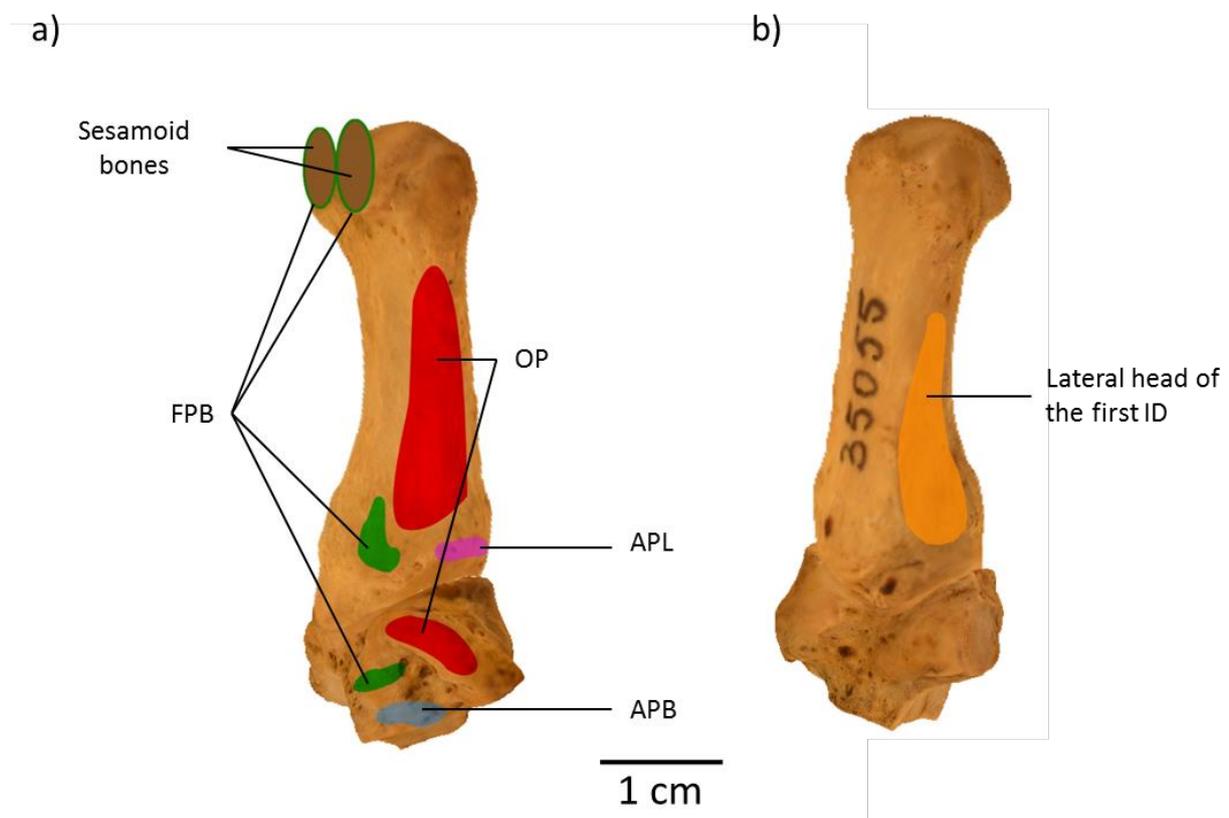


Figure 16. Illustration of a right trapeziometacarpal complex of *Homo sapiens* (specimen MNHN 35055) showing the location of the insertions of tendons on the thumb in a) latero-ventrally and b) medio-dorsal views. OP, *Opponens pollicis* (red); APB, *Abductor pollicis brevis* (blue); FPB, *Flexor pollicis brevis* (green); APL, *Abductor pollicis longus* (purple); ID, *Interosseus dorsalis* (orange).

2.1.1.1. Trapezium

The trapezium is a carpal bone situated on the second distal row of carpal bones in the radial side (Figure 15), and is articulated with four bones (scaphoid, trapezoid, second metacarpal and first metacarpal). It presents six faces, with four joints surfaces (Figure 17): the TMC joint (saddle-shaped) on its distal surface; the joint with the trapezoid and the joint with the second metacarpal on its medial surface; the joint with the scaphoid on its proximal surface. The lateral face of the trapezium is broad and provides attachment of ligaments. The volar face has a deep groove, bounded laterally by the tubercle of the trapezium, where transmits the *Flexor carpi radialis* muscle. This face provides also origin to the *Opponens pollicis*, *Abductor pollicis brevis*, and *Flexor pollicis brevis* muscles. The dorsal surface presents neither articular surfaces nor muscles insertions, but presents the attachment of dorsal ligaments.

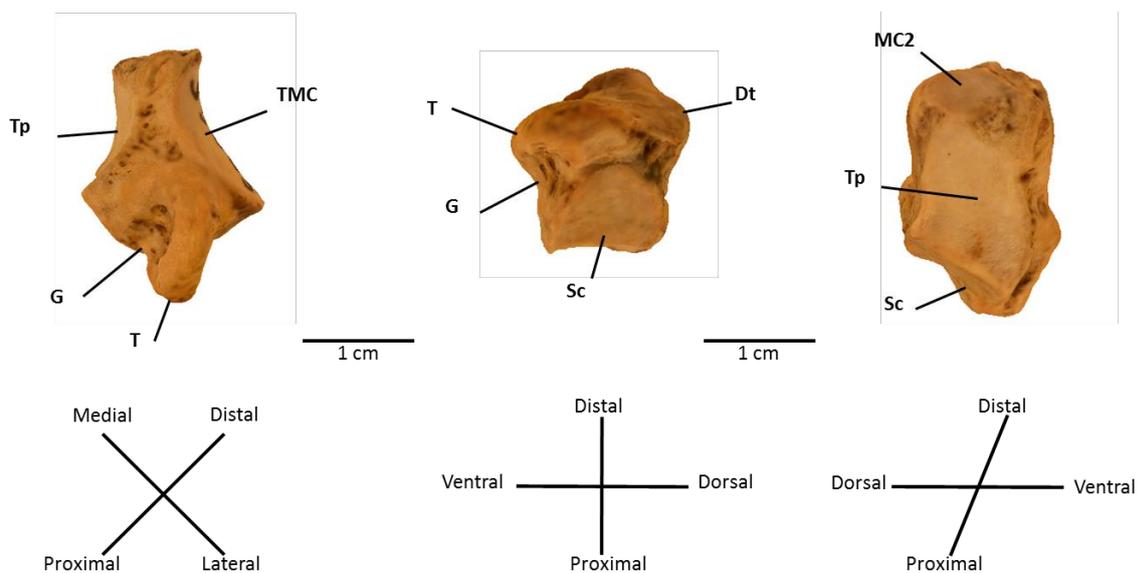


Figure 17. Right trapezium of *Homo sapiens* (specimen MNHN 35055), ventral view on the left, proximal view in the middle, and medial view on the right. Dt=dorsal tubercle; T=tubercle of the trapezium; TMC= trapeziometacarpal joint; MC2= joint surface articulated with the second metacarpal; Tp= joint surface articulated with the trapezoid; Sc= joint surface articulated with the scaphoid; G=groove of the *Flexor carpi radialis* muscle tendon.

2.1.1.2. First metacarpal

The first metacarpal (MC1) is shorter and more robust than the other metacarpals. It presents two articulations, one with the trapezium and one with the proximal phalange of the thumb (Figures 15 and 18). The volar surface is concave from above downward, and the dorsal surface is flat and broad. The radial side presents a crest for the insertion of the *Opponens pollicis* muscle and the ulnar side gives origin to the lateral head of the first *Interosseus dorsalis*. The proximal surface is saddle-shaped for the TMC joint and its radial side presents a tubercle for the insertion of the *Abductor pollicis longus* muscle. The distal surface is convex but less than in the other metacarpal bones and presents on its volar surface two articular eminences, with the lateral being larger than the medial one, for the two sesamoid bones, and for the tendons of the *Flexor pollicis brevis*, respectively.

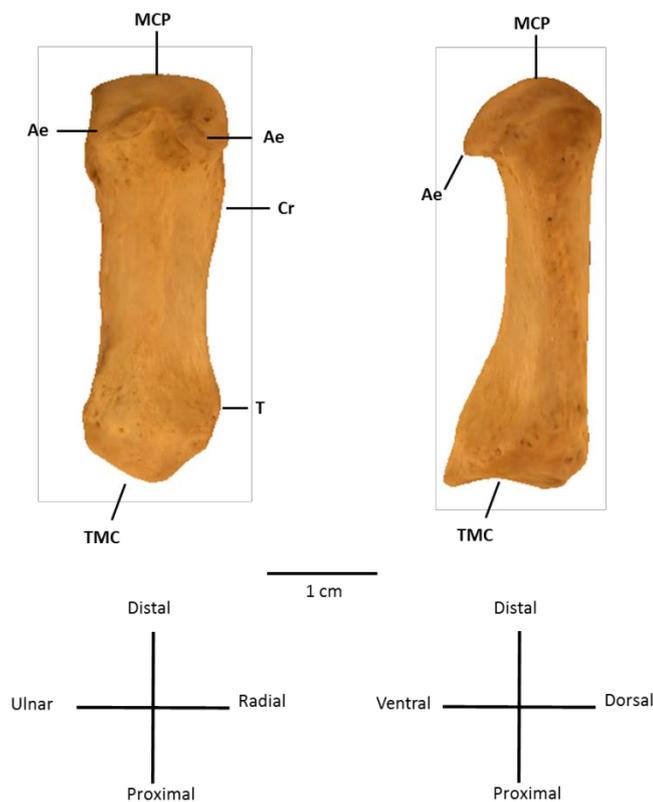


Figure 18. Right first metacarpal of *Homo sapiens* (specimen MNHN 35055), ventral view on the left and radial view on the right. MCP=metacarpophalangeal joint; TMC= trapeziometacarpal joint; Ae= articular eminences for the two sesamoid bones for the tendons of the *Flexor pollicis brevis*; Cr=crest for the insertion of the *Opponens pollicis* muscle; T= tubercle for the insertion of the *Abductor pollicis longus* muscle.

2.1.2. Specimens

We used 230 bones of the TMC complex (trapezium and first metacarpal) of 73 specimens (Table S2): 27 *Homo sapiens* specimens including three fossils of Cro-Magnon (two specimens from “Abri Pataud” estimated to 35-20000 years old and “La Dame du Cavillon” estimated to 30000 years old), three *Homo neanderthalensis* (“Ferrassie 1” and “Ferrassie 2” estimated 70-50000 years old, and “Kebara” or KMH2 estimated 61-59000 years old), nine *Pan troglodytes*, 14 *Pan paniscus*, 11 *Gorilla gorilla gorilla*, and nine *Pongo pygmaeus*. Bones of both right and left hands were available for 42 specimens, only one side was used for the other 31 specimens. All the specimens come from adult individuals, and we included males and females as well as specimens of unknown sex. All specimens of *Homo* used are housed in the collections of “Anthropologie” from the Musée de l’Homme in Paris (France). The specimens of *Pan troglodytes* and most of the *Gorilla gorilla gorilla* specimens are housed in the collections of “Anatomie comparée” from the Muséum National d’Histoire Naturelle in Paris (France). Specimens of *Pan paniscus* and two *Gorilla gorilla gorilla* specimens are housed in the collections of “Mammalogie” from the Royal Museum for Central Africa in Tervuren (Belgium), and specimens of *Pongo pygmaeus* are housed in the collections of “Birds & Mammals” in Naturalis Biodiversity Center in Leiden (Netherlands). For great apes, specimens come from wild and captivity.

2.2. Methods

2.2.1. Acquisition of the 3D models

The 3D digitized bones were produced using photogrammetry. The general principle of photogrammetry is to reproduce an object in 3D from pictures. Compared to other 3D model building methods such as laser scanners, techniques of photogrammetry are low cost (Cunningham et al., 2014), and portable, since it requires a minimal equipment such as a conventional camera (Fau et al., in press). Therefore it constitutes a convenient method to work directly in the museum collections. Moreover, 3D models obtained by photogrammetry can be of as high quality as 3D models obtained with laser scanners (Koutsoudis et al., 2013; Fau et al., in press). Photogrammetry uses algorithms that find matching points between overlapping pictures taken from different viewpoints to build a sparse point cloud model. This model is used as a basis to compute a denser point cloud model, which is submitted to a

triangulation algorithm to generate the polygonal mesh model (3D mesh). This final model is then used for the geometric morphometric analyses.

Fifty pictures were captured on both side of the object from different viewpoints. Viewpoints are located on three different virtual circles, defining three different inclinations of the camera. Pictures were acquired with the maximum lighting possible on the object. We used a Nikon D5500 DSLR camera with a resolution of 24.20 megapixels. The focal length was set to 55 mm (Objectif AF-S DX NIKKOR 18–55 mm VR II) for all pictures. For the reconstruction of our bones we used the Agisoft PhotoScan software (© 2014 Agisoft LLC). Each model was decimated to 90 000 triangles in order to obtain homogeneous 3D surface models. As we used right and left bones, we mirrored the left bones, using the MeshLab software (Cignoni and Ranzuglia, 2014), in order to obtain right bones only.

2.2.2 Geometric morphometrics

To quantify shape variation between specimens, we used a 3D geometric morphometrics approach (Zelditch et al., 2012) using both anatomical landmarks and sliding semi-landmarks (Gunz and Mitteroecker, 2013). Anatomical landmarks are defined as point locations that are biologically homologous between species. Because of the shape complexity of the two bones (trapezium and first metacarpal) and the scarcity of anatomical landmarks, we used sliding semi-landmarks of curves and surfaces (Gunz and Mitteroecker, 2013). Indeed, sliding semi-landmarks allow to accurately describe anatomical zones of high biological interest (like joint surfaces for example) even if devoid of anatomical landmarks (Cornette et al., 2013). To describe the margin of the articular surfaces we used semi-landmarks sliding on curves. Semi-landmarks sliding on surfaces were used to describe articular surfaces and non-articular surfaces. The sliding step permits to place in a geometrical homologous position the landmarks on curves and surfaces while minimizing the bending energy between a model used as a reference (named template) and the specimens (see Gunz et al., 2005 for details). After this step, all landmarks and sliding semi-landmarks can be analyzed as traditional 3D landmarks.

To achieve an accurate description of the trapezium and the first metacarpal, we created templates (Souter et al., 2010) detailed in Figure 19, Table 10 and Table 11. The curves were defined at the margins of articular surfaces and were bordered by anatomical landmarks (Gunz et al., 2005). The 3D landmarks' coordinates, curve and surface sliding semi-landmarks were digitized on the templates using the Landmark software package (Wiley et

al., 2005). The template used for the trapezium contains a total of 1344 points including six anatomical landmarks, 309 semi-landmarks sliding on curves, and 1029 semi-landmarks sliding on surfaces (Figure 19a and Table 10). The template used for the first metacarpal contains a total of 957 points including three anatomical landmarks, 285 semi-landmarks sliding on curves and 669 semi-landmarks sliding on surfaces (Figure 19b and Table 11). For each bone we digitized manually the anatomical landmarks and sliding semi-landmarks on curves using the Landmark software package (Wiley et al., 2005). The sliding procedure was realized using the software R (R Core Team 2016) and the package “Morpho” (Schlager, 2013) considered one of the most efficient packages available for this procedure (Botton-Divet et al., 2015). The sliding semi-landmarks were projected and slid into the surface by minimizing the bending energy between the template and the specimen (Gunz and Mitteroecker, 2013).

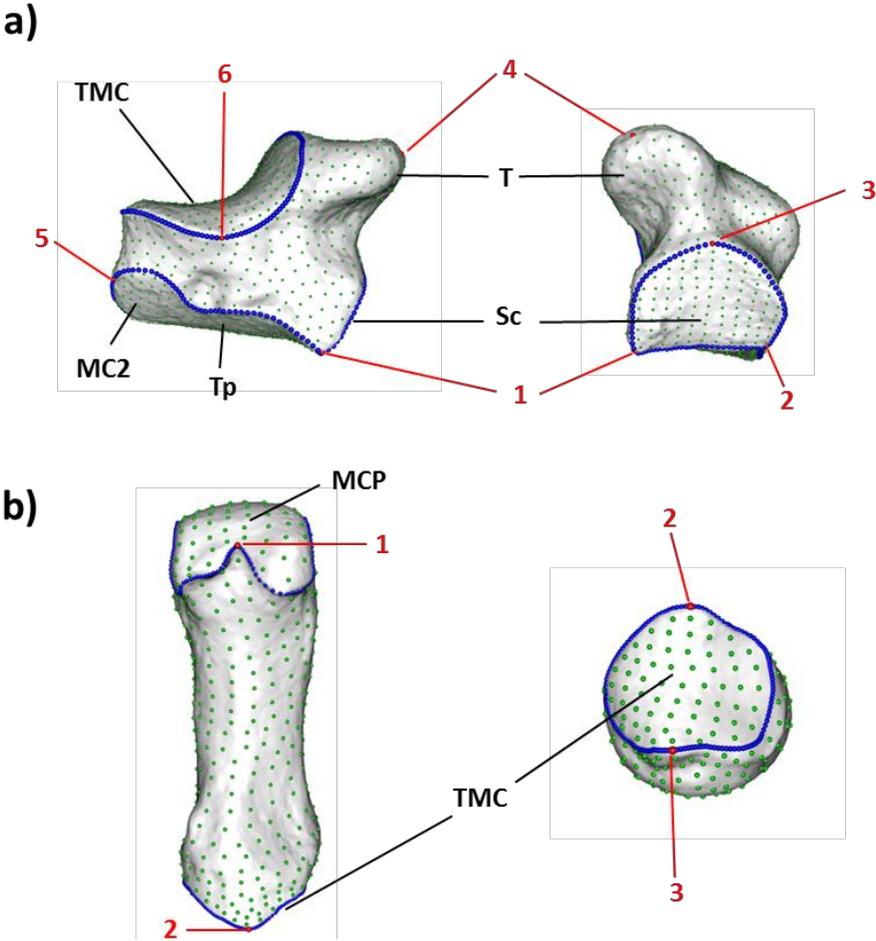


Figure 19. Illustration of the templates for the two bones: a) trapezium of a bonobo (specimen RMCA-27698) in ventral view on the left and proximal view on the right; b) first metacarpal of a human (specimen MNHN-35055) in ventral view on the left and proximal view on the right. Red points and numbers indicate anatomical landmarks defined in tables 10 and 11. Blue points are semi-landmarks sliding on curves. Green points are semi-landmarks sliding on surfaces. Mc=metacarpal; TMC= trapeziometacarpal joint; MCP= metacarpophalangeal joint, T=tubercle of the trapezium, MC2= joint surface articulated with the second metacarpal; Tp= joint surface articulated with the trapezoid; Sc= joint surface articulating with the scaphoid.

Table 10. Definition of the landmarks and curves of the trapezium. The curves 4 and 5 which border the joint surfaces of the trapezoid and the second metacarpal, include also the joint surface for the os central for orangutans (only present in *Pongo* for great apes and merged with the scaphoid for the other Hominins).

	Landmark	Definition
	1	Most medio-proximal point of the joint surface for the scaphoid
	2	Most latero-proximal point of the joint surface for the scaphoid
	3	Point of maximum of curvature of the distal part of the joint surface for the scaphoid
	4	Point of maximum of curvature of the tip of the tubercle of the trapezium
	5	Point of maximum of curvature of the distal part of the joint surface for the second metacarpal
	6	Point of maximum of curvature of the medial border of the trapeziometacarpal joint
<i>Curves</i>	1-3	Joint surface for the scaphoid
	4-5	Joint surface for the trapezoid and the second metacarpal
	6	Trapeziometacarpal joint surface

Table 11. Definition of the landmarks and curves on the first metacarpal.

	Landmark	Definition
	1	Point of maximum of curvature between the 2 articular eminences of the metacarpophalangeal joint surface
	2	Point of maximum of curvature of the anterior border of the trapeziometacarpal joint surface
	3	Point of maximum of curvature of the posterior border of the trapeziometacarpal joint surface
<i>Curves</i>	1	Metacarpophalangeal joint surface
	2	Trapeziometacarpal joint surface

To assess the repeatability of the manual placement of the anatomical landmarks, we placed the landmarks ten times on three specimens showing the lowest shape variability (same species and same sex). A Principal Component Analysis (PCA) shows variability among the repetitions on a specimen much lower than inter-specimen shape variability.

2.3. Analysis

Shape variability analyses were performed using Principal Component Analyses (PCA). 3D shapes associated with the extremes of axes were plotted to visualize the shape deformations along each axis. In order to compare shape co-variation between the trapezium and the first metacarpal, Two-Block Partial Least-Squares (2B-PLS) (Rohlf and Corti, 2000) were performed. It allows to quantify and visualize 3D shape co-variation between two datasets of 3D bones (Polly, 2008; Cornette et al., 2013) by finding common axes of shape variation between the two bones. Visualizations of each PLS axis were realized in order to help understanding shape co-variation between bones. Neighbor joining trees computed on Mahalanobis distances were used to visualize the whole shape variability of the two bones.

MANOVA (Multivariate analysis of variance) were performed on shape data to test significance of differences between species. All the analyses were performed in the software R (R Core Team 2016). The “Ape” package (Paradis et al., 2004) was used to produce the Neighbor joining tree, the “Rmorph” library (Baylac, 2012) for the PCA and 2B-PLS, and the package “Morpho” (Schlager, 2013) for the 3D visualizations of the shapes of the bones.

3. RESULTS

3.1. Shape variation of the trapezium

The first principal component axis (PC1) accounts for 37 % of total shape variation while the second (PC2) accounts for 13 %. The distribution of the different species in the morphospace defined by PC1 and PC2 shows groups structured according to the species (Figure 20). Result of the MANOVA on the shape of the trapezium indicates statistically significant differences between species (MANOVA: $P < 0.05$). The *Homo* group (combining modern and fossil *H. sapiens*, and *H. neanderthalensis*) contains more individuals and is the most compact group. *Homo* specimens are situated on the positive side of PC1 while the *Pongo* group is situated on the negative side (Figure 20). The *Pan* (bonobos and chimpanzees) and *Gorilla* groups are between *Homo* and *Pongo* on the PC1, and are overlapping (Figure 20), indicating similar trapezium shapes, intermediate between those of *Homo* and *Pongo*. All the fossils clearly group with modern *H. sapiens* except for one *H. neanderthalensis* (Kebara) which presents the highest value on PC1. Along PC2, the *Pongo* group is situated on the positive side while the *Pan* group is more on the negative side (Figure 20), indicating opposite shape of the trapezium between them. The other group containing gorillas and *Homo* occurs

in the intermediate place on PC2 between *Pongo* and *Pan*. All the fossils are clearly grouped with modern *H. sapiens*. When we take into account the global variability of the trapezium shape, the neighbor joining tree shows that *Homo* and *Pongo* are the most distant, and bonobos are closest to *Homo* followed by chimpanzees and *Gorilla*. The distance between bonobos and chimpanzees appears the same as that between *H. sapiens* and *H. neanderthalensis* (Figure 21).

Shape deformations associated with the positive side of PC1 (Figure 20), where the *Homo* group (*H. sapiens* and *H. neanderthalensis*) is situated, show a relatively flat and large trapezium, with broad joint surfaces. This trapezium shape shows differences in the joint surfaces, a) plane TMC joint surface; b) transversally orientated articular surface articulating with the scaphoid; c) curved and palmary oriented volar bordering the surface articulating with the trapezoid; d) sagittally orientated articular surface articulating with the second metacarpal. Concerning the non-articular surfaces of the trapezium that present insertions of tendons and ligaments, the volar surface shows e) a thin tubercle of the trapezium laterally oriented; f) on its superior part a deep groove bounded laterally by the oblique ridge of the tubercle of the trapezium; g) a convex surface on the inferior part. The lateral surface shows h) a concave surface oriented down that articulates with the scaphoid. Shape deformations associated with the negative side of PC1 (Figure 20), where the group of *Pongo* is situated, present, when compared to the mean shape, a relatively short and robust trapezium with the opposite morphology as the one described above for the positive side of PC1 (Figure 20).

Shape deformations associated with the positive side of PC2 (Figure 20), where *Pongo* group is situated, show a short and broad trapezium. Moreover we observe differences in the articular surfaces, a) a strongly curved TMC joint surface; b) a broad and extended articular surface articulating with the scaphoid; c) a large articular surface articulating with the MC2 that is fully oriented toward the volar surface of the trapezium; d) a surface articulating with the trapezoid less curved at the proximal part than at the distal part. Concerning the non-articular surfaces with insertions of tendons and ligaments, the volar surface shows e) a small tubercle of the trapezium with its low part concave; f) a small groove bounded laterally by the oblique ridge of the tubercle of the trapezium; g) a thin distal part between the surfaces articulating with the first and the second metacarpals. The dorsal surface shows h) a small dorsal tubercle concave on its distal part, and i) the lateral surface shows a concave surface oriented down. Shape associated with the negative side of PC2 (Figure 20), where the *Pan* groups are situated, correspond to a relatively long and thin trapezium when compared to the

mean shape, with the opposite morphology than described for the positive side of PC2 (Figure 20).

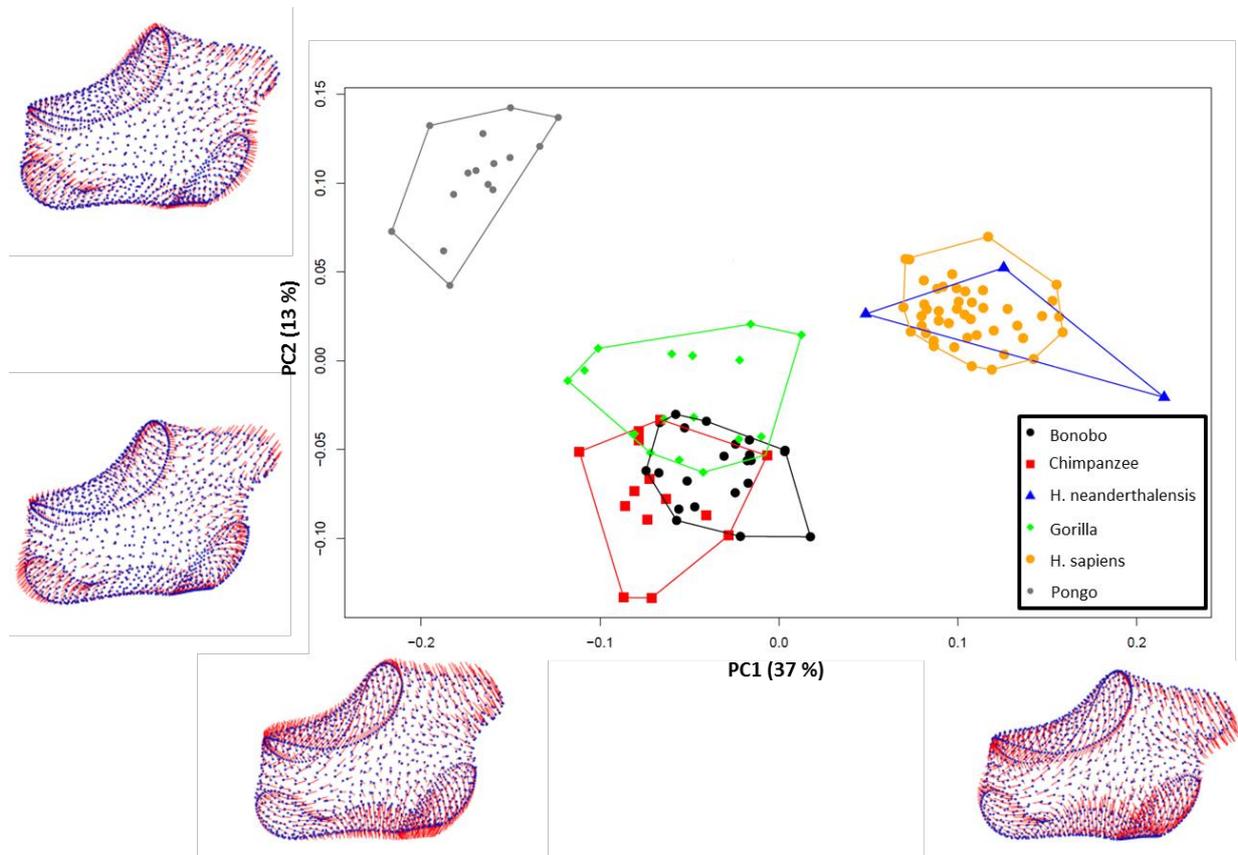


Figure 20. Results of the two first axes (PC1 and PC2) of a PCA performed on the shape variation of the trapezium for all the species. Shape deformations associated with the extremes of the axes are given with mean shape in blue and deformations represented by red vectors in ventral view. Polygons represent species and points specimens. PC1 distinguishes the shape of the trapezium of *Homo* (modern and fossils) from the Asian apes (*Pongo*) one and from the African apes (*Pan* and *Gorilla*) in the middle of the morphospace. PC2 distinguishes the shape of the trapezium of Asian apes (*Pongo*) from the African apes, and *Homo* (modern and fossils) are in an intermediate place.

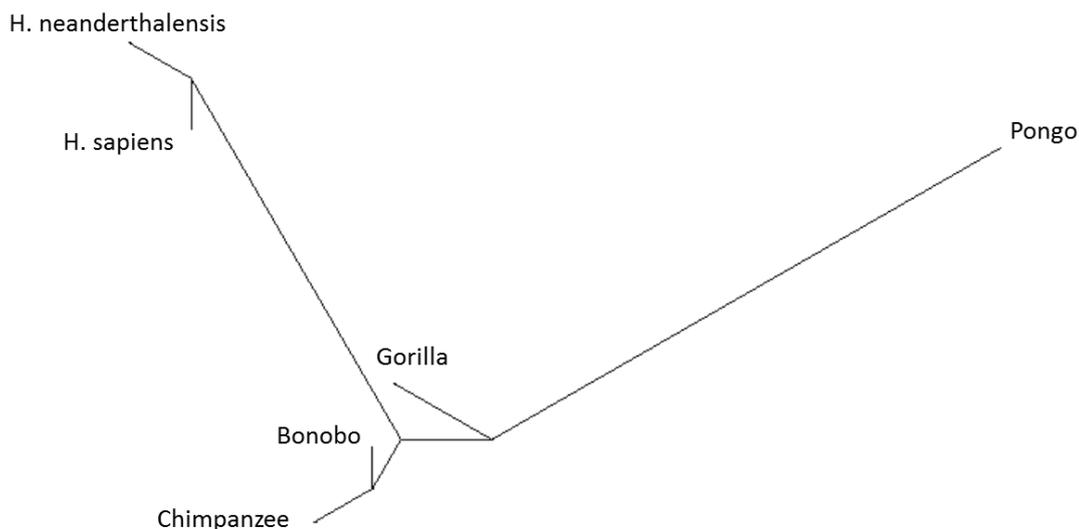


Figure 21. Neighbor joining tree computed on the phenotypic distances between species' trapezium shapes. *Pan* (bonobo and chimpanzee) are the closest to *Homo* (*H. sapiens* modern and fossils, and *H. neanderthalensis*), followed by *Gorilla*, and *Pongo* is the most distant.

3.2. Shape variation of the first metacarpal (MC1)

The first principal component axis (PC1) accounts for 35 % of total shape variation while the second (PC2) accounts for 12 %. The distribution of the different species in the morphospace defined by PC1 and PC2 shows different groups structured according to the species but the overlapping between the species is larger than for the trapezium (Figure 22). This indicates less inter-species variability for MC1 than on the trapezium. Result of the MANOVA on the shape of the MC1 indicates statistically significant differences between species (MANOVA: $P < 0.05$). Modern and fossil *Homo* are situated on the positive side of PC1 and are overlapping with the *Gorilla* group while *Pongo* and *Pan* groups are situated on the negative side (Figure 22). All the fossils clearly group with modern *H. sapiens*. Along PC2, the *Pongo* group is situated on the positive part while the *Pan* and *H. neanderthalensis* groups are on the negative part (Figure 22). *H. sapiens* and *Gorilla* are overlapping, and are in the intermediate place and expanded toward the negative and positive sides of PC2 (Figure 22). When we take into account the global variability of the MC1 shape, the neighbor joining tree shows that, as for the trapezium, *Homo* and *Pongo* are the most distant taxa (Figure 23). Differently as for the trapezium, *Gorilla* is closer to *Homo* than *Pan*. The distance between bonobos and chimpanzees appears smaller than the distance between *H. sapiens* and *H. neanderthalensis*.

Shapes associated with the positive side of PC1 (Figure 22), where *Homo* group and most of the gorillas are situated, show a robust first metacarpal (MC1) with broad and plane joint surfaces. The proximal TMC joint surface shows a broad tubercle on its radial side. The distal metacarpophalangeal (MCP) joint surface shows two robust articular eminences in the volar surface of the MC1 with the lateral eminence prominent compared to the medial one. The radial surface is globally broad with a prominence of the *Opponens pollicis* insertion crest, and an ulnar surface especially broad on its distal part. Shapes associated with the negative side of PC1 (Figure 22), where *Pongo* and *Pan* (bonobos and chimpanzees) are situated, show, when compared to the mean shape, a relatively fine MC1 with the opposite morphology than described for the positive side of PC1 (Figure 22).

Shapes associated with the extreme positive side of PC2 (Figure 22), where *Pongo* group is situated, show a MC1 with thin articular surfaces, with different orientations as compared to the mean shape. The proximal TMC joint surface is thin in its dorso-ventral direction and it is orientated toward the radial side. The dorsal part of the MCP joint surface is orientated and inclined toward the radial side, its distal part is inclined toward the ulnar side. Shapes associated with the extreme negative side of PC2 (Figure 22), where are situated principally *Pan* and *H. neanderthalensis* with some gorillas and *H. sapiens*, show a MC1 with large articular surfaces and orientations opposed to those described for the extreme positive side of PC2 (Figure 22).

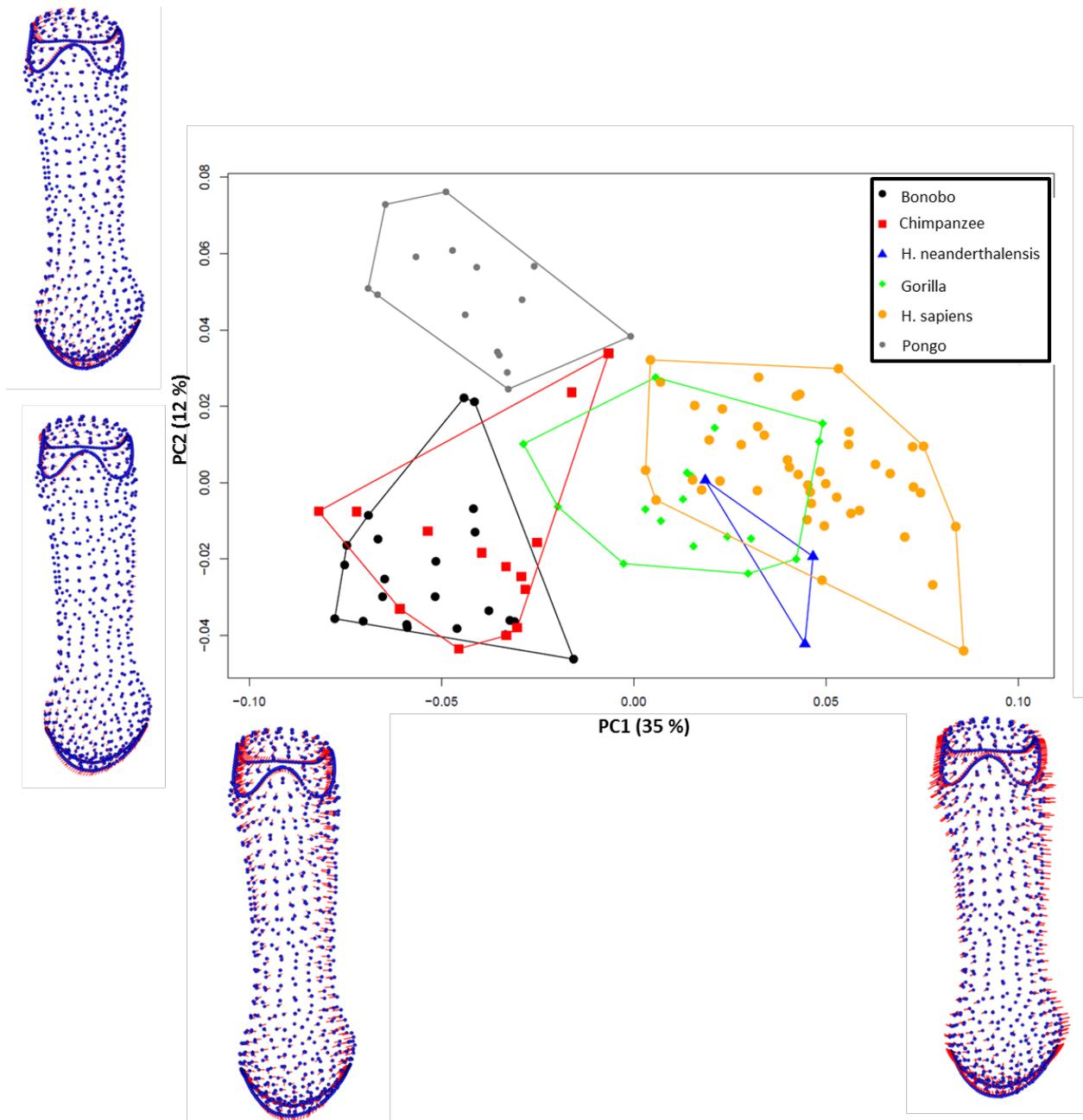


Figure 22. Results of the two first axes (PC1 and PC2) of a PCA performed on the shape of the first metacarpal (MC1) of all the specimens. Visualizations of shape deformations associated to the extremes of axes are given in ventral view (mean shape in blue and deformations represented by red vectors). PC1 distinguishes the shape of MC1 of *Homo* (modern and fossils) overlapping with most of the gorillas from *Pongo*, *Pan* and some gorillas. PC2 distinguishes the shape of MC1 of *Pongo* from almost all *Pan* specimens and *H. neanderthalensis*, and from *Gorilla* and *H. sapiens* (modern and fossil) that are overlapping and situated in the middle.

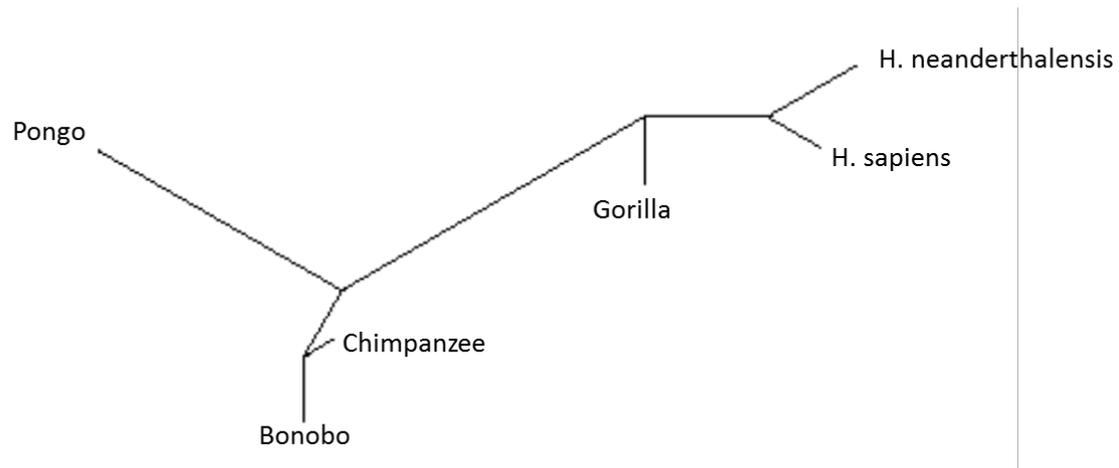


Figure 23. Neighbor joining tree computed on the phenotypic distances between species' mean MC1. *Gorilla* is the closest to *Homo* (modern and fossil), followed by *Pan* (bonobo and chimpanzee), and *Pongo* is the more distant to *Homo*.

3.1. Shape co-variation of the trapeziometacarpal articulation

The first PLS axis (PLS1) describes 83 % of the total shape co-variation between the trapezium and the MC1, and distinguishes *Homo* (combining modern and fossil *H. sapiens* and *H. neanderthalensis*), African great apes (*Pan* and *Gorilla*), and *Pongo* (Figure 24). The *Homo* group is situated on the negative side of PLS1, *Pongo* is on the positive side, while African great apes overlap in the intermediate place, with *Gorilla* also overlapping with *Homo* and *Pan* also overlapping with *Pongo*. On the negative part of the PLS1, where *Homo* is situated, a relatively robust first metacarpal with broad and plane joint surfaces is associated with a proportionally flat and large trapezium presenting larger joint surfaces for TMC joint and for the trapezium/scaphoid joint (Figure 24, shapes in blue). At the opposite end of this PLS1, where *Pongo* is situated, corresponds a relatively fine first metacarpal with small joint surfaces and a concave TMC joint associated with a robust and a proportionally small trapezium presenting a small TMC joint surface but a large trapezium/MC2 joint surface (Figure 24, shapes in red). *Pan* and *Gorilla* appear to share the same pattern of shape co-variation, intermediate between those of *Homo* and *Pongo*.

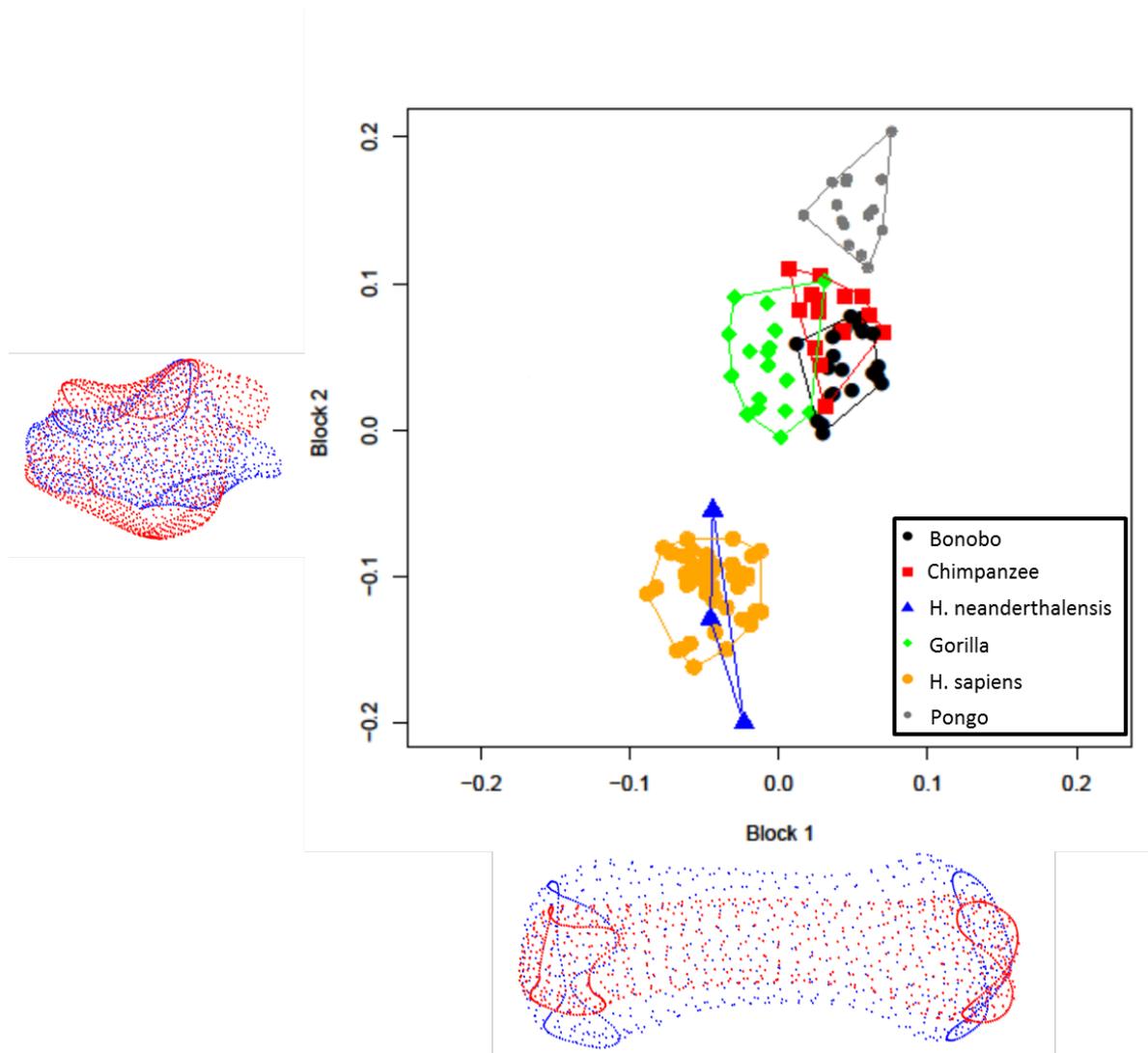


Figure 24. Results of the first PLS axis describing 83 % of the total shape co-variation between the trapezium and the MC1. The block 1 corresponds to shape variability of the MC1 associated with the shape variability of the trapezium in the block 2. The shape deformations are in ventral view and correspond in blue to the shape co-variation associated with the negative part of the PLS1 and in red to the shape co-variation associated with the positive part of PLS1.

The second PLS axis (PLS2) describes 12 % of the total shape co-variation between the trapezium and the MC1, and distinguishes especially *Pongo* to the other species (Figure 25). The *Pan* groups are situated on the negative side of PLS2, *Pongo* is on the positive side, with *Homo* (modern and fossil *H. sapiens* s, and *H. neanderthalensis*) and *Gorilla* overlapping at an intermediate place. On the negative part of the PLS2, where *Pan* groups are situated, a relatively dorsally flat MC1, with a proximal part convex and elongated, and with a radio/ulnar large TMC joint, is associated with a proportionally elongated trapezium with large TMC and trapezoid joint surfaces but small joint surfaces articulating with the scaphoid

and the MC2 (Figure 25, shapes in blue). At the opposite end of this PLS1, where *Pongo* is situated, a relatively MC1 with broad proximal and distal parts where are situated the TMC and MCP joints, which are oriented to the radial side, and with a large MCP joint surface, is associated with a proportionally short and robust trapezium with a small tubercle of the trapezium, a small TMC joint compared to broader joints articulating with the MC2 and the scaphoid (Figure 25, shapes in red). *Homo* (*H. sapiens* modern and fossils, and *H. neanderthalensis*) and *Gorilla* appear to share the same pattern of shape co-variation, intermediate between *Pongo* and *Pan* but closer to *Pan*.

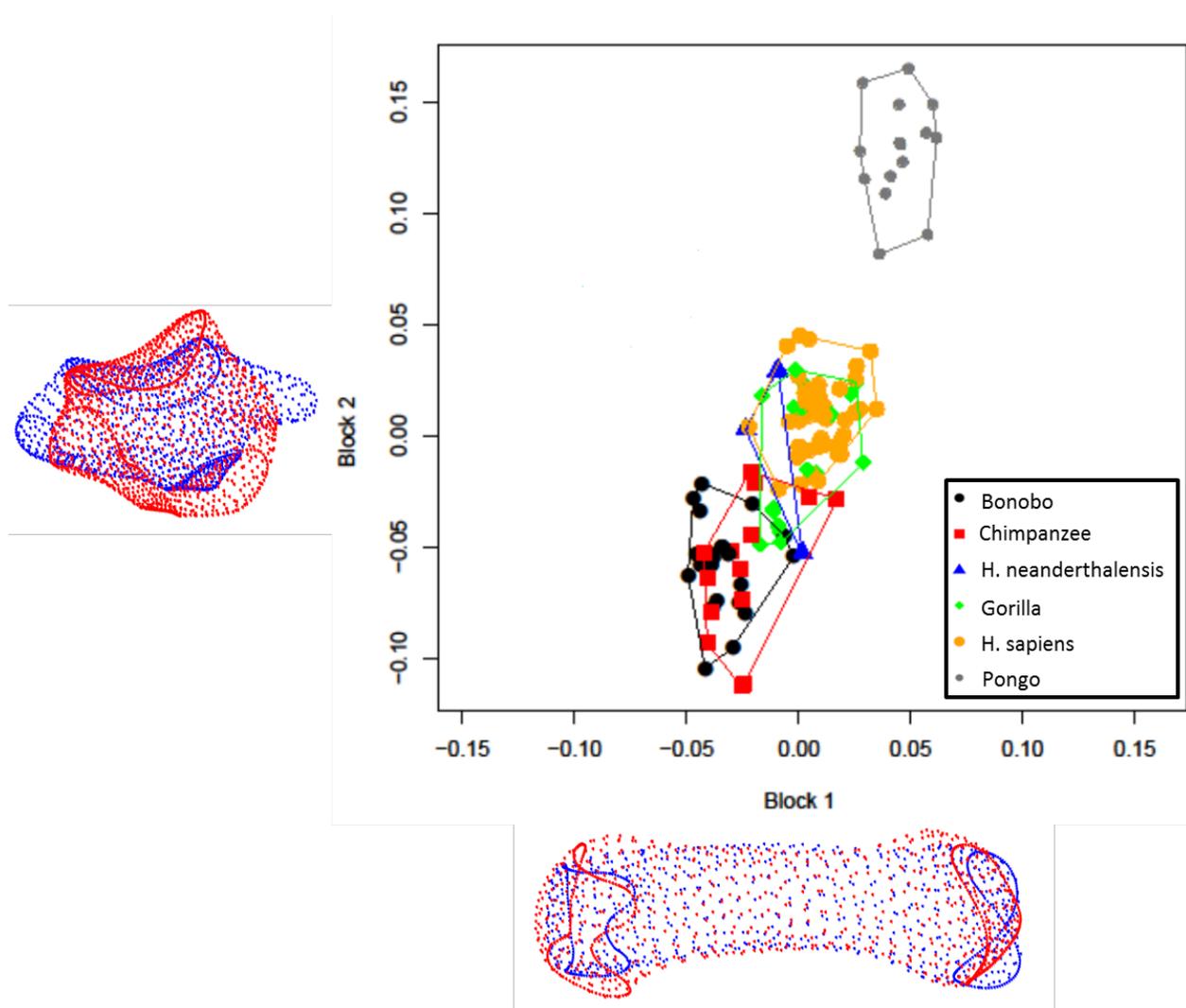


Figure 25. Results of the second PLS axis describing 12 % of the total shape co-variation between the trapezium and the MC1. The block 1 corresponds to shape variability of the MC1 associated with the shape variability of the trapezium in the block 2. The shape deformations are in ventral view and correspond in blue to the shape co-variation associated with the negative part of the PLS2 and in red to the shape co-variation associated with the positive part of PLS2.

4. DISCUSSION

We find shape differences of the two bones according to the species, and several aspects of the quantitative evidence present here support previous qualitative studies (Lewis, 1977; Marzke, 1997). However, multivariate analyses of the trapezium shape variations clearly distinguish *Homo* (*H. sapiens* modern and fossils, and *H. neanderthalensis*) from great apes and, especially, *Pongo* (Figure 20), whereas multivariate analyses of the first metacarpal shape variations almost place *Gorilla* with *Homo* (Figure 22). These results appear to partially reflect the phylogeny. The results of shape co-variation are not only dominated by variations of joint surfaces and muscle attachments zones, but are driven by the overall shape variations of the two bones. Moreover, shape co-variation differ between species, certainly constrained or favored by various factors. We find the same pattern of shape variations for the two bones between modern and fossil *Homo*, suggesting similar functional interaction and potential similar manual abilities. Our results are explained according to the different shapes and shape co-variation observed by species, and are discussed in link with possible functional involvements. Finally, we discuss how these morphological results could explain our behavioral data on manipulatives abilities observed in some Hominids (in the previous chapters 3 and 4).

4.1. Inter-species shape variations of the trapezium and the first metacarpal

Our results of the trapezium shape analysis in Hominids show an inter-species variability with a different global shape between *Homo* (*H. sapiens* moderns and fossils, and *H. neanderthalensis*) and great apes, and also between great apes' genera (Figure 20). We find structured groups that partially reflect the phylogeny with *Pan* closest to *Homo*, followed by *Gorilla* and *Pongo* the more distant (see, e.g., the review of Herlyn, 2016). A combination of morphological patterns on the *Homo* trapezium is clearly different from that quantified in great apes and especially between *Homo* and *Pongo*. *Homo* shows a relatively flat and large trapezium with especially broad joint surfaces compared to *Pongo* which displays a relatively short and robust trapezium. *Homo* shows especially a broad and plane TMC joint surface as compared to *Pongo* which shows the opposite shape. Moreover, we observe different orientations of joint surfaces in the trapezium, particularly between these two species, as previously shown by Tocheri and collaborator (Tocheri et al., 2003, 2005; Tocheri, 2007). Shape analysis of human's trapezium also shows stronger support for the tendon of the

Flexor carpi radialis (FCR) which flexes and abducts radially the hand from the wrist and stabilizes the scaphoid (Jantea et al., 1994). Moreover, the convex inferior part of the volar surface of the *Homo* trapezium, where the FCR comes along, could provide a high support to the attachment of the FCR on the second metacarpal. The specific *Homo* morphology also shows patterns which could favor the insertion of ligaments and thus could involve strong attachment of the trapezium with the bones surrounding it. Considering *Pan* and *Gorilla* groups, they show fewer differences with *Homo* than *Pongo*, and appear to show an intermediate shape of the trapezium between these species. All the fossils are clearly clustered with modern *Homo* except the specimen of *H. neanderthalensis* Kebara (KMH2). These specimens show the same morphology of trapezium than modern *Homo sapiens* but, compared to them, they have a relatively very plane trapezium with a transversally extended tubercle in the ventral surface. This specific shape can limit abduction and flexion of the thumb as for hylobatids which have a large tubercle of the trapezium (e.g. Lewis, 1977).

Our results for the first metacarpal shape analysis in Hominids show an inter-species variability with a different global shape between three groups: *Homo* with *Gorilla*, *Pan* and *Pongo* (Figure 22). Compared to the trapezium shape *Gorilla* are closest to *Homo* (Figure 23). It also appears that there is less inter-species variability for the first metacarpal than for the trapezium. Some morphological features on the *Homo*'s first metacarpal appear still different from those quantified in *Pan* and *Pongo*. Moreover, *Homo* and *Gorilla* show a robust first metacarpal with large and plane joint surfaces compared to a gracile bone with small joint surfaces for *Pan* and *Pongo*. The *Homo* and *Gorilla* relatively robust first metacarpal tends to present more surfaces for muscular insertions as compared to *Pan* and *Pongo*'s. In fact, *Homo* and *Gorilla* show a broad tubercle for the insertion of the *Abductor pollicis longus*, robust articular eminences for the two sesamoid bones in the tendons of the *Flexor pollicis brevis*, prominence of the *Opponens pollicis* insertion crest, and a broad surface insertion for the lateral head of the first *Interosseous dorsalis* (called also “*interosseous volaris primus* of Henle”) which appears to be a muscle only present in humans (Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012). Thus, this particular *Homo* and *Gorilla* morphology could favor a more robust thumb than in *Pan* and *Pongo*.

4.2. Shape co-variation between the two bones of the trapeziometacarpal complex

Shape co-variation between the trapezium and the first metacarpal in our Hominids' sample involves variations of the overall shape of both bones. Indeed, shape co-variation are not only dominated by variations of joint surfaces and muscle attachments zones, but are driven by the overall shape variations of the two bones. This result shows a strong global morphological relationships probably due to the fact that the trapezium and the first metacarpal need to interact functionally to allow movements of the thumb. Moreover, shape co-variation show differences associated with the species (Figures 24, 25). In fact, the species distribution for shape co-variation on the first PLS (PLS1) corresponds to their distribution in the morphospace of the PCA for the trapezium (Figures 20, 24). The distribution of the species on the PLS2 corresponds to their distribution in the morphospace of the PCA for the first metacarpal with *Gorilla* that shows a similar shape co-variation pattern with *Homo* as previously explained (Figures 22, 25). Thus, shape co-variation of the two bones of the TMC complex may not be only constrained by the phylogeny but by other factors (e.g. functional requirements and development). These results confirm the importance to quantify together the overall shape variability of the two bones of the TMC complex in Hominids in order to show 1) the strong morphological and functional relationships between them and 2) different shape co-variation patterns between Hominids with maybe some similar features between *Homo* and *Gorilla*.

4.3. Functional involvement on shape variations and co-variation

The different shape variations of the trapezium and of the first metacarpal, and the different patterns of shape co-variation among Hominids may result from a variety of factors: development, functional requirements, genetics, and evolutionary history (Cheverud, 1996; Klingenberg, 2008, 2009, 2010, 2014). We are especially interested in this study in functional involvements of the different shapes of the TMC complex in Hominids and in discussing the potential evolutionary history of this complex. In fact, our data do not allow us to discuss developmental factors, since we only work on adult specimens. Moreover, the strong morphological and certainly functional relationships between the trapezium and the first metacarpal suggest common developmental origin. The mechanisms of the development of the autopod (carpal bones and fingers) are poorly known (Rolian, 2016). It appears that the more proximal bones of the hand are established before the more distal bones (Rolian, 2016).

Thus, according to our results, we suppose that the trapezium and the first metacarpal could be developing together and with more developmental constraints on the trapezium. Indeed, the trapezium develops being surrounded by four bones, versus only two bones for the first metacarpal. Moreover, the carpal bones are ossified in humans at 12 years in girls and 14-15 years in boys (Scheuer and Black, 2000) and the most carpal bones are totally ossified in great apes at 10-12 years (Kivell, 2007 cited in Kivell, 2016a). As manipulative abilities are observed in Hominids before the end of the total ossification of their carpal bones, it appears that both developmental and functional constraints affect shape co-variation of the TMC complex. The overall shape of the TMC complex in Hominids could be constrained or facilitated by functional factors.

Two major functional constraints could explain the different shapes of the trapezium and the first metacarpal that we quantify between our sample of Hominids: (1) their different mode of locomotion and/or (2) their different manual abilities.

4.3.1. Locomotion constraints

In our sample of Hominids we have different lifestyles, more terrestrial for humans (modern and fossil specimens) and gorillas, highly arboreal for orangutans and a mix of terrestriality and arboreality for *Pan* (bonobos and chimpanzees) (Fleagle, 1988). Thus, part of the differences in shape that we observe in this study could be explained by differences between terrestrial locomotion versus arboreal lifestyle. During terrestrial locomotion in Hominids (bipedalism and knuckle walking locomotion) the thumb is not involved and thus can be available for only food and object manipulation. We observe a relatively robust first metacarpal with more surfaces for muscular insertions in *Homo* and *Gorilla*, while we observe a gracile first metacarpal for *Pongo* and both *Pan* species. Consequently, terrestrial locomotion could favor the development of a strong musculature of the thumb while arboreal lifestyle could reduce the musculature of the thumb. Indeed, it was often suggested that the reduction of the thumb was an adaptation for increased forelimb suspension and for the improvement of hook grips during suspensory behavior (e.g. Tuttle, 1972). Additionally, we find different orientations of the joint surfaces on the trapezium and on the first metacarpal between species. Tocheri and collaborators (Tocheri et al., 2005; Tocheri, 2007) find different orientations of the radial carpal bones between humans and great apes. For great apes, the orientations observed can help the transition of the load in the wrist during knuckle-walking

or suspension, whereas the different orientations observed in humans can provide better loading in the wrist from the thumb during manipulative behaviors (Lewis, 1989; Tocheri et al., 2003; Tocheri et al., 2005; Tocheri, 2007). Additionally to this finding, we quantify also different orientations in the two joints surfaces of the first metacarpal related to the specific shape of the trapezium of the species. These results suggest that not only the first metacarpal or the trapezium could be functionally constrained by locomotion but that the overall TMC complex shows functional relationships according to the locomotor mode. In fact, it appears that we find different patterns of shape co-variation according to the different locomotor modes of the species. Especially, we observe for shape co-variation a total opposition between *Homo* and *Pongo*, which opposes the more terrestrial Hominids to the more arboreal one.

4.3.2. Manual abilities constraints

On the other hand, the different overall shapes and shape co-variation of the TMC complex between Hominids could also be due to functional constraints related to manipulative abilities. In fact, since the thumb is not involved during terrestrial locomotion in Hominids and since the other fingers are more involved than the thumb during suspensory behavior (e.g. Tuttle, 1972), we may suppose greater constraints due to manipulative abilities on the TMC complex. We know that the TMC complex plays an important role during manipulative and grasping behaviors (e.g. Taylor and Schwarz, 1955; Marzke et al., 2010). The specific morphology of the TMC complex quantify here in *Homo*, and describe previously, appears to offer greater grasping and manipulative abilities with a greater potential of thumb mobility, than in great apes, especially *Pongo*, which shows the most distinct morphology of the TMC complex to that of *Homo*. *Pongo* with the most distinct morphology of the trapezium to *Homo*, may not be able to develop strong grips with the thumb and may be limited in its thumb movements. In fact, the shape of the TMC complex of *Pongo* appears to restrain its thumb movements because of the strong curved TMC joint, as compared to *Homo*'s. However, orangutans are able to also use grasping postures involving the thumb, such as the thumb lateral grip (e.g. Christel, 1993). Their particular thumb morphology and their first metacarpal radially oriented could be an advantage to oppose the thumb and the index finger during precision grips. We did not quantify in-hand movements in orangutans during the maze task (chapter 4). According to these morphological results, it could be because of the morphology of the orangutans' thumb could prevent them to use dynamically

their thumb to move an object in one hand. Orangutans reposition the tool in their hand during the maze task most of the time with their mouth, which is probably due to their highly arboreal lifestyle but it could be also explained by their thumb morphology. African great apes (gorillas, chimpanzees and bonobos) show a TMC shape intermediate between *Pongo*'s and *Homo*'s, and show fewer differences with *Homo* than *Pongo* does. Thus, the TMC morphology of the African great apes can allow more freedom of the thumb movements than in *Pongo* but not in the same way as humans. In fact, we observed in-hand movements in bonobos and gorillas during the maze task (chapters 3 and 4) with principally flexion and extension of the thumb. Their movements appear simpler than those observed in humans (chapter 4). It could be explained by their relatively curved TMC joint surface, whereas the humans' plane surface allows more freedom of movements (Marzke et al., 2010). This is also in agreement with the study in chimpanzees of Crast et al. (2009), showing that this species use in-hand movements but simpler than those used by humans.

The particular *Homo* and *Gorilla* morphology of the first metacarpal could favor stronger manipulative abilities with the thumb than in *Pongo* and *Pan*. In fact, differences in robustness across Hominids' first metacarpal may be related to different forces and pressures experienced by the joint between the first metacarpal and the trapezium during object grasping and manipulation (e.g. Cooney and Chao, 1977; Bettinger et al., 1999). We did not measure the force during tool manipulation in the previous studies (chapters 3 and 4) but we observed that gorillas use a stronger grip with faster movements than bonobos, which use more controlled and slower movements.

The results for the shape variability of the two bones in *Homo* show that fossils *H. sapiens* ("Cro-Magnons") are at the core of the modern *H. sapiens* distribution while *H. neanderthalensis*'s specimens are also in the variability space of *H. sapiens* but by surround them. One specimen of *H. neanderthalensis* (Kebara, KMH2) presents a very plane trapezium with a much transversally extended tubercle, which can limit the manual abilities of this specimen by restraining the thumb movements in flexion and adduction. The other specimens show morphology similar to that of modern *H. sapiens* and thus could have presented the same manual abilities. Different morphological features are showed between modern humans and Neandertals' hands (e.g. Niewoehner, 2006), notably a flatter TMC joint in Neandertals. The results in this chapter present inter-species variability. In order to quantify the real differences between modern humans and Neandertals, intra-species variability analyses are needed in future studies.

4.4. Future directions

We did not develop the studies on the fossils in this dissertation and further investigations on behavioral and morphological variability between modern and fossil species are necessary, e.g. regarding stone tool making. In fact, stone tool making is also possible for great apes, as showed by the studies on the trained bonobo (Kanzi) and a trained orangutan (Wright, 1972; Schick and Toth, 1993; Schick et al., 1999). Analysis of the overall hand morphology, and not only of the thumb, of modern species in the light of their manual abilities during stone tool making could allow to better understand and infer the potential manual abilities of fossil taxa. Further studies exploring the effect of the sex, the age and the side of the bones (left or right) on shape variations and shape co-variation on the TMC would be of interest to understand the potential effect of these parameters. For example, it will be interesting to test the potential functional asymmetry effect due to the laterality, with more pressure exerted by the bones of the preferred body side (see Lazenby, 2002). In fact, it was shown that lateralization has an effect on the shape of different bones, such as the humerus and the second metacarpal (e.g. Lazenby et al., 2008; Stock et al., 2013) or in the trabecular architecture in the first metacarpal of *Pan* (chimpanzees and bonobos) and *H. sapiens* (Stephens et al., 2016). Does the lateralization have an effect on the shape and the trabecular architecture of the TMC complex? These kinds of analyses could be interesting in regard to the possible inference of laterality on fossils in association with the manipulative abilities.

Finally, Rolian et al. (2010) suggested that the evolution of the human hand is not linked to an adaptation for tool use or any other function, but rather that the hominin hand and feet coevolved. They suggested that the evolution of long robust big toes and short lateral toes for bipedalism led to changes in hominin fingers that may have facilitated the emergence of stone tool technology. To test this hypothesis, it will be interesting to compare in different species of primates the overall shape co-variation of their trapezium and their first metacarpal with the overall shape co-variation of their cuneiform bone and their first metatarsal bone associated.

5. CONCLUSION

The TMC complex presents different patterns of shape variability according to the species and clearly distinguishes *Homo* from great apes and especially from *Pongo*. The differences between species could be explained by their different lifestyle and manipulative abilities. Indeed, the morphologies of the TMC complex of *Homo* and African great apes (chimpanzees, bonobos, and gorillas) appear to offer greater grasping and manipulative abilities with a greater potential of thumb mobility than *Pongo*. Moreover, the shape of the TMC complex seems to be linked to the manipulative abilities previously quantified (chapter 4), showing more thumb involvement in humans and African apes than in orangutans. Shape co-variation highlight the strong morphological and functional relationship of the two bones of the TMC complex and different shape co-variation patterns between Hominids with maybe some similar features between *Homo* and *Gorilla*. Thus, shape co-variation of the two bones of the TMC complex are constrained by the phylogeny but also by other factors (e.g. functional requirements and development). The results show the importance of quantitatively analyzing the overall morphology of the trapezium and of the first metacarpal together to highlight the real quantitative differences between Hominids and the functional interaction between these two bones. Finally, these results suggest that manipulative abilities can be associated with important constrains on the shape of these two bones, which could be very useful to infer these abilities in fossils based on the TMC morphology.

SUPPLEMENTARY TABLE

Supplementary table S2. Specimens used in analyses.

Species	Specimen	Sex	Hand(s)	Native country (Locality)
<i>H. sapiens</i>	MNHN-HA-35047-1	F	R and L	France (Paris)
<i>H. sapiens</i>	MNHN-HA-35055-1	F	R and L	France (Paris)
<i>H. sapiens</i>	MNHN-HA-35060-1	F	L	France (Paris)
<i>H. sapiens</i>	MNHN-HA-35061-1	F	R and L	France (Paris)
<i>H. sapiens</i>	MNHN-HA-35068-1	F	R and L	France (Paris)
<i>H. sapiens</i>	MNHN-HA-35071-1	F	R and L	France (Paris)
<i>H. sapiens</i>	MNHN-HA-35073-1	F	R	France (Paris)
<i>H. sapiens</i>	MNHN-HA-35080-1	F	R and L	France (Paris)
<i>H. sapiens</i>	MNHN-HA-18003	F	R and L	Russia (Iaroslavl)
<i>H. sapiens</i>	MNHN-HA-10254	F	R and L	United States (Santa Cruz Island)
<i>H. sapiens</i>	MNHN-HA-18449-1	F	L	Central Africa (Oubangui)
<i>H. sapiens</i>	MNHN-HA-34992-1	M	R and L	France (Paris)
<i>H. sapiens</i>	MNHN-HA-34997-1	M	L	France (Paris)
<i>H. sapiens</i>	MNHN-HA-35003-1	M	R and L	France (Paris)
<i>H. sapiens</i>	MNHN-HA-35009	M	R and L	France (Paris)
<i>H. sapiens</i>	MNHN-HA-35015-1	M	R and L	France (Paris)
<i>H. sapiens</i>	MNHN-HA-35018-1	M	R and L	France (Paris)
<i>H. sapiens</i>	MNHN-HA-35026-1	M	R and L	France (Paris)
<i>H. sapiens</i>	MNHN-HA-18002	M	R and L	Russia (Tver)
<i>H. sapiens</i>	MNHN-HA-28907	M	R	France
<i>H. sapiens</i>	MNHN-HA-28913-2	M	L	France
<i>H. sapiens</i>	MNHN-HA-17762-2	M	R and L	Central Africa (near Nola and Bangui)
<i>H. sapiens</i>	MNHN-HA-17980-2	M	R and L	Congo (Ouéssou)
<i>H. sapiens</i>	MNHN-HA-22257-1	M	L	Equatorial Africa
<i>H. neanderthalensis</i> (Ferrassie 1)	MNHN-HA-23645	M	R	France (La Ferrassie)

<i>H. neanderthalensis</i> (Ferrassie 2)	MNHN-HA-23646	F	R	France (La Ferrassie)
<i>H. neanderthalensis</i> (Kebara)	MNHN-HA-28123		L	Israel (Kebara)
<i>H. sapiens</i> (Cro-magnon, abri Pataud)	MNHN-HA-26227		L	France (Les Eyzies- de-Tayac)
<i>H. sapiens</i> (Cro-magnon, abri Pataud)	MNHN-HA-26230-A-9		L	France (Les Eyzies- de-Tayac)
<i>H. sapiens</i> (Cro-magnon, La Dame du Cavillon)	MNHN-HA-3809		L	France (Menton)
<i>Pan troglodytes</i>	MNHN-ZM-AC-1966- 332	F	L	?
<i>Pan troglodytes</i>	MNHN-ZM-AC-2000- 424	?	R and L	?
<i>Pan troglodytes</i>	MNHN-ZM-AC-2000- 425	?	R and L	?
<i>Pan troglodytes</i>	MNHN-ZM-AC-1944- 227	F	R and L	?
<i>Pan troglodytes</i>	MNHN-ZM-AC-2007- 1449	?	R and L	?
<i>Pan troglodytes</i>	1901-659	?		?
<i>Pan troglodytes</i>	1966-330	F	R and L	?
<i>Pan troglodytes</i>	1921-47	F	R	?
<i>Pan troglodytes</i>	1959-35	M	L	?
<i>Gorilla gorilla gorilla</i>	MNHN-ZM-AC- A12747	M	R and L	?
<i>Gorilla gorilla gorilla</i>	MNHN-ZM-AC-1929- 503	M	R and L	?
<i>Gorilla gorilla gorilla</i>	MNHN-ZM-AC-1981- 20	M ?	L	?
<i>Gorilla gorilla gorilla</i>	MNHN-ZM-AC-1906- 443	?	R and L	?
<i>Gorilla gorilla gorilla</i>	MNHN-ZM-AC-A 12748	M	L	?
<i>Gorilla gorilla gorilla</i>	MNHN-ZM-AC-1856- 67	F	R and L	Gabon (Makokou)
<i>Gorilla gorilla gorilla</i>	MNHN-ZM-AC-1912- 475	M	L	?

<i>Gorilla gorilla gorilla</i>	MNHN-ZM-AC-1931-657	M	R and L	?
<i>Gorilla gorilla gorilla</i>	MNHN-ZM-2007-1458	M	R and L	?
<i>Gorilla gorilla gorilla</i>	RMCA-9291	M	R	?
<i>Gorilla gorilla gorilla</i>	RMCA-17202	F	R	Gabon (zoo Leopoldville)
<i>Pan paniscus</i>	RMCA-13201	F	R and L	R. D. Congo
<i>Pan paniscus</i>	RMCA-13202	M	L	R. D. Congo
<i>Pan paniscus</i>	RMCA-15293	F	R and L	R. D. Congo
<i>Pan paniscus</i>	RMCA-15294	M	L	R. D. Congo
<i>Pan paniscus</i>	RMCA-15295	F	R and L	R. D. Congo
<i>Pan paniscus</i>	RMCA-15296	F	R and L	R. D. Congo
<i>Pan paniscus</i>	RMCA-23509	M	L	R. D. Congo
<i>Pan paniscus</i>	RMCA-27696	M	R and L	R. D. Congo
<i>Pan paniscus</i>	RMCA-27698	F	R and L	R. D. Congo
<i>Pan paniscus</i>	RMCA-29040	F	R and L	R. D. Congo
<i>Pan paniscus</i>	RMCA-29042	F	R and L	R. D. Congo
<i>Pan paniscus</i>	RMCA-29045	F	L	R. D. Congo
<i>Pan paniscus</i>	RMCA-29047	M	R	R. D. Congo
<i>Pan paniscus</i>	RMCA-29052	M	R	R. D. Congo
<i>Pongo pygmaeus</i>	NBC-ZMA-1059	M	R and L	R. D. Congo
<i>Pongo pygmaeus</i>	NBC-ZMA-063	F	R and L	Rotterdam Zoo
<i>Pongo pygmaeus</i>	NBC-ZMA-2854	F	R and L	Borneo
<i>Pongo pygmaeus</i>	NBC-ZMA-7128	M	L	Rotterdam Zoo
<i>Pongo pygmaeus</i>	NBC-ZMA-9340	M	R and L	Borneo
<i>Pongo pygmaeus</i>	NBC-ZMA-16935	F	L	?
<i>Pongo pygmaeus</i>	NBC-ZMA-23720	F	R and L	Borneo
<i>Pongo pygmaeus</i>	NBC-ZMA-24449	F	R	Sumatra, Sanctary Ketambe
<i>Pongo pygmaeus</i>	NBC-ZMA-37726	M	R and L	Borneo

Institutional abbreviations are as follows: MNHN= Muséum National d'Histoire Naturelle, Paris; RMCA=Royal Museum for Central Africa, Tervuren; NBC=Naturalis Biodiversity Center, Leiden, M= male, F= female, R= right, L= left. *Homo sapiens* specimens come from Paris have died in Paris but could be native to another country.

SUMMARY OF THE CHAPTER 5

Title: Morphological variability of the trapeziometacarpal complex among Hominids and its functional involvement.

Question: Do different pattern of variation and co-variation exist according to the species? What constraints could explain the differences, or not, between species? Will the pattern observed for shape variation is similar as for our behavioral data? And similar in the two bones?

Model: Modern human (*Homo sapiens*) and fossils (*H. sapiens* “Cro-Magnon” and *H. neanderthalensis*), chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla gorilla*), orangutans (*Pongo pygmaeus*).

Method: Collect of 3D bones shape (MNHN, Paris; Royal Museum for Central Africa, Tervuren; Naturalis Biodiversity Center, Leiden) and Multivariate analysis of the shape of the trapezium and first metacarpal (MNHN, Paris).

Results: Multivariate analysis of the shape of the trapezium clearly distinguishes *Homo* (with a greatest potential of thumb mobility) from great apes and especially from *Pongo*, while the first metacarpal shape distinguish *Homo* from *Pan* and *Pongo*. Shape co-variation are not only dominated by variations of joint surfaces and muscle attachments zones, but are driven by the overall shape variations of the two bones, and differ between species.

Discussion: The morphologies of the two bones of the TMC complex of *Homo* and African great apes (chimpanzees, bonobos, and gorillas) seems to offer greater grasping and manipulative abilities with a greater potential of thumb mobility than *Pongo*. Shape co-variations highlight the strong morphological and functional relationship of the two bones of the TMC complex. Moreover, the shape co-variations show differences associated with the species and appears to partially reflect the phylogeny with maybe some similar features between *Homo* and *Gorilla*. These differences between Hominids are certainly constrained or favored by various factors (e.g. lifestyle and manipulative abilities). Finally, the shape of the trapeziometacarpal complex seems to be linked to the manipulative abilities previously quantified, showing more thumb involvement in humans and African apes than in orangutans.

Perspectives: Next investigations should focus on the consequences of the overall morphometric of Hominids’ hands on tool grasp abilities using a musculo-skeletal model. Such a preliminary approach is conducted in the next chapter.

Chapter 6 – Biomechanical analyses of the consequences of different hand morphometric on tool grasp abilities using musculo-skeletal simulation: a preliminary study

Biomechanical analyses of the consequences of different hand morphometric on tool grasp abilities using musculo-skeletal simulation: a preliminary study

Journal of The Royal Society Interface, in preparation.

ABSTRACT

Differences in grip techniques between primates are most of the time attributed to different morphometric of the hand and different muscular anatomy. However, on the contrary to humans, we don't really know the influence on the biomechanical constraints (force, kinematics, muscles' activities) required to grasp an object for non-human primates because in vivo measures are impossible or very complex to set up. Musculo-skeletal model is a way to access to these biomechanical constraints of the hand of non-human primates by simulating them and thus avoiding in vivo experiments. The main objective of this chapter is to investigate the influence of the morphometric of the primates' hands on the biomechanical constraints associated with different grasping techniques. Typical grasping techniques observed in the previous chapters (3 and 4) on humans, bonobos, gorillas and orangutans during the maze task, are simulated using muscular-skeletal model in which the morphometric is adapted to each species. The simulations of the grips' techniques show a strong influence of morphometric on kinematics, joint net moments and muscles coordination. Some grips appear very difficult for some species in terms of motion range by requiring strong muscle forces. Orangutans' simulations show particularly more biomechanical constraints than the other species. The different manipulative abilities of primates can thus be a consequence of the different mechanical constraints according to the morphometric of the overall hand. This preliminary study provides a new approach to better understand the manipulative abilities of primates and to improve the techniques to infer the potential manipulative abilities of fossils.

1. INTRODUCTION

The previous chapters 3 and 4 show a large diversity of grip techniques (e.g. precision, power, hook grips) used during the maze task, with specific grip techniques according to the hominid species. The different use of grip techniques can be attributed to several factors such as, for example, the different morphometrics of the hand (e.g. Marzke and Wullstein, 1996), the different muscular anatomy (Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012) or social influences as social learning (Whiten and Ham, 1992). The morphometric of the great apes' hands especially compared to those of other primates shows longer and curved fingers and a shorter thumb that could limit the pad to pad contact in thumb opposition (e.g. Napier and Napier, 1967; Marzke and Wullstein, 1996). Moreover, gorillas (and gibbons) have the highest thumb-forefinger index among hominoids, while orangutans have the lowest (Shultz, 1930). This suggests that gorillas could involve more their thumbs than orangutans during manipulative abilities, which is consistent with our behavioral results (chapter 4). Besides, the differences between humans and great apes could be due to the absence of several anatomical features. It appears that some human hands' muscles such as the *flexor pollicis longus* and the *extensor pollicis brevis* which are related to the movement of the thumb, are not present or not independent in the hands of great apes, excepted hylobatids (Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012). However, in non-human primates, on the contrary to humans (Vigouroux et al., 2011; Goislard de Monsabert et al., 2012), we don't exactly know the hand biomechanical functioning during object grasping from muscular action to grip force exertion. Consequently, it remains difficult to directly attribute one or other anatomical characteristics (such as the size and shape of a bone, or the length of a specific muscle) to the use or the non-use of a specific grip technique.

From a biomechanical point of view, performing a given grip technique (such as pinch or power grip) and applying the appropriate grip force on an object requires to: 1) adapt joint kinematics (joint angles) to place the fingers in contact with the object; 2) adapt muscles coordination to generate appropriate tendon and muscle forces to applied the required grip force and to balance the joints; 3) have adapted outer and inner bone's structure to endure the mechanical constraints and to allow required range of motions. In humans, this set of mechanical variables is extensively studied using biomechanical experimentations combining kinematics, electromyography and force sensors as well as using musculo-skeletal modeling (e.g. Sancho-Bru et al., 2003; Vigouroux et al., 2011; Goislard de Monsabert et al., 2012). However, such an investigation in non-human primates is particularly difficult to elaborate

due to i) the difficulty associated to animal's instrumentation (Oishi et al., 2008) ii) the lack of a common method of quantified morphometric data of muscles architecture (e.g. Marzke et al., 1999; Myatt et al., 2011, 2012) and iii) the lack of a common method for the nomenclature of the muscles (e.g. Marzke et al., 1999; Myatt et al., 2011, 2012). Consequently, the joint angles, the muscles coordination and the mechanical constraints required by each typical grip techniques are not entirely quantified in non-human primates.

This lack of data for our main problematic prevents us from a total understanding of the reasons which lead the different species to the use of selected grip techniques. Moreover, these biomechanical variables are subject to change significantly according to the morphometric of the hand. Depending especially on the size of the fingers and hands (which differ importantly between the species), for example the joint constraints applied on the trapezium may be different for the same used grip techniques, suggesting different articular shapes. Vice versa, a same articular shape may lead to different grip techniques according to the hand's morphometric. This point is particularly important as most of the hominins' and hominids' hand grip behavior is deduced from the bone shape information, without taking into account the morphometric and its potential influence on biomechanical constraints. Moreover, the size and the shape of an object could lead to different grip techniques and different biomechanical constraints which could changes according to the morphometric. Consequently, we suggest that the interpretation of the bone shapes should also take into account these constraints' variables which would take place in case of the use of one or other grip techniques.

As a first step for contributing to a better understanding of the non-human hand grip biomechanics, this chapter aims to investigate the influence of the morphometric of the primates' hands on the biomechanical constraints associated with different grip techniques. Typical grip techniques previously observed (chapters 3 and 4) in humans, bonobos, gorillas and orangutans during the maze task, are simulated using musculo-skeletal model in which the morphometric is adapted to each species. Musculo-skeletal model is a practical way to access the biomechanical constraints of the hand in non-human primates by simulating them and thus without measuring them *in vivo*. To answer our questionings we have thus developed a musculoskeletal model based on hominid morphological (e.g. size of the segments) and biomechanical data (e.g. force, kinematics, muscle activities), as it is already use for humans (see Fernandez et al., 2016). According to our behavioral and morphological results obtained on hominids (chapters 3, 4 and 5), we hypothesize that the morphometric of humans',

bonobos', gorillas' and orangutans' hands involves different biomechanical constraints during grasping actions, such as the various fingers' joint angles, corresponding to the different moments arms probably engage different joints and muscles loadings.

2. MATERIAL AND METHODS

2.1. Species and conditions

All musculo-skeletal models were representative of adult individuals. Four hominids species were proposed: humans and three species of great apes: bonobos (*Pan panicus*), Gorillas (*Gorilla gorilla gorilla*), orangutans (*Pongo pygmaeus*). We did simulations of six main grasping postures previously quantified during the maze task among the four species (chapters 3 and 4): dynamic tripod grip, thumb lateral grip, interdigital 2/3 brace grip, power grip, hook grips, scissor grip (Figure 26). Briefly, the Figure 26 represents the percentage of use of each grip techniques according to the species. The dynamic tripod grip, which is the common pencil grip (Wynn-Parry, 1966), was more used by humans, while great apes showed other preferences. Gorillas used more the interdigital 2/3 brace where the tool held by flexed index and exits the hand between the proximal or middle phalanges of the index and third fingers. Orangutans used more the power grip (tool held in opposition between the palm and flexed fingers with a possible pressure applied by the thumb) and bonobos used more hook grips (tool held transversally by flexed fingers). The thumb was not involved during the scissor grip and we considered here that it was not involved also during the hook grip.

2.2. Hand model

The geometry of the hand model was based on the morphometric measures of bones hands from literature for humans (Buchholz, 1992) and from database of T. Kivell (Kent University, UK) for primates. The initial musculo-skeletal model resulted from anthropometric measurements of the right human hand and was further adapted of the hand of each primate species. The articulations (wrist, fingers, and thumb) of the model include 23 degrees of freedom and were mobilized by 42 muscles (Goislard de Monsabert et al., 2012). These degrees of freedom and the data for the muscles locations were taken from human anthropometric data (Chao et al., 1989). As several data are lacking to adapt the model for

primates, the muscles locations were not modified and were only scaled according to the hands' length. This choice results from the fact that we have not enough accurate details available in the literature and our attempt to adapt the model to the primate's muscles morphology resulted in too large assumptions and approximations. Thus, the obtained simulated variables were not an estimation of the accurate muscle force intensity of primates but more an estimation of the muscle strength/capacities required to perform the tested grips (e.g. required finger flexor strength). To perform such an analysis, we considered the results of the net joint moments (function of the forces applied on the fingers and the finger joint positioning, expressed in N.cm) which represent the summed muscular efforts applied on the joints during the grip. We also analyzed the required coordination during the grip by considering the muscle force intensities. Because the muscular architecture is not identical between the species, the results of individual muscle forces could be too expectative and are subjects to too large limitations. We have thus chosen to analyze more global information which was the summed muscle forces of the eight main muscle groups of the hand instead of analyzing each muscle independently. The considered muscle groups are presented in the Table S3 and are: fingers flexors, FF; fingers extensors, FE; intrinsic of the fingers, FI; thumb flexor, TF; thumb extensors, TE; intrinsic of the thumb, TI; wrist flexors, WF; wrist extensors, WE. The muscle group's force informed us on the global coordination required by each grip and we considered that this information was valuable to answer our questionings on the influence of morphometric.

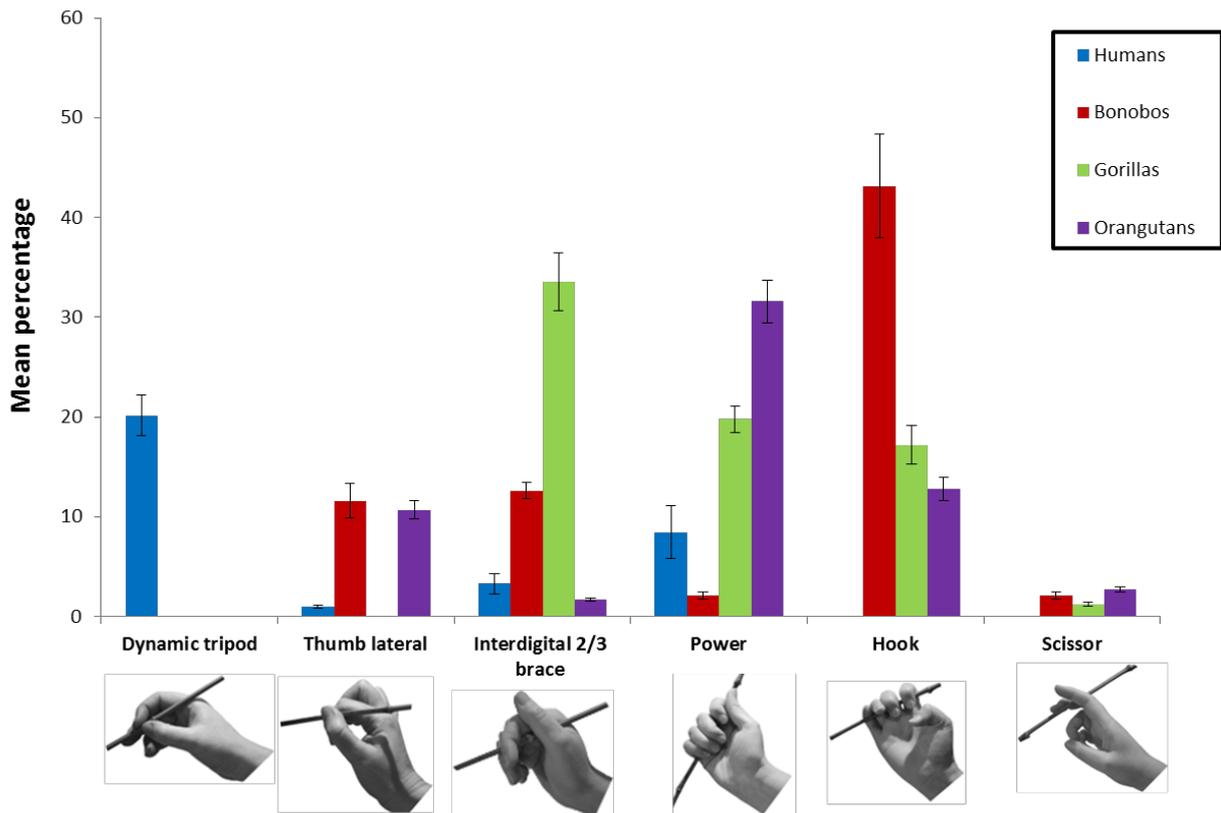


Figure 26. Mean percentage of the main grip techniques used by each species during the maze task. These techniques were first performed by the human subject in order to record experimental data and were secondly simulated in each Ape species.

2.3. Input model data

The 3D Kinematics data were first collected in humans for each grip technique. A set of 32 markers were used to record the human hand joint posture of one participant (age: 37; size: 177 cm; body weight: 72 kg; hand length: 19.4 cm). This data set was measured using an optoelectronic system (Vicon, Marseille, France). The participant was asked to manipulate a bamboo using the grips techniques described above. This data set was then used to analyze the biomechanical constraints in humans using the initial human hand model.

The 3D Kinematics data for primates were obtained using the 3D kinematical representation of the adapted hand model. Starting from the initial joint angles obtained with the human participant, the joint angles were adjusted in order to fit best the postures observed in videos (chapters 3 and 4). Kinematical adjustments also took into account the requirements and the specificities of each posture, especially the contact points with the bamboo. For the simulation, the force applied to the bamboo was distributed between the fingers that were in contact with the bamboo and equal to 40 N. As no force data exists on the force intensity

applied on a bamboo when manipulating it, we have chosen to perform our simulations with a quite enough important force intensity in regards to maximal hand capacities (40 N represents almost 30% of the maximal pinch grip force in humans, Goislard de Monsabert, 2014) and representative of the intensity used during manipulating activities (Domalain et al., 2008). The same intensity of force was applied to all the grasping postures and to all the species to standardize the grip force conditions. Using the input joint forces and the obtained 3D kinematics, an optimization process was used to solve the equations of mechanical joint equilibrium in order to determine the muscle strength required for each grip and each species.

2.4. Output model data

The simulations (realized with the software MATLAB ®) for all the species and for each grasping postures, allowed us to obtain data on: the kinematics of thumb and index finger (Figure 27); the net joint moments of thumb and index finger (sum of the force moments developed by each muscle acting around a joint, expressed in N.cm); the muscle coordination (Figure 28). The kinematics of thumb and index fingers provided information on the position of the joints during the six grasping postures studied, which can help us to better understand the net joint moments. The net joint moments provided information on the intensity of required forces to stabilize the joints according to contact point between the fingers and the bamboo. The muscle coordination provided information on the number of muscles involved during each grasping posture with the intensity of required forces in each muscle group (Figure 28). We considered that a group of muscles was fully involved during a grasping posture when its intensity exceeded 20 Newton. We decided to focus here on the kinematics and the net joint moments of the thumb and index fingers as the opposition of these two fingers was considered important during human's manipulative abilities (e.g. Taylor and Schwarz, 1955; Marzke et al., 2010).

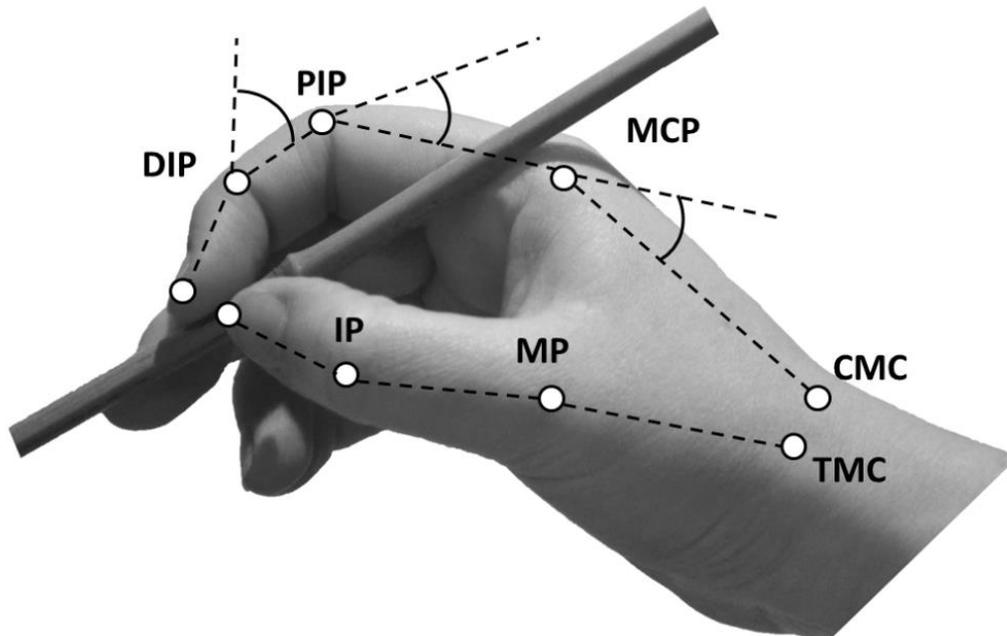


Figure 27. Markers positioned on the thumb and the index fingers, during the dynamic tripod grip, that allowed to record 3D Kinematics. Angles represent here for recording on joints angles for flexion/extension. Joints: CMC, carpometacarpal; MCP, metacarpophalangeal joint; PIP, proximal interphalangeal joint; DIP, distal interphalangeal joint; TMC, trapeziometacarpal (first CMC); MP, metacarpophalangeal joint; IP, interphalangeal joint.

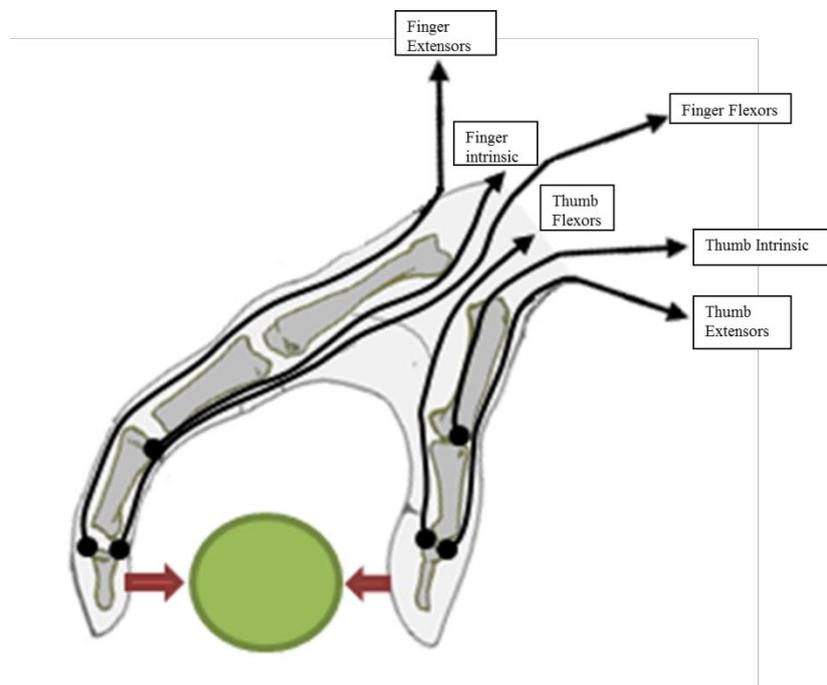


Figure 28. Representation of the six main muscles groups used in the study for the fingers and the thumb during the grip of the bamboo (in green). The two muscular groups for the wrist are not represented. Red arrows represent the force of 40 N applied on the bamboo, here on the distal phalanges of the thumb and the index.

3. RESULTS

3.1. Kinematics of the thumb and the index

3.1.1. Kinematics of the thumb

The thumb joint angles differ largely between species during the power grip, the interdigital 2/3 brace grip, the thumb lateral grip and fewer during the dynamic tripod grip, indicating an influence of the morphometric on the kinematics of the thumb according to the grip techniques. The Figure 29a shows the results during the power grip. Humans show an abduction of the trapeziometacarpal joint (TMC) while great apes don't. Moreover, humans require more flexion at the interphalangeal joint (IP) than great apes. Orangutans and humans show more flexions at the metacarpophalangeal (MP) joint than gorillas and bonobos. During the interdigital 2/3 brace grip (Figure 29b), humans flex higher the IP and MP joints than great apes especially gorillas and bonobos. During the thumb lateral grip bonobos show fewer flexions at the IP joint than the other species and humans abduct more the TMC joint than the other species. Moreover, orangutans flex more the TMC joint than the other species and especially than humans. The principal difference during the dynamic tripod grip is that great apes require more flexions at the TMC joint than humans.

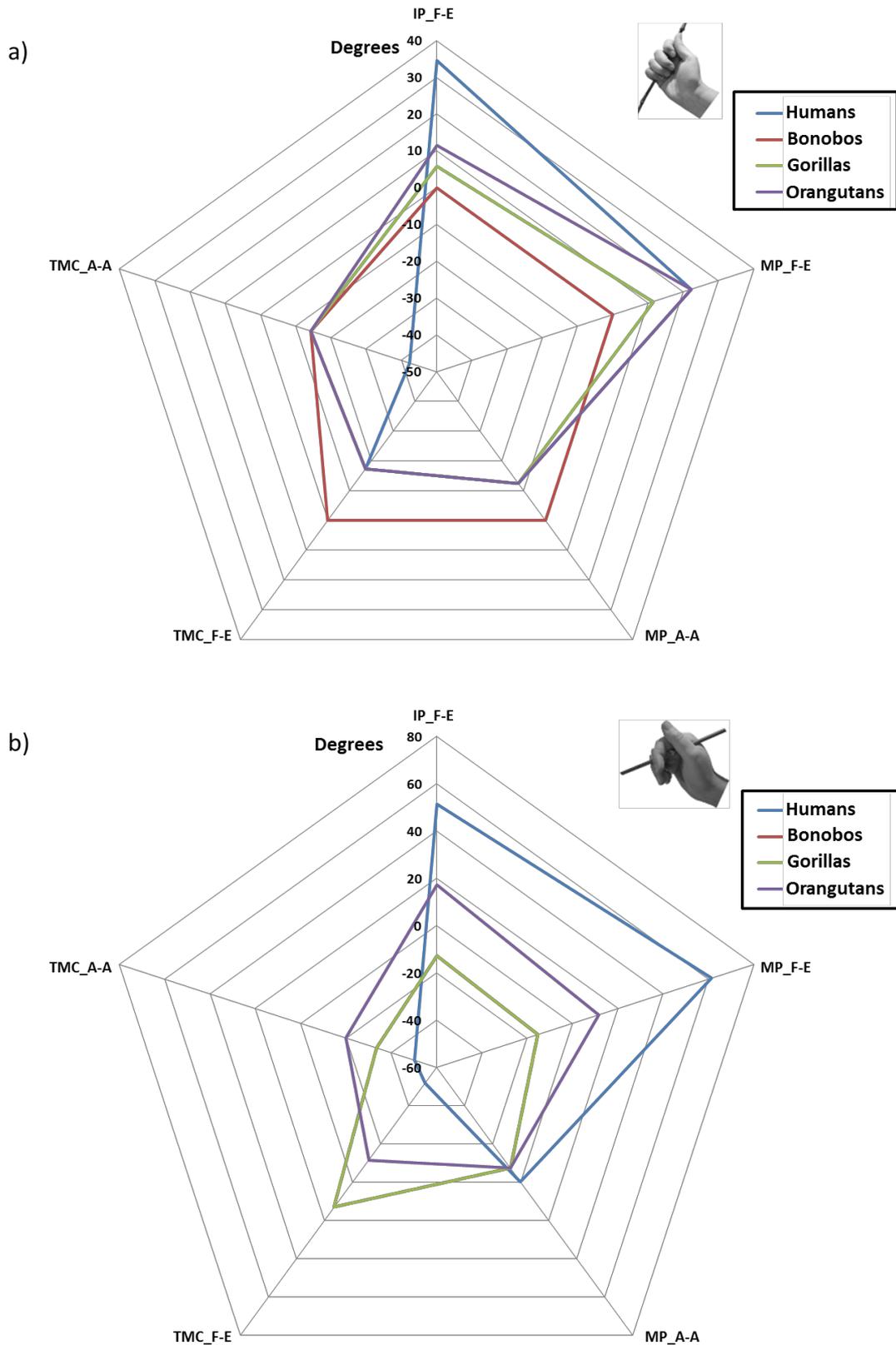


Figure 29. Results on the kinematics of the thumb during the simulations for the a) power grip and b) interdigital 2/3 brace grip, for all the species. a) Great apes show less abduction of the TMC joint than humans which show more flexion at the IP joint than great apes. Orangutans and humans flex more the MP joint than gorillas and bonobos. b) Species show different kinematics of the thumb except bonobos and gorillas which show the same joints' angles. TMC, trapeziometacarpal; MP, metacarpophalangeal joint; IP, interphalangeal joint; A-A, abduction/adduction; F-E, flexion/extension.

3.1.2. Kinematics of the index finger

The largest differences between species appear during the dynamic tripod grip, the interdigital 2/3 brace grip and the thumb lateral grip, indicating an effect of the morphometric on the kinematics of the index finger according to some grip techniques. During the dynamic tripod grip (Figure 30), bonobos and orangutans require more flexion at the metacarpophalangeal joint (MCP) than humans and gorillas, while gorillas show more flexion at the PIP with fewer flexion for humans. Humans require fewer flexion at the distal interphalangeal joint (DIP) than bonobos and gorillas. During the interdigital 2/3 brace grip, orangutans show more flexion at the proximal interphalangeal joint (PIP) and MCP joints than the other species. Concerning the thumb lateral grip, great apes require more flexion at the MCP than humans.

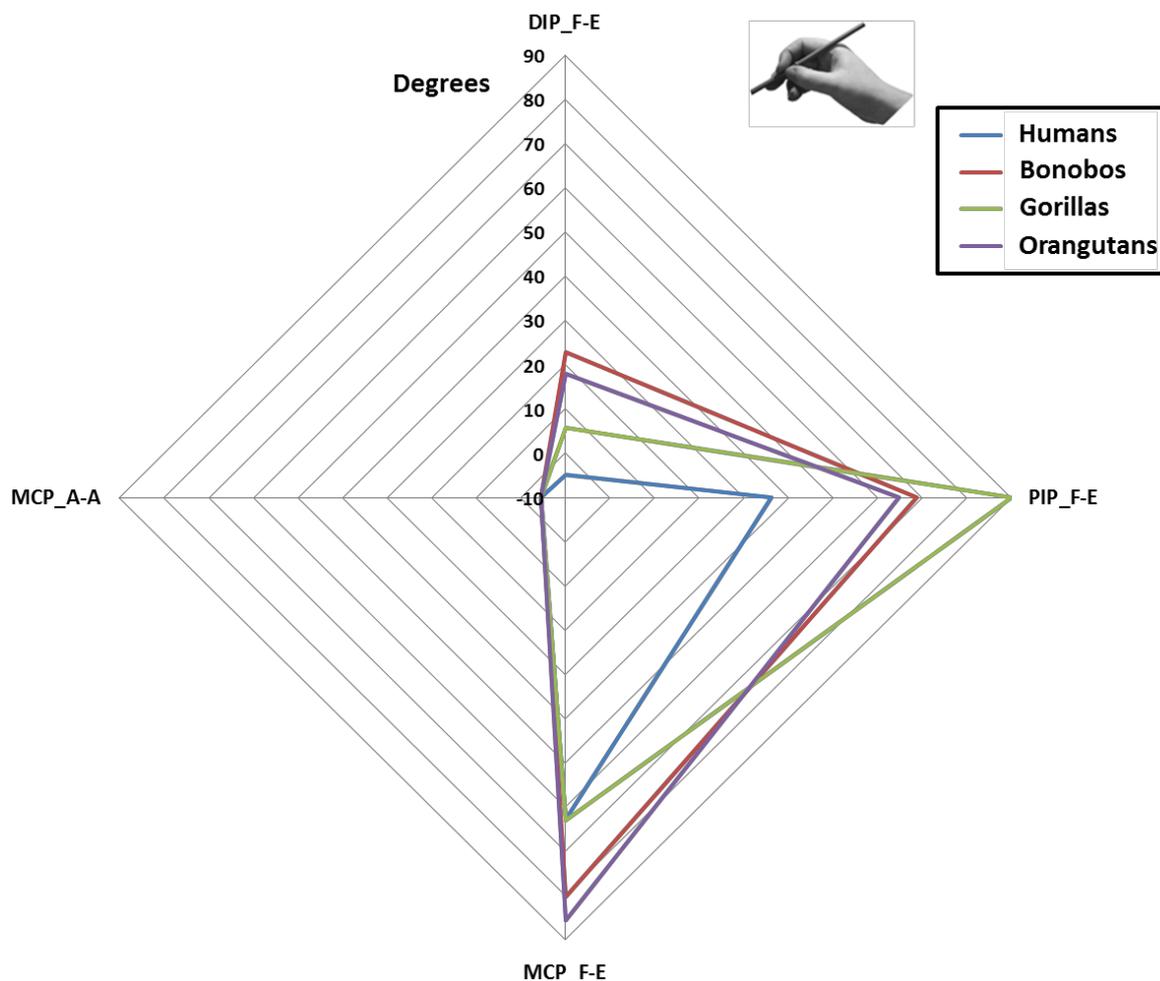


Figure 30. Results on the kinematics of the index finger during the simulations for the dynamic tripod grip for all the species. Differences appear between species in the DIP, PIP and MCP joints in flexion. MCP, metacarpophalangeal joint; PIP, proximal interphalangeal joint; DIP, distal interphalangeal joint; A-A, abduction/adduction; F-E, flexion/extension.

3.2. Net joint moments

3.2.1. Net joint moments of the thumb

Differences between species are observed for the dynamic tripod grip, the interdigital 2/3 brace and fewer for the power grip. On the contrary to these four grips techniques, there is no influence of the morphometric in the net joint moments of the thumb during the thumb lateral grip. The dynamic tripod grip generates different thumb constraints for gorillas with higher net joints moments than the other species (Figure 31a). More specifically, gorillas require more muscular efforts to stabilize the trapeziometacarpal joint (TMC) and MP joint in adduction while it requires less muscular moments for the same two joints in flexion. During interdigital 2/3 brace grip, the TMC of humans involves fewer muscular moments in flexion while orangutans require higher muscular moments in flexion for this joint (Figure 31b). Moreover, humans show higher muscular moments in abduction in the TMC joint while gorillas and bonobos require fewer muscular moments. During the power grip, the main difference is in the TMC joint where humans require fewer muscular moments in flexion than great apes.

3.2.2. Net joint moments of the index finger

We observe the largest differences between the species during the power grip, the thumb lateral grip, the dynamic tripod grip and the interdigital 2/3 brace grip, indicating a strong influence of morphometric in the net joint moments of the index fingers during these four grip techniques. The power grip involves less muscular moments in the PIP joints in flexion for humans and bonobos while orangutans require higher muscular moments (Figure 32a). Moreover, orangutans require more muscular moments in the MCP joint in flexion than bonobos (Figure 32a). The thumb lateral grip involves less muscular moments in the MCP joint in adduction for humans than great apes and especially orangutans which require higher muscular moments in this articulation (Figure 32b). The dynamic tripod grip involves higher muscular moments in the PIP joint in flexion for humans than great apes. The interdigital 2/3 brace grip involve higher muscular moments in the PIP joint in flexion for orangutans than the other species.

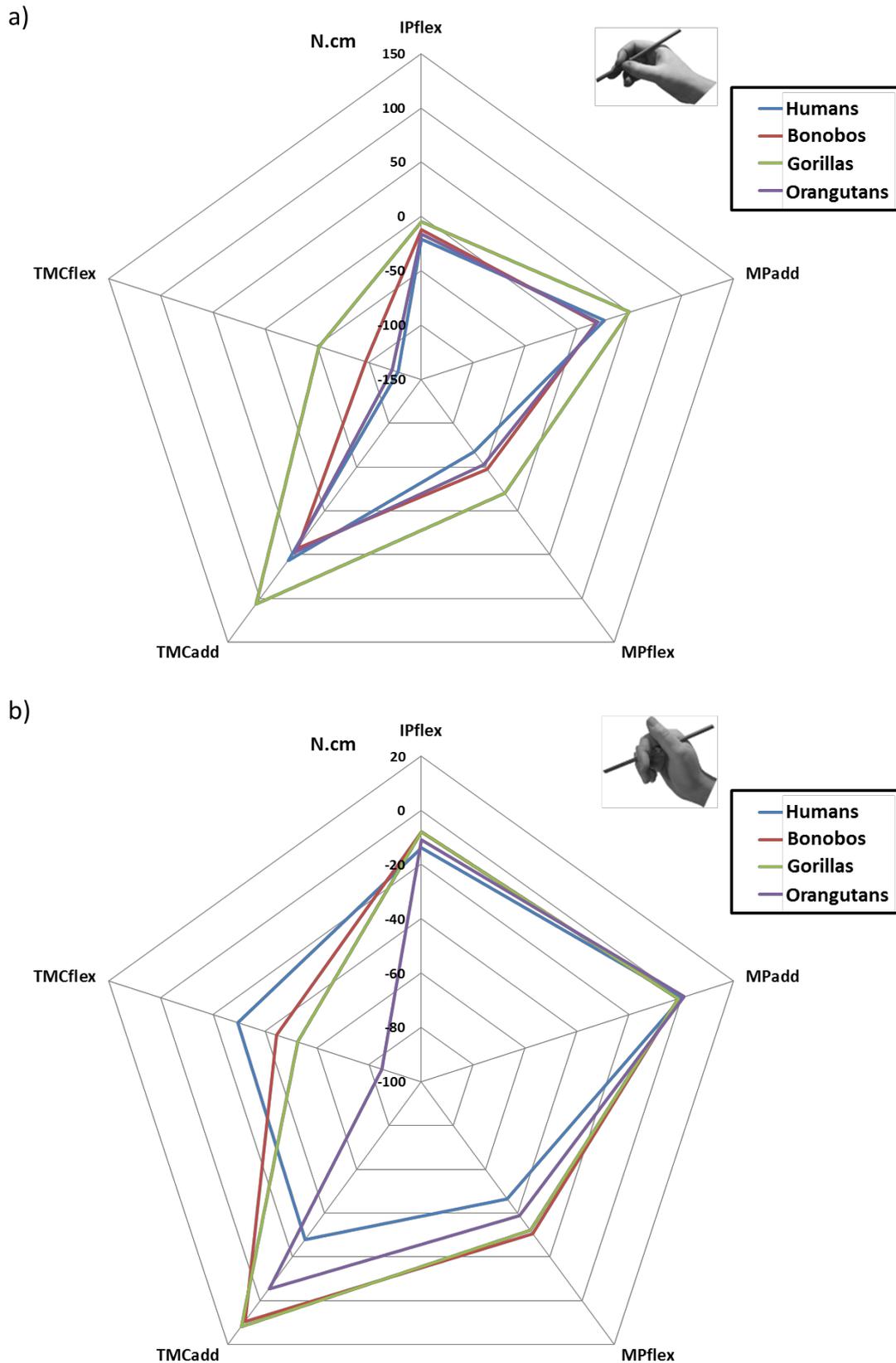


Figure 31. Results on the net joint moments of the thumb during the a) dynamic tripod grip and b) the interdigital 2/3 brace grip, for all the species. a) Gorillas show different net joint moments of the thumb compare to the other species. b) Species show different net joint moments of the thumb principally in the TMC joint in adduction and flexion. TMC, trapeziometacarpal joint; MP, metacarpophalangeal joint; IP, interphalangeal joint; flex, flexion; add, adduction.

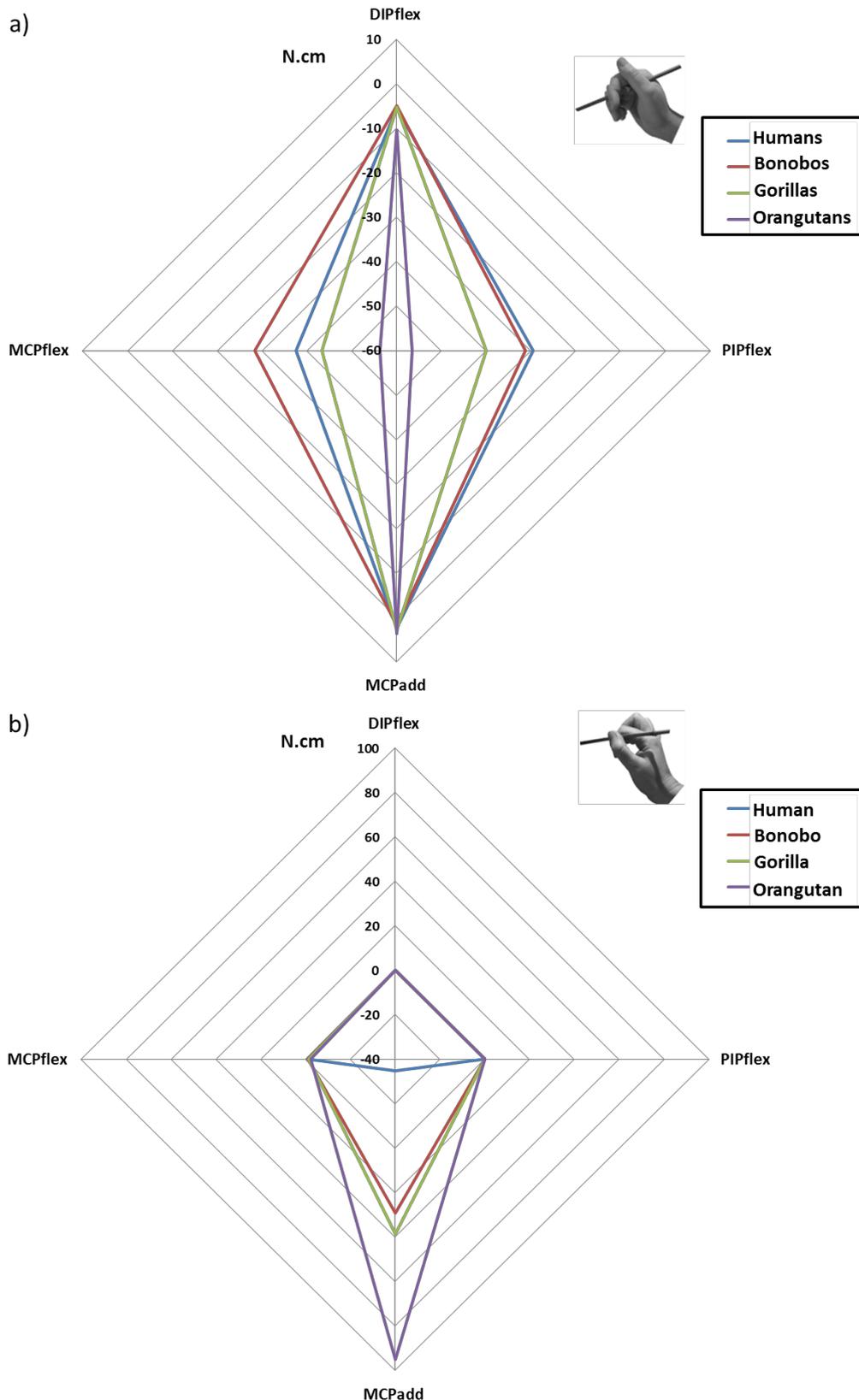


Figure 32. Results on the net joint moments of the index finger during a) the power grip and b) the thumb lateral grip, for all the species. a) Species show different net joint moments of the index finger in the MCP and PIP joints in flexion. b) Species show different net joint moments of the index finger in the MCP joint in adduction. MCP, metacarpophalangeal joint; PIP, proximal interphalangeal joint; DIP, distal interphalangeal joint; add, abduction/adduction; flex, flexion/extension.

3.3. Muscle group coordination

The different grip techniques require different sets of muscle groups' coordination and different muscle force intensities according to the species (Table 12). The two grip techniques which involve the most complex set of muscle coordination and the largest muscle force intensities are the dynamic tripod grip (Figure 33) and the thumb lateral grip (Table 12). The dynamic tripod and the thumb lateral grips involve larger muscle force intensity of the intrinsic muscles of the thumb. The power grip requires a larger muscle force intensity in the extensors of the wrist, the flexors of the fingers and the intrinsic of the thumb. The interdigital 2/3 brace grip require larger muscle force intensity in the extensors of the fingers and in the intrinsic of the thumb.

Interestingly, the two grip techniques which are the most influenced by morphometric are the dynamic tripod grip and the interdigital 2/3 brace grip (Figure 33 and Table 12). The dynamic tripod grip involves less muscle force intensity for humans while orangutans require more muscle force intensity with a strong ratio (> to 3 times) according to the 40 N force applied on the bamboo (Figure 33a). Gorillas require higher muscle force intensity for the thumb extensors muscles (TE) and fewer for the thumb flexor muscles (TF). The interdigital 2/3 brace involves more the TF muscles for orangutans than humans (Figure 33b). Moreover, humans and orangutans require more the intrinsic of the thumb muscles (TI) than gorillas and bonobos, with a strong ratio (> to 2 times). The thumb lateral grip involves more muscle force intensity with a strong ratio in the extensors of the fingers (FE) and the intrinsic muscles of the fingers (FI) for orangutans (FE and FI, both > to 2 times) than the other species (Table 12). Besides, orangutans require less muscle force intensity in the extensors of the wrist muscles (WE) while humans require higher intensity in the WE muscles (ratio > to 2 times). Concerning the power grip, orangutans require higher muscle force intensity with a strong ratio (> to 2 times) while humans need lowest intensity. The hook grip and the scissor grip do not differ significantly in muscle force intensity involved between the species.

Table 12. Summary of the results for the simulations on the muscle coordination^a and muscle force intensity^b requires by grip techniques and for each species.

	Dynamic tripod	Thumb lateral	Power	Interdigital 2/3 brace	Hook	Scissor
Number of involved muscle groups ^a	6 (FI, FE, TF, TI, TE, WF)	6 (FI, FE, TF, TI, TE, WE)	6 (WF, FI, FE, TF, TI, WE)	5 (FF, FI, FE, RF, TI)	3 (FF, FI, FE)	3 (FF, FI, FE)
<i>Thumb</i>	TI +++ ^b TF +	TI+++ TF++	TI +	TI +		
<i>Fingers</i>	FI ++ FE ++	FE + FI +	FF ++	FE +++		FI +++ FE +++
<i>Wrist</i>	WF+	WE+	WE ++			
Humans	FF + WF 0	WE+++	TF -	FI+ TF - TI+++ WF +		
Bonobos			TI ++	WF+		
Gorillas	TE+ TF-		TI +++	WF -		
Orangutans	FI +++ FE+++	WE - FE +++ FI++	TI +++ FE++	TI +++ TF + WF -		

^a Acronyms. Fingers flexors, FF; fingers intrinsic, FI; fingers extensors, FE; thumb flexors, TF; thumb intrinsic, TI; thumb extensors, TE; wrist flexors, WF; wrist extensors, WE. ^b Muscle force intensity requires: -, < 20 Newton (N); +, intensity > 40 N; ++, intensity > 70 N; +++, intensity > 100 N; 0 = absent.

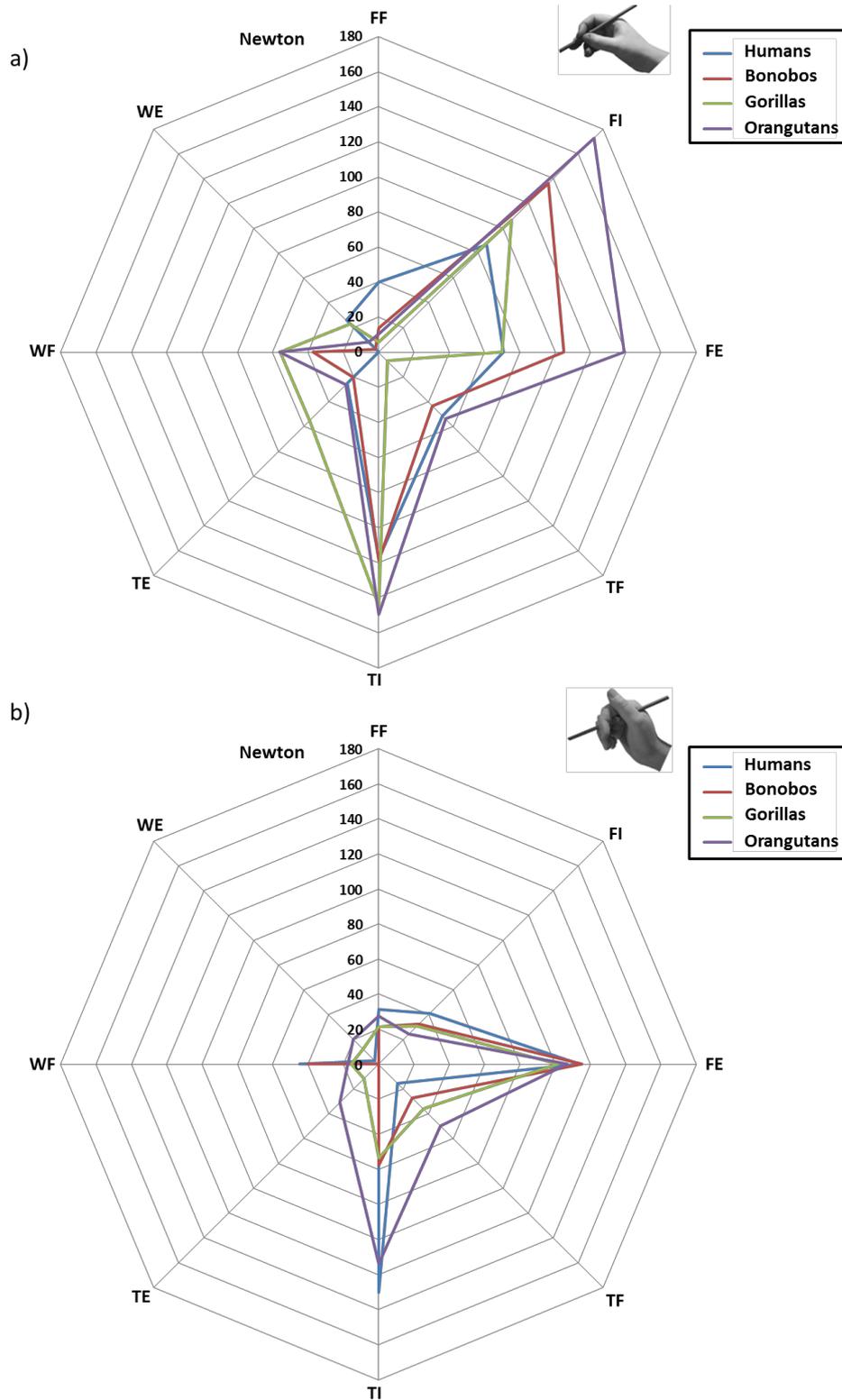


Figure 33. Muscle coordination and different muscle force intensities require according to the species during the simulations of a) the dynamic tripod grip and b) the interdigital 2/3 brace grip. a) The dynamic tripod grip requires less muscle force intensity for humans while orangutans require higher muscle force intensity. Gorillas need higher muscle force intensity for the TE muscles and fewer for the TF muscles. b) The interdigital 2/3 brace grip involves higher muscle force intensity of TF muscles for orangutans and fewer for humans. Moreover, humans and orangutans require more the TI muscles than gorillas and bonobos. Fingers flexors, FF; fingers intrinsic, FI; fingers extensors, FE; thumb flexors, TF; thumb intrinsic, TI; thumb extensors, TE; wrist flexors, WF; wrist extensors, WE.

4. DISCUSSION

Our main objective was to investigate on the influence of the morphometric of the primates' hands on the biomechanical constraints associated with different grip techniques observed during the maze task (chapters 3 and 4). The results of the simulations show a strong influence of morphometric on kinematics, joint net moments and muscle coordination especially on the four grip techniques involving the thumb (dynamic tripod, thumb lateral, power, interdigital 2/3 brace). These results validate our hypothesis that the morphometric of humans', bonobos', gorillas' and orangutans' hands involves different biomechanical constraints during the same different grip techniques previously observed (chapters 3 and 4). These results help us to better understand why some grip techniques are not used by all the species, such as the dynamic tripod which is only used by humans during the maze task (Figure 26).

Generally, the simulations inform us that some grip techniques seem very difficult in terms of range of motions for great apes compare to humans. For example, we observe that some grip techniques involve more or less muscle groups according to the different requirements as the use of the thumb and/or the wrist. These muscles' requirements present different muscle force intensity between species (Table 12). Even if no data exists on the muscle forces capacities of each species, some results showed very high force intensity which appeared as non-physiological and hardly feasible. Indeed, some species demonstrate a high ratio of muscle force intensity according to the force applied basically on the tool (i.e. same intensity of grip force for all the species and all grips). Moreover, the simulations show that some grip techniques induce also different fingers joints angles which appear to be not realizable for some great apes. In fact, according to the size of their fingers, humans and great apes require different finger joint angles to hold the tool with specific grips techniques. These different angles correspond to the different moments arms which engage different joints and muscle loadings. Consequently, the rare use of fingertips for great apes could be the results of a choice based on biomechanical loadings, which cannot be balanced by their musculature when grasping with their thumb. For example, orangutans' simulations generally demonstrate higher biomechanical constraints than the other species. Compared to the other species, they require more flexion and adduction of their thumb and their index finger to hold the tool according to the grip technique, causing more joints and muscles loading than the other species. Indeed, for example, the muscle force intensity requires in the muscles of the fingers for the orangutans is higher and can be with a ratio between 2 and 3 times of the force applied

on the bamboo. Moreover, humans and great apes show different biomechanical constraints during the same tool grip techniques. These different biomechanical constraints are discussed for each grip techniques involving the thumb (dynamic tripod, thumb lateral, power, interdigital 2/3 brace) in order to better understand the use or not of these grip techniques.

The dynamic tripod grip was only used by humans during the maze task (Figure 26). This grip represents the common human pencil grip (Wynn-Parry, 1966), i.e. how children learn to write between four and six years old (Schneck and Henderson, 1990). This grip technique appears to be the most “complex” and constraint in the simulations, and shows the most differences between species (Table 12 and Figures 30, 33). During this grip technique the tool is stabilized against the radial side of the third finger by the thumb pulp with index pulp on top of the tool. The simulation of this grip shows more requirements of the intrinsic muscles of the thumb involving more support of the trapeziometacarpal joint of the loaded thumb. Moreover, the simulations show that during this grip great apes need to flex more the trapeziometacarpal joint of the thumb than humans (Figure 30), and bonobos and orangutans need to flex more the metacarpophalangeal joint of the index finger than humans and gorillas (Figure 30). According to their morphometric, great apes need to position differently their fingers compared to humans, which involve different muscle efforts on the articulations to stabilize them and different muscle force intensity on the muscle groups of the hand. According to these results and the fact that only humans used this grip technique, the biomechanical constraints engage by this grip cannot be balanced by the musculature of great apes. In fact, the robust thumb of humans helps to resist increased joint forces due to their strong thumb musculature (Susman, 1994) whereas great apes show less musculature in their thumb (Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012). Consequently, in addition to the learning effect, the biomechanical simulations show that it is almost impossible for great apes to realize the dynamic tripod grip.

The interdigital 2/3 brace grip is used by all the species but more by the gorillas during the maze task (Figure 26). This grip technique is defined in human studies as an inefficient variant of pencil grip (Selin, 2003). This grip appears particularly difficult in terms of motion range of the thumb for the orangutans (Figure 31b). Orangutans need more net joint moments in the trapeziometacarpal joint during flexion than the other species and need more muscle force intensity in the flexors of the thumb. According to their small thumb and the absence of a true *flexor pollicis longus* muscle (Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012), this muscle force intensity can be too strong for them and so this grip cannot be

realizable. Gorillas, according to their highest thumb-forefinger index among hominoids, with gibbons (Schultz, 1930), require less muscle force intensity in the intrinsic and flexors muscles of the thumb than orangutans. These biomechanical results can explain why gorillas use more this grip technique than the other great apes during the maze task.

The thumb lateral grip (called also pinch grip, e.g. Byrne et al., 2001) is considered important during stone tool making and use in humans (e.g. Marzke and Shackley, 1986; Marzke, 1997). The human thumb anatomy and morphology, as the presence of an independent *flexor pollicis longus* muscle (e.g. Susman, 1988, 1994; Marzke, 1992), is supposed to allow a more important strength during this grip than great apes, by facilitating contact between the thumb and the index. However, this grip technique used by all the great apes in various activities (e.g. Christel, 1993; Marzke and Wullstein, 1996; Byrne et al., 2001; Pouydebat et al., 2011) is more used by bonobos and orangutans during the maze task than humans and gorillas (Figure 26). Furthermore, the simulations demonstrate that the index finger show more differences between species than the thumb and reveals more constrains on its net joint moments than the thumb. Great apes require more flexion of the metacarpophalangeal joint of the index finger than humans. This strong flexion involves for great apes an adduction of the metacarpophalangeal joint of the index finger according to the oppose force of the thumb applied on it. According to this, great apes require higher net joint moments to stabilize their metacarpophalangeal joint of their index finger than humans. It appears thus difficult for them to realize this grip technique according to the force applied on the object grasped. In other words, it is possible for great apes to use this lateral grip technique during the manipulation of a bamboo, but it may be impossible for them to use it if more force is required as during stone making. Additionally to the finger muscles, humans require more muscle force intensity of the extensors muscles of the wrist, with a ratio of 2 times to the force applied on the bamboo, than great apes. The orientations of the carpal bones in humans are supposed to facilitate the loads on the wrist during strong grip in stone making (Tocheri et al., 2007, 2008). Thus, during the lateral thumb grip the morphometric of the human hand and the orientation of their carpal bones can allow them to better control the loads in the wrist during stone making than great apes. However, stone tool making was also possible for great apes, as showed by the studies on the trained bonobo Kanzi and a trained orangutan (Wright, 1972; Schick and Toth, 1993; Schick et al., 1999). However, Williams et al. (2010) showed that the human wrist joint was important on the efficiency in knapping strategy during stone making. Thus, great apes can produce abundant muscle force intensity during bamboo manipulation but may not be

sufficient during stone making according to the morphometric and morphology of their hand which could prevent enough mobilization of the wrist. It would be interesting to quantify hand and finger postures used by Kanzi in order to test how this lateral grip and the wrist are involved according to the various tool using tasks it accomplishes, taking into account that with its experience, Kanzi may have developed an adapted morphology of its upper limb. We could then also quantify the muscle force intensity and mechanical constraints involved during stone making in trained great apes.

The power grip appears, as the thumb lateral grip, important in human tool manipulation. Humans seem to use more efficiently the power grip than great apes, by grip with power an object according to some specific human morphological features (Marzke et al., 1992). The power grip is used by all the species during the bamboo manipulation (Figure 26). The simulations show that during the power grip the intrinsic muscles of the thumb, the flexor of the fingers and the extensors of the wrist are strongly involved, and different muscle force intensity are required between species. Our results especially demonstrate stronger activation of the intrinsic muscles of the thumb for great apes than humans. All the great apes need more net joint moments to flex the trapeziometacarpal joint of the thumb than humans, but more differences between species appear for the index finger (Figure 32a). For example, orangutans require more net joint moments in the index finger in flexion to stabilize the metacarpophalangeal and proximal interphalangeal joints. Moreover, the power grip requires more muscle force intensity in all the muscle groups needed during this grip for orangutans than the other species. Thus, orangutans appear during the power grip to present more biomechanical constraints than the other species (e.g. strong joint and muscle loadings) but orangutans endure these constraints without difficulties as they use more the power grip than the other species during the maze task (Figure 26). This result shows the importance to compare the real manipulative abilities of primates with the associate potential biomechanical constraints of their morphometric hand to better understand the evolution of the manipulative abilities of humans. It would be interesting to perform the simulations with more force applied on the tool and with different size of the tool to test if orangutans differ strongly from other primates. This could allow us to better understand the muscle coordination and the muscle force intensity involved during stone tool making. As during the power grip the fifth finger plays an important role to stabilize stone during stone tool making (Marzke and Shackley, 1986; Marzke et al., 1998), it appears important to also study its biomechanical constraints by

simulations and to compare them between primates to better understand their full hand abilities.

5. CONCLUSION

This preliminary study provides new results and a new approach to better understand the manipulative abilities of primates. This study clearly shows that the morphometric of the overall hand can involve different biomechanical constraints. The differences between species observed in kinematics, net joint moments and muscle coordination also demonstrate the high difficulty to infer preferred manual postures. These simulations can provide also new information to better understand the evolution of manual abilities in primates. For example, the simulations for the bonobos place them in a middle place with mean results compared to the other species. The morphometric of the bonobos' hands could provide a good compromise to use different grasping postures without the strongest biomechanical constraints (e.g. strong joint and muscle loadings) undergone by the other species. Thus, according to our results and the fact that stone making is possible by the bonobo Kanzi (Schick and Toth, 1993; Schick et al., 1999), we parsimoniously suggest that the intensification of complex manipulation in primates leading to stone making in the genus *Homo* may be originated at least from the last common ancestor of *Pan* (chimpanzees and bonobos) and *Homo* (between 8 and 4 Ma; Tocheri et al., 2008). By including such a biomechanical constraint analysis, we would like to improve the inference of the potential manipulative abilities of some fossils. Moreover, we would like to use this musculo-skeletal model during stone making in order to test the potential manipulative abilities of primates for this important behavior in human evolution. To conclude, the different manipulative abilities of primates can be not only a consequence of the different shape morphology of the trapeziometacarpal joint but also a consequence of the different mechanical constraints according to the overall hand morphometric.

SUPPLEMENTARY TABLE

Table S3. Muscles groups used in the simulations for all the species.

Muscles groups	Muscles ^a
FF - Fingers flexors	FDPI, FDPM, FDPR, FDPL, FDSI, FDSM, FDSR, FDSL, FDQ
FE - Fingers extensors	EDCI, EDCM, EDCR, EDCL, EIP, EDQ
FI -Fingers intrinsic	LU1, LU2, LU3, LU4, DIO1 (RI), DIO2 (RI), DIO3 (UI), DIO4 (UI), PIO1 (UI), PIO2 (RI), PIO3(RI), ADQ (UI)
TF - Thumb flexors	FPL, FPB
TE - Thumb extensors	EPL, EPB, APL
TI - Thumb intrinsic	OPP, APB, ADPt, ADPo
WF - Wrist flexors	FCR, FCU, PL
WE - Wrist extensors	ECRL, ECRB, ECU

^a Acronyms. FDP, flexor digitorum profundus; FDS, flexor digitorum superficialis; FPL, flexor pollicis longus; FPB, flexor pollicis brevis; OPP, opponens pollicis; EDI, extensor digitorum indicis; EDC, extensor digitorum communis; DIO, dorsal interosseous; APB, abductor pollicis brevis; ADPt, adductor pollicis transverse head; ADPo, adductor pollicis oblique head; PIO, palmar interosseous; ECRB, extensor carpi radialis brevis; ECRL, extensor carpi radialis longus; ECU, extensor carpi ulnaris; FCU, flexor carpi ulnaris; FCR, flexor carpi radialis; PL, palmaris longus; APL, abductor pollicis longus; EPL, extensor pollicis longus; EPB, extensor pollicis brevis; EDQ, extensor digiti quinti; FDQ flexor digiti quinti, LU, lombrical; ADQ abductor digiti quinti.

SUMMARY OF THE CHAPTER 6

Title: Biomechanical analyses of the consequences of different hand morphometric on tool grasp abilities using musculo-skeletal simulation: a preliminary study.

Question: What are the influences of the morphometric of the Hominids' hands on the biomechanical constraints associated to different grip techniques?

Model: Humans (*Homo sapiens*), bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla gorilla*), orangutans (*Pongo pygmaeus*).

Method: Experimentation in human and Musculo-skeletal simulation using human 3D biomechanical study (MNHN & ISM Marseille).

Results: The simulations of the grip techniques show a strong influence of morphometric on kinematics, joint net moments and muscles coordination. Some grips appear very difficult for some species in term of range of motion by requiring strong muscle forces.

Discussion: This preliminary study provides new results and a new approach to better understand the manipulative abilities of Hominids. This study clearly shows that the morphometric of the overall hand can involve different biomechanical constraints. The different manipulative abilities used by Hominids cannot only be a consequence of the different morphology of the trapeziometacarpal joint but also a consequence of the different mechanical constraints related to the overall hand morphometric.

Perspectives: We would like to improve the simulation to infer the potential manipulative abilities of some fossils by including such biomechanical constraint analysis. It would be interesting to perform the simulations with more force applied on the tool and with different size of the tool to better understand the muscle coordination and the muscle force intensity involved for example during stone tool making. These simulations could provide new information to better understand the evolution of manual abilities in Hominids.

Chapter 7 – General discussion, conclusion & perspectives

General discussion, conclusion & perspectives

1. GENERAL DISCUSSION

The aim of this doctoral dissertation is to better understand the Hominids' manipulative abilities related to their hand anatomy and hand function by developing an interdisciplinary framework around three principal research questions: **(1) What are the real manual abilities of Hominids? (2) Do humans really have unique manual abilities? And if yes, why? (3) Which morphological and mechanical parameters are associated with these manual abilities?**

To answer these questions, I combined three different approaches: ethology, functional morphology and modelling. The results of the different chapters show that even if great apes also display great manipulative abilities in the context of tool use, humans present specific manual abilities. Moreover, the results clearly show that the different manipulative abilities of Hominids cannot only be a consequence of the different shapes of the trapeziometacarpal joint but also a consequence of the different mechanical constraints related to the overall hand morphometric. To conclude this work, I will draw the link between all my results and replace them in an evolutionary framework.

1.1. What are the real manual abilities of Hominids?

In the chapter 2 of this work, I tested hand preference in bonobos regarding the hypothesis proposing both tool use and bipedalism as selective pressures for hand preference in humans (Kimura, 1979; Frost, 1980). I showed that bonobos can exhibit a strong hand preference for the right hand during a complex tool use task (the maze task) independently to body posture. Task complexity might have contributed more than bipedal posture in the emergence of human lateralization and the preponderance of right-handedness. A larger sample size and additional data on other species could be useful to reinforce this hypothesis.

It is unlikely that bipedalism had such an important role in the elaboration of tool use and in the preponderance of the right hand preference in humans. Indeed, a recent neurological study

conducted by Hashimoto et al. (2013:1) suggested that “adaptations underlying tool use evolved independently of those required for human bipedality.” Hand preference might be older than bipedalism in origin and appears rather linked to an arboreal lifestyle that requires complex body postures and manipulation. In fact, a link might have existed between the mode of locomotion and manipulative abilities, with a tendency for an exaptation of manipulation for arboreal species (Sustaita et al., 2013). In this context, the capacity to grasp is proposed as a “critical adaptive innovation” for arboreal primates (Kivell et al., 2010:1549) and a “key feature” of primate evolution (Ravosa and Dagosto, 2007:18). An arboreal lifestyle could have led to the elaboration of manual skills and tool use in primates, and hand preference could have emerged from arboreal ancestors coming down to the ground to use tools like some apes today.

My data set did not allow testing the hypotheses on hand preference in chapter 4 but we can mention that only humans and bonobos (chapter 2) are right handed during the maze task. Hand preference varies across individuals for gorillas (4 left handed and 2 right handed) and orangutans (2 left handed and 5 ambidextrous). These results are in accordance with previous data on orangutans (O’Malley and McGrew, 2006) but not on gorillas (Pouydebat et al., 2010). Thus, according to the variability of the results in the literature, we expect that plasticity of the brain and hemisphere specialization is underestimated. Moreover, gorillas perform the maze task in seated posture, as bonobos do for one of the conditions in chapter 2, whereas orangutans change their body posture during the task (seated, hanging on the wire netting, and bipedal postures). It is really difficult to conclude about hand preference and tool use because of the many parameters that can influence hand preference (e.g. task complexity, body posture, experience, object position, properties of the object grasped, grasping techniques, object movement, social context, environment, etc.). It appears important to study hand preference with a better control of the potential parameters that can influence the results. That was the aim of my second chapter on bonobos. Indeed, I recorded data when the individuals were truly seated and in a true bipedal posture (which I defined as the position where the angle between the trunk and the thigh was greater than 90° with the knee extended), and I also recorded data only when the subject was facing the experimental apparatus. For orangutans and gorillas, I tried to control the body posture by placing the maze low enough to force the seated posture but it did not work for orangutans. We need to think about new experimental designs that could take into account the natural needs of arboreal species.

As task complexity and tool use appear fundamental in the specialization of the hand of bonobos (chapter 2), the chapter 3 quantified the functional and behavioral strategies used by these species during two different tool use tasks varying in complexity. I showed that bonobos use a great variety of grip techniques, demonstrate dynamic manipulation, and respond to task constraints by selecting and modifying tools appropriately, usually before they start the tasks. Moreover, more complex manipulation is observed for the more complex task (i.e. the maze task) and bonobos demonstrate individual strategies. The manual abilities observed in bonobos suggest that they have the neuromuscular and morphological requirements that give them the necessary neuromotor control for complex fingers' manipulation, like chimpanzees (Craut et al., 2009). Moreover, even if bonobos do not use tools into the wild during food process (Ingmanson, 1996), they have the cognitive abilities to anticipate and plan the use of appropriate tools according to the task. This point needs to be investigated with a larger sample size and on different groups of bonobos.

In order to better understand the manipulative abilities of Hominids related to the increase of tool use complexity and to test if humans are really unique, I compared in chapter 4 the manipulative abilities of humans, gorillas, and orangutans during the same complex task (maze task). The complexity of the maze task requires complex coordination of motor demands, which could be expressed differently between species according to their motor skills and their morphology (Wainwright et al., 2008). I showed that during the maze task, humans perform better than gorillas and orangutans, with performance linked to in-hand movements and specific grip types. These results could have suggested a lack of efficiency and precision of wrist movements for gorillas and orangutans. However, some individuals among humans and gorillas performed better than others according to their grip types and the use of in-hand movements. Thus, the use of in-hand movements could involve better manipulative control with less repositioning of the tool in the grid, and enable a better performance. Moreover, gorillas present more in-hand manipulation than orangutans that show more mouth manipulation. This difference between great apes could be explained by many factors, such as the morphology of their hands (Marzke and Wullstein, 1996; Marzke et al., 2010), their different lifestyles (Tuttle, 1972), and their social process, like social learning (Whiten and Ham, 1992). Indeed, gorillas (and gibbons) have the longest thumb relative to the size of their other fingers among hominoids, while orangutans have the shortest (Schultz, 1930). It is often suggested that the reduction of the thumb is an adaptation for increased forelimb suspension and for the improvement of hook grip during suspensory behavior

(Tuttle, 1972). During terrestrial locomotion in Hominids (bipedalism and knuckle walking locomotion) the thumb is not involved and thus can be available for food and object manipulation. I showed that gorillas, the most terrestrial of the great apes, use their thumb more often during in-hand movements than orangutans, the most arboreal great apes. Orangutans use specific grip types including ones involving the mouth and the foot, probably due to their arboreal lifestyle as it is shown that orangutans demonstrate a strong preference for oral tool use over manual tool use (O'Malley and McGrew, 2000). Bonobos and gorillas show a preferred grip technique during the maze task whereas orangutans show more intra-specific variability in the grip techniques. Orangutans frequently change their body posture during the maze task. This could force them to change their grasping postures and could also induce more repositioning of the tool, especially with the mouth. Species could have developed and adapted manual abilities according to the demands of their foraging niche. One study suggested that humans have the most complex foraging niche and so that they have developed complex manual abilities, with the idea that the manipulation complexity would have coevolved with brain size and territoriality in primates (Heldstab et al., 2016). Though an analysis with a large sample size including many arboreal and terrestrial species would be necessary to test this hypothesis, the results of the chapters 3 and 4 are partly consistent with this previous study and with the hypothesis that territoriality facilitates the development of complex tool use (Meulman et al., 2012). Indeed, humans, bonobos and gorillas show more complex manipulation skills during the maze task than orangutans, like the use of in-hand movements, a bias for a preferred hand, and more stable technique use (i.e. technique used for a long time).

It appears difficult to quantify manipulation with a common method to compare species. The method of time based sequence analysis of contact areas (Borel et al., 2016a) that I used in my PhD does not imply direct contact with the observed individuals or the use of markers which could impact their behavior. Therefore, even if it is based on time consuming video analysis including a few limitations (see Borel et al. [2016a] for complete discussion about advantages and limitations) it is a good compromise to obtain comparable data between different species. It allows to describe in detail the grip types and their variability. It also provides a dynamic view of the manipulation strategies and thus allows not only to record the

number of occurrences of grasp types but also to quantify their duration of use. It is possible to show that some grasp types are used longer than others. Individual differences are also examined and quantified with this method. This is a relevant approach to compare tasks and species in future studies, and to investigate more thoroughly inter and intra-individual variability. Moreover, combining data obtained by the method of time-based sequence analysis of contact areas with the trabecular architecture of hand bones in extant Hominids (see the review of Kivell [2016b]) could provide new information in their manipulative abilities. In fact, we can test for possible correlations between contact areas on the fingers and the trabecular architecture of the metacarpals and/or carpals bones (e.g. trapezium and first metacarpal) to show a possible signal in the inner structure linked to contact and loading areas in the fingers. This approach could help to better understand the use of preferred grip techniques in Hominids according to their functional abilities, and could also provide new information to infer manual abilities in fossils (Skinner et al., 2015a).

1.2. Do humans really have unique manual abilities? And if yes, why?

I showed in chapter 4 that humans demonstrate specific manual abilities during tool manipulation (the maze task). Only humans use the bimanual grip type, pad-to-pad precision grip and in hand-movements involving fingertips. Human specificities quantified here, but also differences quantified between gorillas and orangutans, could be explained by morphological and/or neuromuscular factors, such as coordination specificities. Indeed, the differences in manipulative abilities between humans and great apes could be due to different morphologies of the hand and to the absence of several anatomical features in the great apes. The shape of the trapeziometacarpal complex appears to allow greater mobility of the carpometacarpal joint of the thumb in humans than in great apes (e.g. Marzke et al., 2010). Thus, according to the morphology of their trapeziometacarpal complex, humans can demonstrate more complex in-hand movements involving the finger pads than great apes. It appears that some human hand muscles, such as the *flexor pollicis longus* and *extensor pollicis brevis*, which are involved in the movement of the thumb, are not present in the hands of great apes, except hylobatids (Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012). Moreover, in contrast to in humans (Vigouroux et al., 2011; Goislard de Monsabert et al., 2012), the muscle activities and muscular coordination required to grasp an object for great apes are not known. According to extremely scarce studies on muscles activities

(Overduin et al., 2008) and on our results, we can expect that the morphometric of humans', bonobos', gorillas' and orangutans' hands involves different biomechanical constraints during grasping. For example, a smaller thumb would generate a different finger joint angle, corresponding to different moment arms and would probably engage different joints and muscle loadings. Consequently, the rare use of fingertips for both great apes could be the result of a choice based on biomechanical loadings, which could not be balanced by their musculature when grasping with the thumb.

However, it is possible that some specific manual abilities observed only in humans during the maze task are absent in non-human primate species due to behavioral choice, rather than an inability to perform these manual abilities. Indeed, during the maze task one of the human specificities is bimanual coordination, which is a very high cost strategy. However, this strategy does not appear to outperform the others. So the lack of bimanual coordination in gorillas and orangutans could be the result of a choice based on the cost at the motor control level. The ability to perform many two-handed tasks routinely exists in both humans (Corbetta and Thelen, 1996) and great apes (e.g. chimpanzees: Marzke et al, 2015; gorillas: Byrne et al., 2001; orangutans: Peters and Rogers, 2008). In the present study, bimanual coordination grips are employed half of the time, only by humans. These bimanual coordination grips increase the complexity of manipulation (MacNeilage et al., 1987; Hopkins, 1995; Heldstab et al., 2016). Humans display symmetrical bimanual coordination, where both hands grasp the same tool, and also asymmetrical bimanual coordination where each hand grasp separate tools. Asymmetrical bimanual coordination appears to be a more difficult task and requires eye coordination with both distant hands. Are humans more used to bimanual strategies conditioned from their childhood than non-human primates? It would be interesting to study a greater sample of humans to test the influence of unimanual and bimanual grip types on their performance during different manual activities.

In order to better understand the morphological and biomechanical effects on the manual abilities in primates, I used 3D geometric morphometrics and comparative approaches on the trapeziometacarpal complex (chapter 5) combined with musculo-skeletal simulations to better interpret the behavioral results and to test the link between hand morphometric and biomechanical constraints during tool grasp abilities in Hominids (chapter 6).

1.3. Which morphological and mechanical parameters are associated with these manual abilities?

In chapter 5, I quantitatively analyzed the shape variations in the trapeziometacarpal (TMC) complex and the co-variations between the two bones of this complex among Hominids. I showed that shape variations of the trapezium appear to partially reflect the phylogeny (see, e.g., the review of Herlyn, 2016), whereas the shape variations of the first metacarpal almost placed *Gorilla* with *Homo* (modern and fossil *H. sapiens*, and *H. neanderthalensis*). I showed that the analysis of the shape variations of the trapezium clearly distinguishes *Homo* from great apes, especially *Pongo*, with a greatest potential of thumb mobility for *Homo*. However, the analysis of the shape variations of the first metacarpal shows a more robust thumb for *Homo* and *Gorilla* than for *Pan* and *Pongo*. Shape co-variations are not only dominated by variations of joint surfaces and muscle attachment zones on each bone, but are driven by the overall shape variations of the two bones. This result shows a strong global morphological relationship probably due to the fact that the trapezium and the first metacarpal need to interact functionally to allow movements of the thumb. Moreover, the shape co-variations show differences associated with the species and appear to partially reflect the phylogeny. Thus, shape co-variation of the two bones of the TMC complex is constrained by the phylogeny but also by other factors (e.g. functional requirements and development) These results confirm the importance of quantifying together the overall shape variability of the two bones of the TMC complex in Hominids in order to show 1) the strong morphological and functional relationships between them and 2) different co-variations patterns between Hominids with maybe some similar features between *Homo* and *Gorilla*. Two major functional constrains could explain these differences between the Hominids studied: their different mode of locomotion and/or their different manual abilities.

According to the results of chapter 4 already discussed and to the fact that *Homo* and *Gorilla* show a more robust thumb than *Pan* and *Pongo*, we can suggest that terrestrial locomotion could favor, in Hominids, the development of a strong musculature of the thumb while arboreal lifestyle in Hominids could reduce it. Additionally, I found different orientations of all the joint surfaces on the trapezium and on the first metacarpal between species, which probably favor the loading in the wrist for the locomotion in great apes and for manipulation with the thumb in humans (Lewis, 1989; Tocheri et al., 2003; Tocheri et al., 2005; Tocheri, 2007). The co-variation show that the overall trapeziometacarpal complex could be

functionally constrained by locomotion with a total opposition between *Homo* and *Pongo*, which opposes the most terrestrial Hominid to the more arboreal one.

On the other hand, the differences between Hominids could also be due to functional constraints related to manipulative abilities. The specific shape of the trapeziometacarpal complex quantified in *Homo* appears to offer greater grasping and manipulative abilities with a greater potential of thumb mobility than in great apes, especially *Pongo*. In fact, *Pongo* shows the most distinct morphology of the TMC complex from that of *Homo*. Thus, *Pongo* may not be able to develop strong grips with the thumb and may be limited in its thumb movements. However, orangutans are also able to use grasping postures involving the thumb, such as the thumb lateral grip (e.g. Christel, 1993). Their particular thumb morphology and their first metacarpal radially oriented could be advantages to oppose the thumb and the index finger during precision grips. However, the fact that I did not quantify in-hand movements in orangutans during the maze task (chapter 4) could be explained by the morphology of the orangutans' thumb, which could prevent them from dynamically using their thumb to move an object in one hand. Orangutans reposition the tool in their hand during the maze task most of the time with their mouth, which is probably due to their highly arboreal lifestyle. This could also be explained by their thumb morphology. African great apes (gorillas, chimpanzees and bonobos) show a TMC shape intermediate between *Pongo*'s and *Homo*'s, and display fewer differences with *Homo* than *Pongo* does. Thus, the trapeziometacarpal morphology of the African great apes can allow more freedom of the thumb movements than in *Pongo* but not in the same way as in humans. In fact, in-hand movements are observed in bonobos and gorillas during the maze task (chapters 3 and 4) mainly with flexion and extension of the thumb. Their in-hand movements appear simpler than those observed in humans (chapter 4). It could be explained by their relatively curved trapeziometacarpal joint surface, whereas the humans' plane surface allows more freedom of movements (Marzke et al., 2010). This is also in agreement with the study in chimpanzees of Crast et al. (2009), showing that this species uses in-hand movements but simpler than those used by humans.

Homo fossil specimens were also incorporated in the comparative analyses of shape in order to test their distribution among Hominids and to discuss their potential manual abilities. The results for the shape variability of the two bones in *Homo* show that fossil *H. sapiens* ("Cro-Magnons") are at the core of the modern *H. sapiens* distribution while *H. neanderthalensis*'s specimens surround the variability space of *H. sapiens*. One specimen of *H. neanderthalensis* (Kebara, KMH2) presents a very plane trapezium with a much transversally extended

tubercle, which could have limited the manual abilities of this specimen by restraining the thumb movements in flexion and adduction. The other specimens show a functional morphology similar to that of modern *H. sapiens* and thus could have presented similar manual abilities.

The morphological analyses in chapter 5 focused on only two bones in the hand but, as previously discussed, the muscle activities and muscular coordination required to grasp an object for great apes are not known. It appears important to take into account the overall hand morphometric. This approach was conducted in the last study of this work (chapter 6) focusing on the consequences of different hand morphometrics on tool grasp abilities (observed in chapters 3 and 4) using musculo-skeletal simulation. The simulations of the grips' techniques show a strong influence of hand morphometric on kinematics, joint net moments and muscles coordination. Some grips appear very difficult for some species in terms of motion ranges by inducing different finger joint angles and by requiring strong muscle forces, which appears not feasible for some great apes. These muscles' requirements are associated with different muscle force intensities between species, preventing the use of some grips in some of them. For example, only humans used the dynamic tripod grip (i.e. the common pencil grip) during the maze task. According to their morphometric, great apes need to position differently their fingers compared to humans during this grip, which involves different muscle efforts on the articulations to stabilize them and different muscle force intensities on the muscle groups of the hand. According to these results and to the fact that only humans used this grip technique, the biomechanical constraints engaged by this grip technique can probably not be balanced by the musculature of great apes. In fact, the robust thumb of humans helps to resist increased joint forces due to their strong thumb musculature (Susman, 1994) whereas great apes show less musculature in their thumb (Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012). Consequently, in addition to the learning effect, the biomechanical simulations suggest that it is almost impossible for great apes to perform the dynamic tripod grip.

Orangutans' simulations especially show more biomechanical constraints than in the other species. Compared to the other species, they require more flexion and adduction of their thumb and of their index finger to hold the tool according to the grip technique, causing more joint and muscle loading than in the other species. Indeed, for example, the muscle force

intensity required in the muscles of the fingers for the orangutans is higher and can reach a ratio between 2 and 3 times the force applied on the bamboo. Orangutans use a diversity of grip techniques, such as the thumb lateral grip (Chrstitel, 1993), which is considered important during stone tool making and used in humans (e.g. Marzke and Shackley, 1986; Marzke, 1997). Trained orangutan and bonobo (Kanzi) have the potential (e.g. functional, morphological, and cognitive) to manufacture stone tools (Wright, 1972; Toth and Schick, 1993; Schick et al., 1999) but their environment may not require to use this skill. Nevertheless, the results of the simulations show that it appears difficult for orangutans to perform some grip techniques if more force is required, such as during stone tool making. Additionally, Williams et al. (2010) show that the human wrist joint is important on the efficiency in knapping strategy during stone making. Thus, great apes can produce abundant muscle force intensity during bamboo manipulation (i.e. maze task in chapter 4) but this force may not be sufficient during stone making according to the morphometric of their hand, which could prevent sufficient mobilization of the wrist.

The simulations for the bonobos place them in a middle place with mean results compared to the other species. The morphometric of the bonobos' hands could provide a good compromise to use different grip techniques without the strongest biomechanical constraints (e.g. strong joint and muscle loadings) undergone by the other species. It would be interesting to quantify hand and finger postures used by Kanzi in order to test how this lateral grip and the wrist are involved depending on the various tool using tasks accomplished, taking into account that with its experiment, Kanzi may have developed an adapted morphology of its upper limb. We could also quantify the muscle force intensity and mechanical constraints involved during stone making in trained great apes.

According to the results on the simulations and the fact that stone making is possible for Kanzi (Schick and Toth, 1993; Schick et al., 1999), we parsimoniously suggest that the intensification of complex manipulation in primates leading to stone making in the genus *Homo* may have originated at least from the last common ancestor (LCA) of *Pan* (chimpanzees and bonobos) and *Homo* (between 8 and 4 Ma; Tocheri et al., 2008). Thus, the LCA of *Pan-Homo*, if he had similar hand morphology to bonobos, may have had similar functional capabilities. However, some authors consider the human hand more primitive than that of extant apes which have high levels of hand disparity explained by different evolutionary processes (Almecija et al., 2015). Thus, the bonobo hand could be more derived. In this context bonobos are interesting because they use different locomotion modes such as

knuckle-walking and bipedalism and use both terrestrial and arboreal substrates (see D'Août et al., 2004 for a review). Thus, they appear adapted for arboreal behavior and terrestrial locomotion. The results of chapter 3 show a variety of grasp types and in-hand movements in bonobos which could be linked to these diverse types of locomotion (Christel et al., 1998). According to Almecija and collaborators (2015) the morphology of the hand of bonobos may have evolved in conjunction with their different modes of locomotion, as in extant apes. This hypothesis is consistent with Rolian and collaborators (2010) who suggest that the evolution of the human hand is not linked to an adaptation for tool use or any other function, but rather that the hominin hand and feet coevolved. They suggested that the evolution of long robust big toes and short lateral toes for bipedalism led to changes in hominin fingers that may have facilitated the emergence of stone tool technology (Rolian et al., 2010). No fossil hand of a much primitive ancestor of Hominids has been discovered yet and the evolution of the human hand during the emergence of manual abilities to produce stone tools remains debated. Recent archeological and paleoanthropological discoveries show that the earliest evidence of intentional stone tool production at 3.3 Ma (Harmand et al., 2015) predate the appearance of the genus *Homo* by at least 0.5 Ma (Skinner et al., 2015b), and that intensified manual manipulation could be linked to an arboreal lifestyle (Kivell et al., 2011; Kivell et al., 2015; Skinner et al., 2015a). These discoveries allow suggest that arboreal species could have the potential to produce and to use stone tools.

2. CONCLUSION

This work provides new information on the manual abilities of Hominids and on the different constraints surrounding these abilities, and new information to better understand the evolution of manual abilities in Hominids. The use of the time based sequence analysis of contact areas allows to highlight new grasping postures and also provides a new method to present a dynamic view of the manipulation strategies. Bonobos and gorillas show more complex dynamic manual abilities than orangutans, and humans show specific manipulative abilities and a better performance. The different lifestyles of the species may explain this variability with possibly higher complex manual abilities related to terrestrial lifestyle. However, in order to really test this hypothesis, it appears essential to analyze a large sample including arboreal and terrestrial primates and to investigate the manipulation in trees, which involves complex postural constraints. The quantitative analyses of the overall morphology of

the trapezium and of the first metacarpal together highlight the real differences between Hominids and the functional interaction between these two bones. Indeed, the TMC complex presents a high variability according to the bone and the species, and different co-variations patterns between Hominids with some similar features between *Homo* and *Gorilla*. The co-variation between the two bones of the TMC complex is constrained by the phylogeny and by other factors (e.g. functional and developmental requirements). Manipulative abilities may also constrain the shape of these two bones, which could be very useful to infer the manipulative abilities of fossils. However, comparative approaches of the overall hand morphology of Hominids, not limited to the thumb, can provide important information on the morpho-functional relationships between hand morphology and manipulative abilities. In addition, the musculo-skeletal model shows that the different manipulative abilities of primates can be a consequence of the different mechanical constraints depending on the morphometric of the overall hand. Indeed, even if no data exist on the muscle forces capacities of each species, some grip types require a very high force intensity, which appeared as non-physiological and hardly feasible for great apes. The morphometric of the hand of some species, such as orangutans, could enhance their grip techniques during suspensory behavior at the cost of manipulation skills. This preliminary study shows the importance of studying the overall morphometric of the hand and provides a new approach to better understand the manipulative abilities of primates. Including such a biomechanical constraint analysis could improve inferences of the potential manipulative abilities of some fossils.

This new integrative approach also clearly shows that the different manipulative abilities of Hominids cannot only be a consequence of the different morphologies of the trapeziometacarpal joint but also a consequence of the different mechanical constraints related to the overall hand morphometric. All the results of this work highlight the difficulty to infer manual abilities in fossils from bone shape information, without taking into account the overall morphometric of the hand and its potential influence on biomechanical constraints. Many questions remain open, in particular on the evolution of the manipulation in humans and on the evolution of the human hand. How the hands of our early ancestors functioned? What were their manual abilities? How can we infer manual abilities in fossils? To bring new information, it appears important to carry on with this type of interdisciplinary approach.

The following work is to test the potential manipulative abilities in fossils (*A. sediba*, *H. naledi*...) by including biomechanical constraint analyses. Moreover, it would be interesting to perform simulations with more force applied on the tool, and with different sizes of the tool, in order to better understand the muscle coordination and the muscle force intensity involved during stone tool making for instance. These simulations could enable to better understand the evolution of this behavior in humans. Additionally, different morphological features are shown between modern humans and Neandertals' hands (e.g. Niewoehner, 2006), notably a flatter TMC joint in Neandertals. In order to quantify the real differences between modern humans and Neandertals, it appears important to treat intra-species variability inside the genus *Homo*. Moreover, it will be very interesting to relate the overall hand morphology of Neanderthals and the potential biomechanical constraints during the use of their microlithic tools. The use of these microlithic tools in Neanderthals appears intentional (Moncel [2004] cited in Borel et al. [2016]) but why they used these tools and how these tools could be held in the hand of Neanderthals remain unknown (Borel et al., 2016b).

In this work, I focused on the inter-species variability of the shape of the trapeziometacarpal complex and a perspective is to analyze my data in the light of a possible intra-species effect such as sex, age and the side of the bone (left or right). For example, it will be interesting to test the potential functional asymmetry effect due to the laterality, with more pressure exerted by the bones of the preferred body side (see Lazenby, 2002). It was shown that lateralization has an effect on the shape of different bones such as the humerus and the second metacarpal (e.g. Lazenby et al., 2008; Stock et al., 2013) and has also an effect on the trabecular architecture of the first metacarpal of *Pan* (chimpanzees and bonobos) and *H. sapiens* (Stephens et al., 2016). Next studies should focus on the potential effect of the lateralization on the shape and the trabecular architecture of the overall TMC complex. These kinds of analyses could be interesting in regard of the possible inference of laterality on *Homo* fossils.

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Annexes

ANNEXES

Annex A: Article

Bardo A., Borel A., Meunier H., Guéry JP., Pouydebat E., **2016**. Behavioral and functional strategies during tool use in bonobos (*Pan paniscus*). *American Journal of Physical Anthropology* **161** (1), 125-140.

Annex B: Article

Bardo A., Pouydebat E., Meunier H., **2015**. Do bimanual coordination, tool use, and body posture contribute equally to hand preferences in bonobos? *Journal of Human Evolution* **82**, 159-169.

Annex C: Abstract

Bardo A., Pouydebat E., 2015. Stratégies de manipulation d'outils lors de la tâche du labyrinthe chez les gorilles et les orangs-outans. *Revue de primatologie* (**6**) document 54. XXVIIIe Conference of the French Society Of Primatology in Strasbourg, 14-16 October **2015**.

Annex D: Abstract

Bardo A., Borel A., Guéry J.P., Lemaire M., Lempereur E., Pouydebat E., **2015**. Manipulative abilities during the same tool use task in different species of primates. *Folia Primatologica* **86** (4): 243. 6th Congress of the European Federation for Primatology Meeting in Rome, August 25-28 2015.

Annex E: Abstract

Bardo A., Borel A., Pouydebat E. Functional strategies during tool use tasks in captive bonobos. The Anthropology of Hands conference in University of Kent (UK), 24-26 June **2015**.

Annex F: Abstract

Bardo A., Borel A., Pouydebat E. Tool making and use by captive bonobos: functional & behavioral strategies. 21st Benelux Congress of Zoology in Liège (Belgium), 11-12 December **2014**.

Annex G: Abstract

Bardo A., Borel A., Meunier H., Lemaire M., Lempereur E., Guery J.P., Pouydebat E., 2015. Stratégies de manipulation d'outil chez les humains et les bonobos. *Revue de primatologie* (**6**) document 8. XXVII Conference of the French Society Of Primatology in Poitiers, 4-7 November **2014**.

Annex H: Abstract

Bardo A., Meunier H., Pouydebat E. Tool making and use by captive bonobos: behavioral strategies, efficiency and tool selectivity. 25th Congress of the International Primatological Society, Hanoi (Vietnam), 11-16 August **2014**.

Annex I: Poster

Bardo A., Pouydebat E., Cornette R. Morphological variability of the trapeziometacarpal joint among Hominids and functional involvements. IX national Symposium of Morphometric and Forms Evolution in Paris, 1-2 June **2016**.

Annex J: Poster

Bardo A., Pouydebat E. How to objectively assess the complexity of a task? 25th Congress of the International Primatological Society, Hanoi (Vietnam), 11-16 August **2014**.

Annex K: Poster

Pouydebat E., **Bardo A.**, Canteloup C., Borel A. Preliminary observation of coconut cracking open among capuchins monkeys and humans: proto tool-use costs and benefits. 25th Congress of the International Primatological Society, Hanoi (Vietnam), 11-16 August **2014**.

Annex L: Poster

Bardo A., Meunier H., Pouydebat E., **2013**. Differential manipulative strategies in great apes during a new complex tool use task. 5th Congress of the European Federation for Primatology. *Folia Primatologica* **84**, 246-247.

ANNEX A

Bardo A., Borel A., Meunier H., Guéry JP., Pouydebat E., **2016**. Behavioral and functional strategies during tool use in bonobos (*Pan paniscus*). *American Journal of Physical Anthropology* **161** (1), 125-140.

Behavioral and functional strategies during tool use tasks in bonobos

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Abstract

Different primate species have developed extensive capacities for grasping and manipulating objects. However, the manual abilities of primates remain poorly known from a dynamic point of view. The aim of the present study was to quantify the functional and behavioral strategies used by captive bonobos (*Pan paniscus*) during tool use tasks. The study was conducted on eight captive bonobos which we observed during two tool use tasks: food extraction from a large piece of wood and food recovery from a maze. We focused on grasping postures, in-hand movements, the sequences of grasp postures used that have not been studied in bonobos, and the kind of tools selected. Bonobos used a great variety of grasping postures during both tool use tasks. They were capable of in-hand movement, demonstrated complex sequences of contacts, and showed more dynamic manipulation during the maze task than during the extraction task. They arrived on the location of the task with the tool already modified and used different kinds of tools according to the task. We also observed individual manual strategies. Bonobos were thus able to develop in-hand movements similar to humans and chimpanzees, demonstrated dynamic manipulation, and they responded to task constraints by selecting and modifying tools appropriately, usually before they started the tasks. These results show the necessity to quantify object manipulation in different species to better understand their real manual specificities, which is essential to reconstruct the evolution of primate manual abilities.

KEYWORDS

grasping postures, in-hand movements, *Pan paniscus*, tool choice, tool manipulation

1 | INTRODUCTION

A high degree of manual function and ability is thought to have been a crucial adaptation in primates and a primordial element in human evolution (Susman, 1994). All primates use their hands for feeding and moving, and during social interaction. In doing so, they show different types of grasping postures and hand movements according to the species (i.e., Frigaszy, 1998; Pouydebat, Laurin, Gorce, & Bels, 2008; Pouydebat, Gorce, & Bels, 2009; Reghem, Ch eze, Coppens, & Pouydebat, 2013; Reghem, Ch eze, & Pouydebat, 2014). In this context, the human hand is traditionally considered unique in the animal kingdom based on its functional characteristics involving the use of a variety of forceful precision grips, opposing the thumb with the pads of the fingers (Napier, 1960; Marzke, 1997; Susman, 1998; Tocheri, Orr, Jacofsky, & Marzke, 2008). However, other primates such as great apes and

capuchins, use different grasping postures that are sometimes comparable to those used by humans, including the precision grip posture involving the tips of the thumb and index fingers (Christel, 1993; Jones-Engels & Bard, 1996; Marzke & Wullstein, 1996; Christel, Kitzel, & Niemitz, 1998; Byrne, Corp, & Byrne, 2001; Pouydebat et al., 2009; Pouydebat, Reghem, Borel, & Gorce, 2011). Moreover, the real dynamic manual abilities of non-human primates are not sufficiently documented to be able to conclude that human hand abilities are unique. In this context, detailed studies of manual abilities in primates are essential to better understand the functional and behavioral strategies of each species in relation with its hand morphology and ecology. These kinds of data are also needed for assessing the evolution of grasping ability in primates more generally.

Several studies have described dynamic human hand movements (i.e., Elliot & Connolly, 1984; Exner, 1992; Santello, Flanders, &

Soechting, 1998; Braido & Zhang, 2004; Bullock & Dollars, 2011) defined as “a form of precision handling in which an object is moved using the surface of the palm and the digits of one hand” (Craet, Fragaszy, Hayashi, & Matsuzawa, 2009: 274). Only a few studies have focused on non-human primates. Preliminary studies in chimpanzees (*Pan troglodytes*) showed the complexity of their dynamic manual abilities in captivity (Craet et al., 2009) and in the wild (Marzke, Marchant, McGrew, & Reece, 2015). Moreover, in non-human primates, dynamic hand abilities have been investigated mainly in chimpanzees (i.e., Boesch & Boesch, 1993; Marzke & Wullstein, 1996; Craet et al., 2009; Marzke et al., 2015) and results for other great apes are lacking. Indeed, while wild chimpanzees and orangutans (*Pongo* sp.) use different tools in a variety of contexts (chimpanzees: Goodall, 1968; orangutans: van Schaik, Fox, & Sitompul, 1996; Fox, Sitompul, & van Schaik, 1999; Bentley-Condit & Smith, 2010; McGrew, 2010; Meulman & van Schaik, 2013), there are few reported examples of tool use in wild gorillas (*Gorilla gorilla* sp.; Breuer, Ndoundou-Hockemba, & Fishlock, 2005; Kinani & Zimmerman, 2014) and bonobos (*Pan paniscus*; Hohmann & Fruth, 2003). It appears thus necessary to explore the manual abilities during tool use in different non-human primates and to focus on lesser known species such as bonobos.

Termite fishing in wild bonobos has never been observed (McGrew et al., 2007), and there is only one report of “ant harvesting tools” discovered near termite mounds (Badrian, Badrian, & Susman, 1981: 179). Bonobos thus do not appear to use tools to manipulate food in their natural environment but do use tools for social functions such as communication, play, cleaning, and protection from the rain (Ingmanson, 1996). The absence of extractive foraging in wild bonobos may be due to the small number of groups studied and/or the limited period of time dedicated to the observation (Gruber, Clay, & Zuberbühler, 2010). This is supported by the fact that studies in captivity indicated that they use a variety of objects as tools for food acquisition (Visalberghi, Fragaszy, & Savage-Rumbaugh, 1995; Boose, White, & Meinelt, 2013). Moreover, the ability to manufacture and use appropriate tools for food extraction has been demonstrated as well (Boose et al., 2013). In addition, bonobos have been shown to be able to produce stone tools in captivity (Toth, Schick, Savage-Rumbaugh, Sevcik, & Rumbaugh, 1993; Schick et al., 1999; Roffman, Savage-Rumbaugh, Rubert-Pugh, Ronen, & Nevo, 2012). Captive bonobos demonstrated the same capacity of understanding the properties of tools as other great apes do (Herrmann, Wobber, & Call, 2008) and tool use in bonobos can be as complex as in chimpanzees (Takeshita & Walraven, 1996; Gruber et al., 2010). Thus, the absence of habitual tool use in wild bonobos cannot be attributed to the lack of manual abilities (Takeshita & Walraven, 1996). Moreover, manipulation abilities in bonobos have been investigated in detail during object grasping (Christel, 1993; Takeshita & Walraven, 1996; Christel et al., 1998) but have never been examined during tool use behavior.

The aim of the present study was to quantify the functional and behavioral strategies used in captive bonobos during two different tool use tasks: a task of food extraction from a large piece of wood, and a task involving food recovery from a wooden maze (Bardo, Pouydebat,

& Meunier, 2015). Our two tasks were defined as simple tool use actions following the definition that “simple tool use includes all instances where a single tool is used to perform all actions necessary to obtain the reward” (Boesch, 2013: 25). The food extraction task was comparable to the termite-fishing task recently described for captive bonobos (Boose et al., 2013). The mazes were different from those used in previous studies focusing on spatial memory (i.e., Paul, Magda, & Abel, 2009), anxiety (i.e., Pinheiro, Zangrossi, Del-Ben, & Graeff, 2007), or virtual cognitive tasks (i.e., in macaque, Washburn & Astur, 2003). They were indeed not virtual but real and used to quantify the different strategies of manipulation in bonobos during tool use to recover food. Even if it is classified as a “simple” tool use task, we consider this task more complex than the food extraction task because it requires several steps (Parker & Gibson, 1977; Meulman & van Schaik, 2013). Indeed, the maze task requires the use of a tool to reach and recover a walnut by facing many obstacles: first, obstacles placed inside the maze to complicate the path of the walnut, and second, wire netting placed between the maze and the subject. These obstacles involved several constraints in terms of forelimb coordination, body posture adjustments, manual abilities, and vision. We expected this variability of constraints between the two tasks to influence the functional and behavioral strategies. We focused on grasping postures, in-hand movements which have never before been studied in bonobos, sequences of postures used, and the kind of tools selected. As we only focused on the process that occurred at the task location, tool manufacture and modification processes are not documented here.

We hypothesized that (a) new types of grasping postures would be observed during tool use tasks compared to those previously observed during food grasping, (b) bonobos would use in-hand movements and complex sequences of postures during both tool use tasks, but possibly with a greater variability for the maze task, (c) following Boose et al. (2013), we also predicted that bonobos would use appropriate tools according to the task.

2 | METHODS

2.1 | Subjects and housing

The study was conducted from February 1, 2012 to April 18, 2012 at the “Vallée des singes” (France). A group of nine captive bonobos (five females and four males) from 4- to 43-year old (15.88 ± 4.12 years) was observed. According to the age classes of bonobos defined by Kano (1982), our group was composed of two adult females, two adult males, two adolescent females and two adolescent males. One juvenile female (4-year old), Nakala, had not yet included tool use in her behavioral repertoire and was excluded from the analyses. The bonobos were housed in an indoor building consisting of a network of eight cages from 30 to 98 m² with a height of 3 to 6 m (the two larger cages were visible to the public while the six smaller cages were not). Several climbing structures were present in each of the cages. This indoor building was connected to an outdoor island with grass and mature trees. However, bonobos could not access this island in February and March. They could go to the island in April, during the afternoon only.

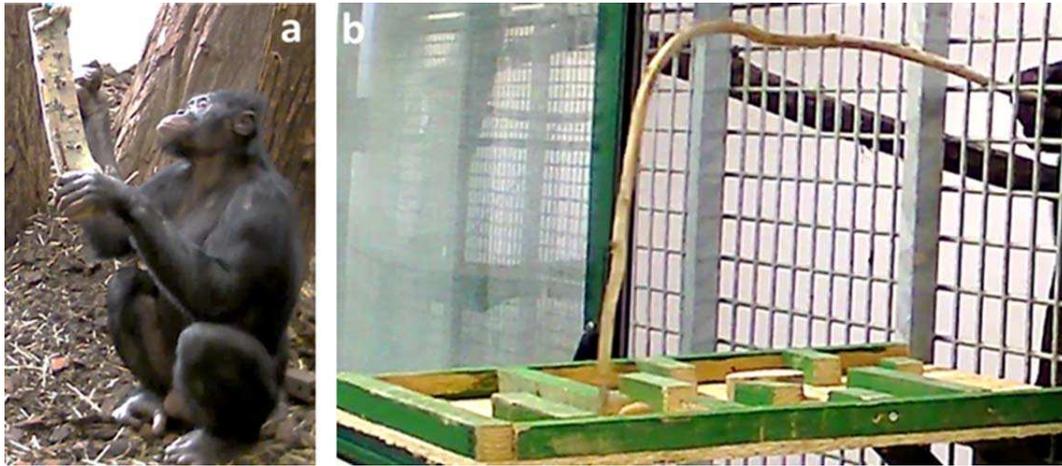


FIGURE 1 Testing situation: (a) food extraction task and (b) maze task. Subject in (a) is holding the log with one hand and holding a stick in an extended transverse hook grasp with the other hand. The subject in (b) is holding a curved tool with one hand with a thumb lateral grasp combined with a passive use of the palm

Water was available *ad libitum* in their pens and they were fed four times a day. The food used for our protocol was part of the daily diet. All subjects were tested within their social group, in cages not visible to the public. Before our study, this group already had experience with food extraction tasks.

2.2 | General procedure

Tree branches of different lengths and shapes (maximum length of 3 m) were provided at the beginning of the experimental period and were freely available to bonobos as raw material for potential tools. Thus, bonobos could manufacture and modify their tools freely. The tools manufactured by bonobos were not discarded during the experimental period and were left in the cages. One task was conducted per day in the morning and lasted until the food was consumed (around 30 min for both tasks). Two cameras (Sanyo® Xacti VPS-HD2000), one fixed and one mobile, were used during the experiments to optimize the recording and obtain detailed data of hand use. Videos were recorded at 60 frames/sec. These recordings were conducted for the study of Bardo et al. (2015) on the hand preferences of bonobos, and in the present study we used the videos to quantify the tool use process.

2.3 | Experimental tasks

2.3.1 | Task 1: Food extraction

Twelve logs (mean length = 53.25 ± 2.90 cm and mean diameter = 9.17 ± 0.88 cm) with 10 holes (1.5 cm in diameter) drilled all around and over their entire length were hung vertically inside the cage (see Figure 1a). The logs were hung at different heights and were placed in every cage to avoid social tensions. Sticky food (fruit puree) was placed inside the holes. Subjects had to use a tool with one hand to be able to extract the food and visual guidance was required to insert the tool into the holes. The other hand was placed on the log or on the bars of the cage. Eleven test sessions were conducted with one session per

day and each subject was observed between five and nine days (mean = 6.87 ± 0.58). The eight subjects performed the task. Some subjects were more rapid to extract food than others, or accessed the logs more easily, so we decided to use a focal sampling method of 2 min (defined here as a sequence). This method was used to ensure an approximately similar number of events between subjects. We decided to record data with the frequencies technique (i.e., Hopkins, 1995), in which each food extraction event is recorded, and not the bout technique in which only the first pattern of a series of identical actions is recorded (i.e., Marchant & McGrew, 1991). Using the frequencies technique allowed us to not lose information on in-hand movements. Food extraction events were recorded if the bonobos were seated. One event was counted each time a subject inserted the tool into a hole, removed it from the hole, and brought it to its mouth with one hand (without bimanual coordination). The parameters observed during each event were the grasping posture, in-hand movements for repositioning the tool within one hand (surface of the palm and the fingers), tool selectivity with the types of tool used (length, diameter, and shape). We recorded 564 events (mean = 70.5 ± 7.47 per subject) of extraction.

2.3.2 | Task 2: The maze

This task consisted of reaching walnuts positioned on a wooden maze (45 cm wide by 60 cm long) with a tool. The mazes were attached to the wire mesh of the cage (size = 5×5 cm) but hung outside the cage (see Figure 1b). To avoid competition and social tension, nine different mazes were placed simultaneously around the cages. These mazes differed in the shape, position, and size of the wooden obstacles. These differences provided different potential spatial adjustment of the walnuts inside each maze. In the study on the hand preferences of bonobos by Bardo et al. (2015), authors observed social pressure or competition during the maze task. Individuals preferred to visit mazes with simple spatial adjustment over more complex mazes. Thus, in this present study, we decided to focus on a specific maze (Figure 1b). This maze constituted a good compromise in term of complexity to observe

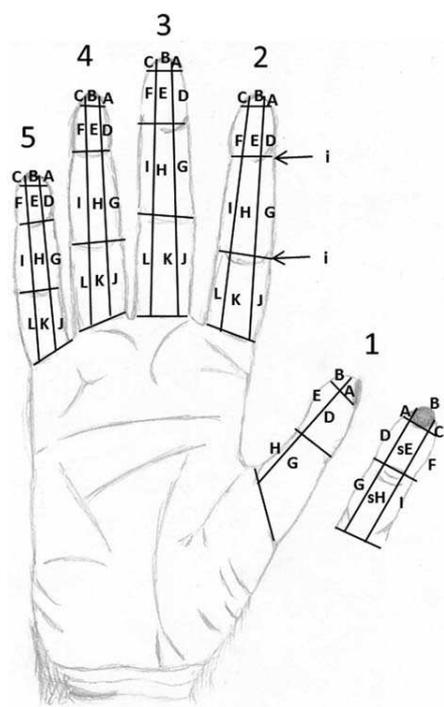


FIGURE 2 Right hand of a Bonobo with the code used for each contact area (Adapted from “Sequence analysis of Grip and Manipulation During Tool Using Tasks: A New Method to Analyze Hand Use Strategies and Examine Human Specificities,” by A. Borel et al., 2016, *Journal of Archaeological Method and Theory*, p. 1.) and with the right thumb in dorsal view. A contact area is indicated with the first letter of the hand (R for right or L for left), the number of the finger and the letter(s) of the contact area (i.e., R1E.2G). For dorsal contact, we added the letter “s” before the letter of contact area (i.e., 2sH for the dorsal area of the middle phalange of the index finger). For interphalangeal contacts, we added the letter “i” between the two letters of phalanx (i.e., 2DiG for contact with the distal interphalangeal joint of the index finger)

a maximum of subjects. This was also a pragmatic choice as the structure of the building did not allow us to film all the mazes at the same time. The maze was positioned 30 cm from the ground to constrain bonobos to a seated posture. It was composed of 11 wooden obstacles of different shapes and sizes. The walnuts were placed at the end of the maze (60 cm away from the subject). Among our eight subjects, a young male (Kelele) never succeeded to access the maze and one male (David) succeeded in reaching the maze only once, restricting the analysis to six subjects only. Three sessions per individual were recorded, one session corresponding to when a subject reached one walnut. On average 2.17 ± 0.31 days were necessary to get the data of one individual. A sequence began when a subject started to go through the maze with the walnut and ended when it could reach the walnut by hand. In addition to the different parameters observed for the food extraction task, during each session we counted the number of hand movements used to reach the walnut (quantified by wrist movements), the number of touched wooden obstacles (placed inside the maze), and the time to reach the walnut and the number of position changes of the tool in the grid. We recorded an event each time a subject moved

its fingers (i.e., displacements), stopped moving the tool for more than 20 s, and when a subject changed the position of the tool in the grid. Among all subjects and for all sessions, we recorded a total of 95 events.

2.4 | Classification system

First, we characterized the strategies of tool grasping using a method recently implemented by Borel, Chêze, and Pouydebat (2016). Each grasping posture was characterized by a combination of hand contact areas with the tool and defined following the anatomical terminology (see Figure 2). To name the grasping postures, we used the Marzke’s typology of grasp (Marzke & Wullstein, 1996; Marzke et al., 2015) and we divided the grasp types into five categories (Table 1):

- *Category 1*: contact between distal phalanges of the thumb and the index finger. This category corresponds to the category called “precision grip” in Jones-Engels and Bard (1996) and “Thumb-index grips” in Pouydebat et al. (2011).
- *Category 2*: contact between the distal phalanx of the thumb, the lateral side of the middle, proximal phalanges of the index finger and the tool. This category included the grasping postures called “thumb lateral” in Pouydebat et al. (2011).
- *Category 3*: contact between one or several fingers, except the thumb, and the tool, called “without thumb” in Pouydebat et al. (2011).
- *Category 4*: contact involving palm, the thumb and one or several part of other fingers and the tool, involving the power grasping posture (Napier, 1956; Jones-Engels & Bard, 1996), and called “palm grips” in Pouydebat et al. (2011).
- *Category 5*: contact types which fell outside the above categories, involving the “hook grip” in Napier (1956) and called “other grips” in Jones-Engels and Bard (1996).

2.5 | Data analysis

Video analysis was performed with VLC® media player using a focal sampling protocol (Altmann, 1974). For multiple comparisons, we used the Friedman chi-squared test and for pairwise comparisons the Wilcoxon signed-rank test, with continuity correction for the maze task as we analyzed a small sample ($N = 6$). We performed statistical tests in the software R (R Development Core Team, 2013). Tests were two-tailed with a significance level set at 0.05.

Time-based sequence analysis was used to quantify and visualize the combinations of the contact areas between hand and tool during tool use tasks. The combinations of the contact areas, with the time associated were exported to the software R (R Development Core Team, 2013) and Time-based sequence analysis were performed with the package TraMineR (Gabadinho, Ritschard, Mueller, & Studer, 2011) modified by Borel et al. (2016).

To describe the strategies used during the maze task on all the sessions ($N = 18$), a Principal Component Analysis (PCA) was performed

TABLE 1 Variability of the grasping postures used to hold a tool during the two tasks and the number of events by task

Category of grasping postures	Grasping postures name	Acronym	Description	Number of observations by task	
				Task 1	Task 2
Thumb-index grips	Two-jaw chuck ^a pad-to-pad side	2JCPPS	Tool held between pad of the thumb and side of the pad of the index finger.	N = 8/564	-
	Two-jaw chuck thumb-to-index	2JC	Tool held between pad of the thumb and the ventral part of middle phalanx of the index finger.	N = 4/564	-
Thumb lateral	Two-jaw chuck tip-to-side	2JCTS	Tool held between tip of the thumb and the side of the index finger.	-	N = 2/95
	Two-jaw chuck pad-to-side ^b	2JCPS	Tool held between pad of the thumb and the side of the index finger.	N = 165/564	N = 9/95
Without thumb	Two-jaw chuck proximal-to-side	2JCPrs	Tool held between proximal phalanx of the thumb and the side of the index finger.	N = 2/564	-
	Scissor hold ^c	SH	Tool held between fingers 2-3.	-	N = 2/95
	3-jaw chuck	3JC	Tool held by flexed fingers 2-3 and between the side of finger 4.	N = 48/564	-
Tool held between flexed fingers 2-3 and the proximal phalanx of finger 5.			-	N = 1/95	
With palm	Thumb lateral with palm	P2JCPS	Tool held between thumb and index finger with passive contact of the palm with the tool.	N = 34/564	-
	Power grip	P	Tool held in opposition between the palm and flexed fingers with a possible pressure applied by the thumb.	-	N = 2/95
Other grips	V pocket ^c	VP	Tool held in web between full thumb and index finger, other fingers were flexed but not in contact with the tool.	N = 103/564	-
			3-jaw chuck with thumb	T3JC	Tool held between the middle phalanges of fingers 2-3 and with a pressure applied by the thumb.
			Tool held between the distal part of the thumb and the palmar aspect of the middle phalanx of fingers 2-3.	-	N = 4/95
			Tool held by flexed fingers 2-3 and with counter pressure applied by the thumb.	-	N = 4/95
			Tool held by lateral and distal part of the thumb, flexed index, and lateral aspect of finger 3.	-	N = 9/95
			Tool held by lateral and distal part of the thumb and between flexed fingers 2-3.	-	N = 1/95
Hook grasping postures	Transverse hook ^b	TH	Tool held by all fingers flexed at interphalangeal joints, the thumb may be adducted or opposed, and the distal part of the palm was not involved.	N = 90/564	N = 11/95
	4-jaw chuck transverse hook	4JCTH	Tool held by fingers 1-2 and 4-5 flexed at interphalangeal joints; finger 3 was straight, and the distal part of the palm was not involved.	N = 3/564	-
			Tool held by fingers 1-4 flexed at interphalangeal joints, and the distal part of the palm was not involved. Contact with any part of phalanx of fingers 1-3 and the side of the middle phalanx of finger 4	N = 45/564	-
	Extended transverse hook ^b	ETH	Tool held by all fingers flexed at all joints and the distal part of the palm was involved.	N = 8/564	N = 30/95
	4-jaw chuck extended transverse hook	4JCETH	Tool held by fingers 2-5 flexed at all joints, the thumb may be adducted or opposed, and the distal part of the palm was involved.	N = 9/564	-
	Diagonal hook ^b	DH	Tool held by decreasingly flexed distal fingers 5-1; the distal part of the palm was not involved.	-	N = 10/95
Extended diagonal hook ^b	EDH	Tool held by decreasingly flexed full fingers 5-1; the distal part of the palm was involved.	-	N = 8/95	

^a“X-jaw chuck” typology of Marzke et al. (Marzke & Wullstein, 1996; Marzke et al., 2015) refers to the number of fingers, X, that clamp an object.

^{b,c}The grasping postures are named and are described for chimpanzees in ^b Marzke and Wullstein (1996) and ^c in Marzke et al. (2015).

on six variables (P): the number of in-hand movements, the number of combinations of contacts areas, the number of hand movements used to reach the walnut, the number of touched wooden obstacles, the

time to reach the walnut, the number of position changes of the tool in the grid. PCA was performed in R (R Development Core Team, 2013), with the raw data normalized for all the sessions of all subjects.

TABLE 2 Percentages of grasping postures used for each subject during the food extraction task

Grasping postures ^a	Daniela	Ukela	Kirembo	Diwani	David	Khaya	Lingala	Kelele
2JCPS	8	26	6	36	8		90	22
TH	21	69	1	1				55
T3JC			10			100		
VP	37				82		10	20
ETH			6	1	3			
3JC			31	24				
P2JCPS	34			15				
4JCTH			45	10				
2JCPPS		6			5			
2JCPrxS					1			2
4JCETH				10				
2JC				2				

^a2JCPS = Two-jaw chuck pad-to-side; TH = Transverse hook; T3JC = 3-jaw chuck with thumb; VP = V pocket; ETH = Extended transverse hook; 3JC = 3-jaw chuck; P2JCPS = Thumb lateral with palm; 4JCTH = 4-jaw chuck transverse hook; 2JCPPS = Two-jaw chuck pad-to-pad side; 2JCPrxS = Two-jaw chuck proximal-to-side; 4JCETH = 4-jaw chuck extended transverse hook; 2JC = Two-jaw chuck thumb-to-index.

3 | RESULTS

3.1 | Grasping postures and combinations of contact areas

A total of 17 grasp types were observed during the two tasks with different variants for some grasp types (Table 1).

3.1.1 | Task 1: Food extraction

We recorded a total of 564 grasping events. Except for Khaya, who used only one grasp type, subjects used from two to eight grasp types (mean = 4.71 ± 0.75) (Table 2). Grasps for which bonobos used their thumbs and index fingers in varying combinations of contact areas (Figure 3) accounted for 50% of all events (282/564). Subjects used their full palm passively (the tool was just in contact with the palm which did not firmly grasp it) combined with a thumb lateral grasp in 6% of cases (34/564), and the distal palm in 3% (17/564) during extended transverse hook grasps and 4-jaw extended transverse hook grasps.

We recorded a total of 37 combinations of contacts areas (see Figure 2 for the method to quantify these combinations) and 81.1% ($N = 30/37$) of these combinations were used by only one individual. Each subject used between one and 12 (mean = 6.38 ± 1.35) different combinations of contacts areas.

The four males used more combinations of contact areas (mean = 8.75 ± 1.88) and various grasp types (mean = 6 ± 0.91) than the four females (combinations, mean = 4 ± 1.08 ; grasping postures, mean = 2.5 ± 0.64).

3.1.2 | Task 2: Maze

We recorded a total of 95 grasping events. Except for Khaya, who used only one type of grasp, subjects used from two to four grasp types (mean = 2.83 ± 0.54) during the total of the three sessions. During one session they used on average 1.28 ± 0.14 grasp types. Compared to the food extraction task, individuals during the maze task used more hook grasping postures (Table 1). Some postures were only

used by one individual and very few individuals used more than one preferred grasp type (Table 3).

We recorded a total of 32 combinations of contact areas, and 31 combinations were used by only one subject, indicating strong intra-variability. Subjects used between three and nine different combinations of contact areas (mean = 5.5 ± 0.99).

The four females used on average more combinations of contact areas (mean = 6.5 ± 1.19) than the two males (see methods section for

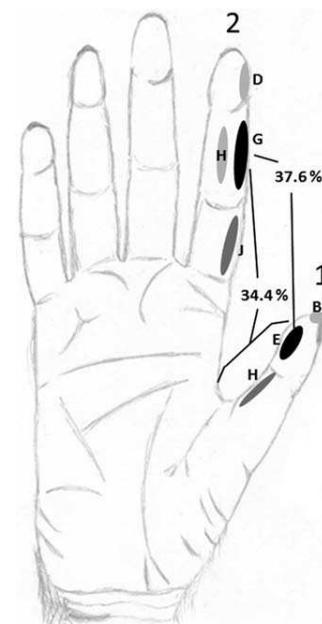


FIGURE 3 Combination of contact areas between the thumb and the index for the food extraction task, whether for the right or left hand. At the group level, the more the area is dark the more this area was used. For example, the two main combinations were 1E.2G and 1EH.2G, corresponding respectively to the Two-jaw chuck pad-to-side and the V pocket grasping postures

TABLE 3 Percentages of grasping postures used for each subject during the maze task

Grasping postures ^a	Daniela	Ukela	Kirembo	Diwani	Khaya	Lingala
T3JC	11		22	67	100	
TH	3	26	44			
DH		35		33		
2JCPS		4				80
EDH		35				
ETH	81					
3JC			11			
2JCTS						20
SH			22			
P	5					

^aT3JC = 3-jaw chuck with thumb; TH = Transverse hook; DH = Diagonal hook; 2JCPS = Two-jaw chuck pad-to-side; EDH = Extended diagonal hook; ETH = Extended transverse hook; 3JC = 3-jaw chuck; 2JCTS = Two-jaw chuck tip-to-side; SH = Scissor hold; P = Power grip.

explanation about less males observed for this task (mean = 3.5 ± 0.5) while both used similar number of grasp types (mean for females = 2.75 ± 0.75 ; mean for males = 3 ± 1).

3.2 | Dynamic tool manipulation: in-hand movements and sequences of contact areas

We quantified 10 in-hand movements and combinations of in-hand movements in this research (defined in Table 4).

3.2.1 | Task 1: Food extraction

We observed in-hand movements only five times during the 564 grasping events. Three kinds of in-hand movements were observed: roll (ROL; used one time by Daniela), thumb extension and flexion (T.EF; used one time by Daniela and two times by Diwani), and extension and flexion of all fingers (EF; used one time by David).

TABLE 4 Definition of the different in-hand movements and their combinations to reposition the tool in the hand observed during the two tasks

Type	Definition
Extension and Flexion (EF) Thumb adduction (TAD) ^a Thumb extension and flexion (T.EF)	<i>Finger movements</i> Opening and closing all fingers (EF), moving away from midline of the hand and the tool slides along the fingers or palm. <i>Thumb movement alone moves tool</i> Thumb moves toward midline of the hand.
Index abduction (IAB) ^a Index extension and flexion (I.EF)	<i>Index movement alone moves tool</i> Index moves away from midline of the hand.
Roll (ROL) ^a	<i>Tool held between two digits</i> Fingers move opposite to one another to twist or roll the tool along one axis.
Extension and Flexion of fingers and Thumb abduction/adduction (EF.TAB/EF.TAD)	<i>Combination of in-hand movements</i> Opening and closing fingers 2 to 5 and thumb moves away (TAB) or toward the midline of the hand (TAD).
Extension of all fingers, releases the tool and takes it later (E.REL)	Opening fingers moving away from the midline of the hand which releases and grasps the tool again.
Extension of all fingers and help of the second hand to repositioning tool (E.H)	Opening fingers moving away from midline of hand; the object slides along the fingers or palm and the second hand helps to repositioning the tool in the hand.

^aNamed and defined in Crast et al. (2009).

During the sequences of extraction, we observed few changes of contact areas between the tool and the hand. Five subjects (four males and one female) changed their contact areas during two or three sequences of extraction (mean = 2.6 ± 0.63). The female (Daniela) just combined the palm with a thumb lateral grasp during two sequences (N total = 6). Males changed their combinations of contact areas between two and four times during one sequence (mean = 2.45 ± 0.21). They also changed the number of fingers placed on the tool, inducing more changes in grasp types than Daniela.

3.2.2 | Task 2: Maze

We recorded a total of 77 in-hand movements events classified in 10 different types (as defined in Table 4). We did not observe statistically significant differences in the number of in-hand movements used between the three sessions (Friedman rank sum test, $Q = 9.5146$, $df = 5$, $p = .09$). Of the six subjects observed for this task, all used in-hand movements. Some movements were not used in every session or by every subject, and some movements were applied between two and five subjects (see Table 5). The in-hand movement applied most by all subjects except Kirembo was T.EF (Table 5). The two oldest females, Daniela and Ukela, used more in-hand movements during the three sessions as well as on average than other subjects (Table 5). Daniela used more different types of in-hand movements ($N = 8/10$) than other subjects. We also noticed that Lingala adjusted the tool in her hand using her lips and Ukela used a foot. This occurred only one time in one session for both subjects.

More changes of combinations of contact areas between hand and tool were observed during a single session for this task (Figure 4) than for food extraction. It was the two adult females which changed more often their combinations of contact areas (nine times for Ukela and six times for Daniela during the first session) (Figure 4). The other subjects changed between zero and two times during one session (Figure 4). Daniela put the most time to reach the walnut (152 s) and Kirembo the least amount of time (20 s) (Figure 4). Females got the walnut on

TABLE 5 Details of in-hand movements used by session (S) by each subject and the mean number of in-hand movements (with standard errors) during one session by each subject

In-hand movements	Daniela			Ukela			Kirembo			Diwani			Khaya			Lingala				
	S1	S2	S3	S1	S2	S3	S1	S2	S3	S1	S2	S3	S1	S2	S3	S1	S2	S3		
	Mean and SE			Mean and SE			Mean and SE			Mean and SE			Mean and SE			Mean and SE				
EF	4	8	8	6.67 ± 1.33	9	5	3	5.67 ± 1.76	2	0	0	0.67 ± 0.67	-	-	-	-	-	-	-	
TAD	1	0	0	0.33 ± 0.33	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
T.EF	4	0	1	1.67 ± 1.2	1	2	2	1.67 ± 0.33	-	-	-	1	1	1	1 ± 0	0	0	1	0.33 ± 0.33	
IAB	-	-	-	-	1	0	0	0.33 ± 0.33	0	1	0	0.33 ± 0.33	-	-	-	-	-	-	-	
I.EF	0	0	1	0.33 ± 0.33	-	-	-	-	-	-	-	-	-	-	-	1	1	3	1.67 ± 0.67	
ROL	0	2	0	0.67 ± 0.67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
EF.TAB	2	1	0	1 ± 0.58	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
EF.TAD	1	0	0	0.33 ± 0.33	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
E.REL	-	-	-	-	-	-	-	-	0	2	1	1 ± 0.58	-	-	-	2	0	0	0.67 ± 0.67	
E.H	0	1	0	0.67 ± 0.67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Total	12	12	10	11.33 ± 0.67	11	7	5	7.67 ± 1.76	2	3	1	2 ± 0.6	1	1	1	1 ± 0	3	1	4	2.67 ± 0.88

Notes: In-hand movements are described in Table 2. EF = Extension and Flexion; TAD = Thumb adduction; T.EF = Thumb extension and flexion; IAB = Index abduction; I.EF = Index extension and flexion; ROL = Roll; EF.TAB = Extension and Flexion of fingers and Thumb abduction; EF.TAD = Extension and Flexion of fingers and Thumb adduction; E.REL = Extension of all fingers, releases the tool and takes it later; E.H = Extension of all fingers and help of the second hand to repositioning tool.

average in 102.75 ± 10.80 s with 119.33 ± 14.04 s for adult females and 86.16 ± 14.37 s for adolescent females. Adult males took on average 70.5 ± 15.70 s.

3.3 | Tools selected

Subjects arrived on the location of the task with their tool already modified in 99.47% of the cases for the food extraction task ($N = 561/564$) and in 83.33% of the cases for the maze task ($N = 15/18$). For the six events of modifications, we observed five individuals who used two techniques. Four individuals grasped the tool with one hand and used their mouth to break the tool thereby shrinking it, and one individual for two events used both hands to break the tool and its mouth to peel bark.

As every tool was different, we classified the tools according to their length, shape, and diameter. Two types of tool shape were identified: curved (see Figure 1b) and straight. For the diameter, tools were classified in two categories: the fine tools with a diameter of less than 1 cm and the coarse tools with a diameter greater than 1 cm. The diameter of the tool did not seem to have a significant effect on the number of fingers used to grasp the tool (for tests with 2 to 5 fingers, Friedman rank sum tests, $N = 8$, $p > .05$).

3.3.1 | Task 1: Food extraction

Subjects used six tools lengths between 10 and 60 cm. No particular length was preferred (Friedman rank sum test, $N = 8$, $Q = 4.1528$, $df = 7$, $p = .76$). However, it seemed that they used more small tools (i. e., less or equal than 30 cm long; $N = 439/564$) than long tools (i. e., more than 30 cm; $N = 125/564$). They used significantly more straight tools (97.2%; $N = 548/564$) than curved tools (2.8%; $N = 16/564$) (Wilcoxon rank sum test with continuity correction, $N = 8$, $W = 0$, $p < .001$). We observed two types of tool tips, "brush tip" and "pointed tips," which were significantly more used (73.05%; $N = 412/564$) than straight tips (26.95%; $N = 152/564$) (Wilcoxon rank sum test with continuity correction; $N = 8$, $W = 59$, $p < .01$). Considering the diameter of the tools, bonobos used significantly more fine tools ($N = 527/564$) than coarse tools ($N = 37/564$) (Wilcoxon signed rank test, $N = 8$, $W = 36$, $df = 7$, $p < .01$).

3.3.2 | Task 2: Maze

We recorded 18 tools differing by their shape, size, and diameter were used by the bonobos. Curved tools (see Figure 1b for an example of curved tool) were used in 66.7% ($N = 12/18$) but were not used statistically significantly more than straight ones (33.3%; $N = 6/18$) (Wilcoxon rank sum test with continuity correction, $N = 6$, $W = 5$, $p = .28$). We observed that all subjects used curved tools and three individuals (Daniela, Ukela, and Diwani) spontaneously chose this type of tool at the beginning (first session). More subjects used curved tools during the third session (Daniela, Ukela, Diwani, Kirembo, and Khaya). Daniela and her son Diwani used curved tools in each session while the others changed between sessions.

We observed two types of length, long tools (more than 60-cm long; 60 cm being the length of the maze) and short tools (less or equal

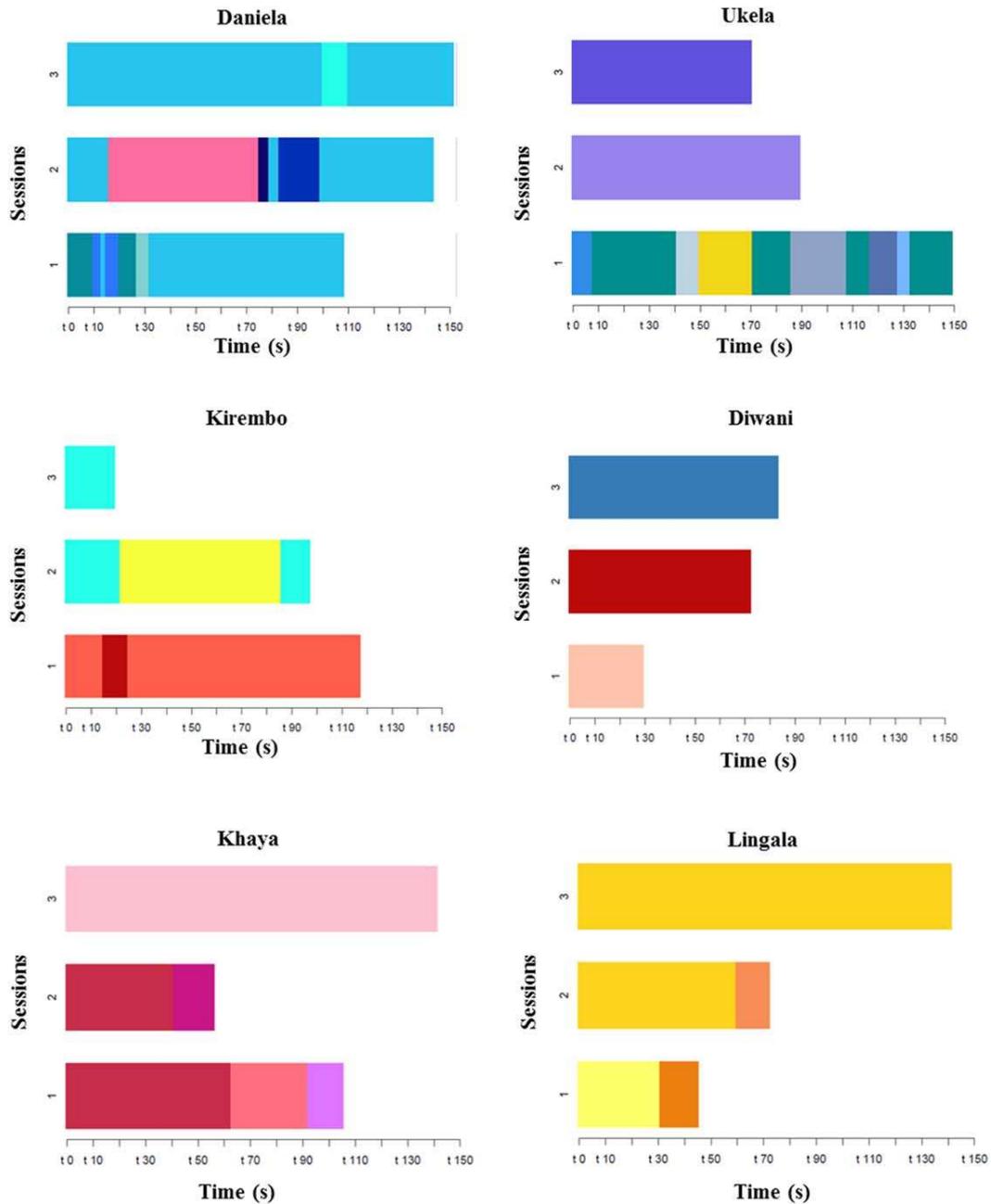


FIGURE 4 Sequences of combinations of contact areas used by each subject and by session for the maze task. Each color corresponds to a specific combination of contact areas (for example the blue in session three of Daniela corresponds to the combination R1E.2EHK.3EHK.4EHK.5EH)

than 60-cm long). Subjects used significant more long tools (77.8%; $N = 14/18$) than short tools (22.2%; $N = 4/18$) (Wilcoxon signed rank-test with continuity correction, $N = 6$, $W = 0$, $p = .03$). We observed three types of tool tips; “pointed tips” (55.6%; $N = 10/18$), “large tips” (22.2%; $N = 4/18$), and “straight tips” (22.2%; $N = 4/18$). No significant statistical differences between these three types of tips were noticed (Friedman rank sum test, $N = 6$, $Q = 0.3846$, $df = 5$, $p = .99$). Considering the diameter of the tools, they used significantly more coarse tools ($N = 16/18$) than fine tools ($N = 2/18$) (Wilcoxon signed rank test with continuity correction, $N = 6$, $W = 0$, $df = 5$, $p < .05$).

3.4 | PCA for the maze task

For the three sessions, subjects needed an average of 35.28 ± 3.32 hand movements to get the walnut. They touched obstacles on average 6.17 ± 0.94 times. They changed the placement of tools in the grid on average 5.67 ± 1.82 times.

The three first axes of the PCA performed on the raw data explained 89% of the total variance. The first axis (44%) was determined by time needed to retrieve the walnut (loading = 0.49), the number of repositioning movements (loading = 0.47), the number of in-

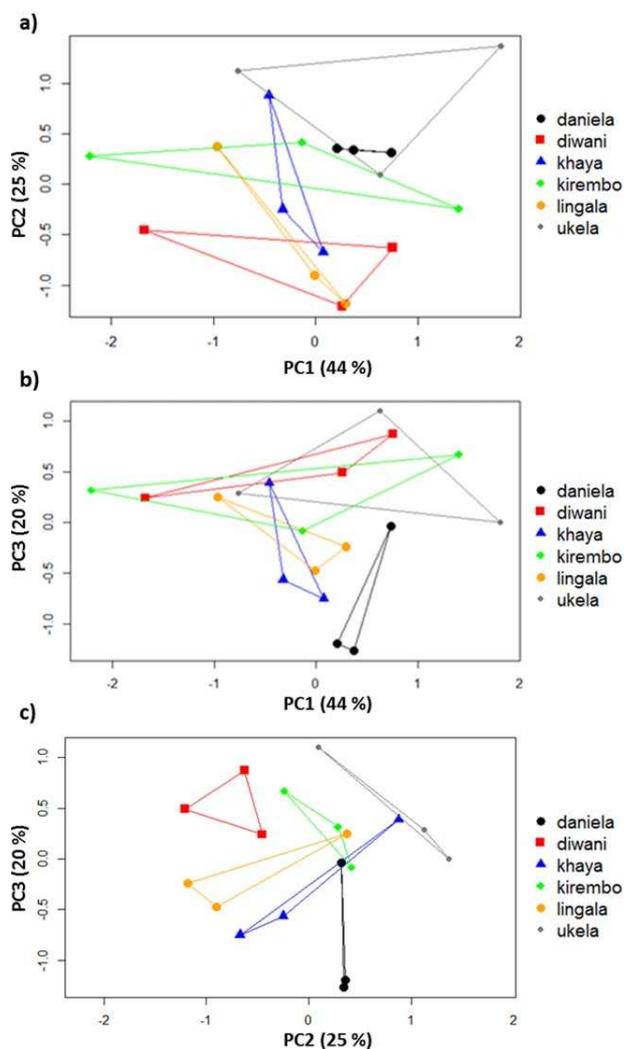


FIGURE 5 Results of the three first axes (PC1, PC2, PC3) of a PCA performed on six variables, with all the data for all the sessions of all individuals. Polygons represent individuals and points sessions. PC1 distinguished sessions within each subject; sessions situated along the positive side of PC1 took more time, more repositioning movements, more in-hand movements and overall hand movements than sessions situated along the negative side of this axis. PC2 attempted to distinguish subjects based on their strategies; subjects situated along the negative side of PC2 touched more obstacles and repositioned their tool more than subjects situated along the positive side of this axis. PC3 also attempted to distinguish between subjects, but mainly separated two sessions of Daniela from all other sessions; sessions situated along the positive side repositioned their tool more and used fewer combinations of contact areas than subjects situated along the negative side of this axis

hand movements used (loading = 0.45), and the total number of hand movements used (loading = 0.35). The second axis (25%) was explained by the total number of obstacles touched (loading = 0.81) and the number of repositioning movements (loading = 0.39). The third axis (20%) was determined by the number of tool repositioning in the grid (loading = 0.74) and the total number of combinations of contact areas used (loading = 0.57). The PCA distinguished between the different

strategies observed for each subject and for some subjects between them (Figures 5a–5c). PC1 attempted to distinguish sessions within each subject. Sessions situated along the positive side of PC1 took more time, more repositioning movements, more in-hand movements, and overall hand movements than sessions situated along the negative side of this axis (Figure 5a). These results indicated intra-individual variation in the strategies used by each subject for these four parameters, except for Khaya and Daniela who seemed to be rather standardized in their strategies with less variation between sessions than other subjects. PC2 attempted to distinguish subjects by their strategies and the differences in the number of obstacles touched and the number of repositioning movements. Subjects situated along the negative side of PC2 touched more obstacles and repositioned their tool more than subjects situated along the positive side of this axis (Figure 5b). These results indicated inter-individual variation in the general strategies used, with specific strategies observed for the four adults with respect to the number of obstacles touched and the number of repositioning movements. Khaya and Lingala seemed not to use stable strategies and showed strong variability between sessions. PC3 attempted to distinguish sessions and subjects but mostly distinguished two sessions of Daniela from all the other sessions. Sessions of the subjects situated along the positive end of the axis were performed with more tool repositioning and fewer combinations of contacts used than sessions situated along the negative side of this axis (Figure 5c). We suggest that each individual can perform the task differently according to the grasp type that they use.

4 | DISCUSSION

Our study revealed three major findings regarding tool manipulation in bonobos. First, bonobos used a great variety of grasp types during tool use tasks. Second, bonobos used in-hand movement, demonstrated complex sequences of contacts, and showed more dynamic manipulation during the maze task than during the extraction task. Finally, they responded to task constraints by selecting and/or modifying tools appropriately, usually before they started the tasks. Our results also indicated that bonobos showed individual manual strategies. These results make this study useful and compelling in spite of our small sample size and show new insights into both functional and behavioral manipulative abilities and possible morphological correlates with these abilities. The following discussion considers the implications of our findings with regard to the specific tasks of the bonobos, the individual differences observed, and the evolution of manual abilities in primates.

4.1 | New grasping postures and functional links

In accordance with our first hypothesis, new grasp types in captive bonobos were observed. In previous studies, respectively four (Christel, 1993) and seven (Christel et al., 1998) variants of grasp types between thumb and index finger were observed. During the two tool tasks, we also observed a grasp type between the thumb and index finger with nine variants but little implication of the tip of the thumb. The two-jaw

chuck pad-to-side grasp type was the most observed in this group of captive bonobos during the food extraction task. This observation is consistent with previous research on herbaceous termite or ant fishing in chimpanzees (i.e., Lesnik, Sanz, & Morgan, 2015; Marzke et al., 2015), and this grip was also used by wild chimpanzees for perforating the opening of a termite nest (Lesnik et al., 2015).

One variant of the 3-jaw chuck with thumb, where the tool was held between the middle phalanges of fingers 2–3 and with pressure applied by the thumb, was observed recently for the first time in wild chimpanzees (Lesnik et al., 2015). Lesnik et al. (2015) called this grasp type “interdigital brace” and in human studies it is defined as an inefficient variant of pencil grasp (Selin, 2003). These authors ranked this grip as being more powerful than the two-jaw chuck pad-to-side grasp type because “it is the bracing of the tool against the hand that gives the grip its greatest strength” (Lesnik et al., 2015: 256). In our study, only one subject (Khaya) used this grasp all the time during the two tasks. Perhaps for bonobos this is not an efficient grasp type for these tasks.

All of the grasp types observed here were also reported in captive and wild chimpanzees for diverse activities such as tool use (Jones-Engels & Bard, 1996; Lesnik et al., 2015; Marzke & Wullstein, 1996; Marzke et al., 2015; Pouydebat et al., 2011). Similar to these previous studies, we observed different grasp types and a tendency to use different grasp types according to the demand of the task. More hook grasp types were observed during the maze task than for extraction. Hook grasps were used by wild chimpanzees during feeding (Marzke et al., 2015) or tool use (Lesnik et al., 2015), and also gorillas during feeding (i.e., Byrne, 1994). It appears that this grasp type with the fingers flexed around the tool applies more force, increasing the force exerted on the tool allowing to push the walnut more efficiently. We suggest that hook grasps might be more efficient than grasp types between the thumb and index finger for the maze task and subjects that used more power than precision succeeded in the maze task more often. Moreover, grasp types between the thumb and the index finger, including the two-jaw chuck pad-to-side grasp, may be more efficient for extraction. In fact, food extraction involved the extraction of food from a small hole with a relatively fine tool, which likely involves more precision during the manipulation. It also appeared that the V pocket grasp type, where the tool was held between the web of the thumb and index finger, was effective during food extraction. The use of the web between the full thumb and index finger could help to stabilize the tool during precise extraction. Moreover, some grasp types, like the scissor hold (tool grasp between fingers 2–3), were used less by bonobos during the maze task. This grip was completely absent during food extraction. Thus, grasp types differed according to the demand of the task.

4.2 | Grasping postures and hand morphology

The reason for the rare use of the thumb’s tip in bonobos performing the two tool use tasks could be due to the shape of the tool. The cylindrical tool needs to be firmly grasped between the fingers, and the distal parts of the fingers are rolled around the tool. It also could be

explained by the fact that bonobos need, when the thumb is involved, all the phalanges and not only the distal one to firmly grasp the tool. Indeed, bonobos used the thumb to hold the tool in general in an opposed position to other fingers which maintained the tool in the hand. The use of the thumb in opposition to other fingers in chimpanzees was explained by the transverse portion of the intrinsic thumb adductor muscle which was well-developed compared to humans (Marzke et al., 1999).

The reason for the rare use of the thumb in bonobos performing the maze task could also be due to the absence of several anatomical features. It appears that some human hand muscles are not present in the hands of great apes (Diogo & Wood, 2011; Diogo, Richmond, & Wood, 2012). Especially two thumb muscles, the *flexor pollicis longus* and *extensor pollicis brevis* which are related to the movement of the thumb and probably important in human tool manipulation (Diogo et al., 2012). These two muscles are only rarely present in great apes (as hylobatids) (Diogo & Wood, 2011; Diogo et al., 2012; Myatt et al., 2012). As the maze required forceful grips from the fingers on the tool to retrieve the walnut, we suggest that the absence of these muscles in the hand of bonobos may prevent them to use the tip of the thumb during grasps which involve strong force. Grasping an object indeed necessitates complex muscular coordination and requires high intensities of muscle forces up to 2 times the force exerted on the object in humans (Vigouroux, Domalain, & Berton, 2011; Goislard de Monsabert, Rossi, Berton, & Vigouroux, 2012). Investigating this coordination and quantifying muscle activities in apes would be of great interest to explore the relationship between hand morphology and hand activities. However, due to the high level of implantation complexity and ethical implications for primates, studies reporting muscles activities during grasping actions in non-human primates are extremely scarce (i.e., Overduin, D’avella, Roh, & Bizzi, 2008). In the framework of this study, we thus can expect that the morphometry of the bonobo’s hand, such as short size of their thumb compared to their long fingers, involves different biomechanical constraints during grasping actions. For example, a smaller thumb would generate different finger joint angle, corresponding to different moment arms and probably would engage different joint and muscle loadings. Consequently the rare use of the thumb for the bonobo could be the results of a choice based on biomechanical loadings, which cannot be balanced by their musculature when grasping with the thumb. Nevertheless, the mechanics of the hand of great apes is poorly understood compared to humans (e.g., for review: Taylor & Schwarz, 1955; e.g. for exhaustive information: Connolly, 1998; Jones & Lederman, 2006) and only the development of a musculoskeletal model based on ape morphological (i.e., size of the segments) and biomechanical data (i.e., force, kinematics, muscle activities) may be appropriate to test this hypothesis.

4.3 | Dynamic tool manipulation

With regard to our second hypothesis, our observations showed that bonobos did indeed use in-hand movements to reposition the tool. These manual abilities suggest that bonobos have the level of neuromotor control with the neuromuscular and morphological requirements

necessary for complex fingers manipulation. These results confirm the recent study in captive chimpanzees (Crast et al., 2009), that showed their abilities to use complex in-hand movements, suggesting that this dynamic ability is not unique to human hands and could be present at least in the last common ancestor of Hominini.

Bonobos used more in-hand movements during the maze task than during food extraction. This result could be explained by the task itself. In fact, the extraction task did not require complex manipulation in contrast to the maze task which involved many obstacles such as the wire netting between the subject and the maze and the obstacles inside the maze. This task involved repositioning and a dynamic manipulation with more changes of the combinations of contact areas compared to the food extraction task. No movements of the objects between the thumb and fingertips were observed during Mahale chimpanzees feeding (Marzke et al., 2015), but they were observed in an experimental context (Crast et al., 2009). Marzke et al. (2015) showed that in-hand movements can be observed during tool-making and tool use behaviors at other chimpanzee sites. According to the taxonomy of Elliot and Connely (1984), bonobos here used more in-hand movements classified as "simple synergies," where the tool was moved by flexing and extending the fingers without changing its orientation. In the study of Crast et al. (2009), chimpanzees showed complex in-hand movements classified as "sequential patterns" (Elliot & Connely, 1984), involving coordination of fingers in a characteristic sequence of movements. This difference could be explained by the tasks differing between our study and the study of Crast et al. (2009) where chimpanzees needed to grasp and insert the adequate small objects in the corresponding shaped cutouts. Thus, tasks necessitating tool or complex object manipulation and repositioning can require more dynamic strategies inside the hand itself according to the number of steps needed to perform the task. However, in-hand movements performed by chimpanzees (Crast et al., 2009) and in our study by bonobos involved the use of the palm whereas humans executed sequential movements without using the palm but the fingertips instead (Elliot & Connely, 1984). This suggests that the different neuromuscular anatomy and the morphometry of the hand between humans and great apes could involve different in-hand movements. However, more studies are needed to conclude this and a comparison between humans and great apes during the same activities is especially needed to better understand the mechanisms of their hands.

It appeared difficult to quantify the manipulation with a common method to compare species. The method of time based sequence analysis of contacts areas (Borel et al., 2016) that we used in our study does not imply direct contact with the observed individuals or the use of markers. Therefore, even if based on video analysis and including few limitations (see Borel et al., 2016 for complete discussion about advantages and limitations) it is a good compromise to obtain comparable data between different species. It allowed us to describe in detail the grasp types variability. It also provided a dynamic view of the manipulation strategies and thus allowed not only recording the number of occurrences of grasp types but also quantifying their duration of use. It has been possible to show that some grasp types were used lon-

ger than others. Individual differences were also examined and quantified with this method. This kind of method is a relevant approach to compare tasks and species in future studies, and to investigate more thoroughly inter and intra-individual variability.

4.4 | Individual strategies

We observed different functional and behavioral strategies between the subjects and stronger differences between subjects during the maze task. These differences may be explained by morphological and/or behavioral effects. There may be other explanations and with other groups of bonobos there may not be any differences. Despite our small sample size, inter-individual variability is an important point to investigate.

A possible hypothesis for these individual preferences is that some subjects may have more experience in tool use and as such they would have developed an individual technique. For example, some individuals showed less grasp variability. We observed that these individuals, such as Daniela, had more access to the enrichments and thus more time to practice. Individuals in this captive group of eight bonobos could thus develop different grasp types and techniques according to: (a) the time spent obtaining food and (b) their experience in food extraction with tools before the onset of the study. Daniela seemed to be standardized in her strategies (i.e., time to retrieve the walnut, number of in-hand movements). Daniela was the oldest individual in this group and the dominant one. Could we expect bonobos to use different strategies according to the hierarchical rank or the age? We could not discuss this point in the present study because of our small sample but we suggest one hypothesis that could be interesting to test in future studies. Indeed, Daniela could have developed a stable strategy according to her social status as she had more time to perform the task and because nobody took her place. The males and adolescent females, might have suffered from a lack of time to practice constraining them to use different strategies to reach the walnut as fast as possible before adult females took their place. We clearly need to work on a large sample of different group of bonobos to test this hypothesis.

One subject (Khaya) used only one grasp type during the two tasks: the 3-jaw chuck with thumb. This grasp type is typical of human pencil grasping and this female was raised by humans. We wonder if the use of this grasp type by Khaya was facilitated by this human proximity. However, this grasp type is also used by wild chimpanzees during termite nest perforation (Lesnik et al., 2015), without the proximity of humans. It would be interesting to study the acquisition and the development of these preferred grasp types in bonobos to investigate the presence of (a) a non-social process, (b) a social influence, or (c) social learning (see Whiten & Ham, 1992).

It could also be relevant to compare the maze task results of bonobos with other species to test if the strong individual preference for specific grasp types is particular to bonobos. Variability in the grasp types used by chimpanzees during a food task (Lesnik et al., 2015) or during different food manipulation tasks (Marzke et al., 2015) has been observed but individual preferences were not investigated. Moreover, in chimpanzees dominant males may show more specialization in their

manual abilities than females. To investigate this, it would be interesting to observe the manual abilities in chimpanzees of both sexes.

4.5 | Selectivity of tools already modified

Bonobos responded to task constraints by selecting and modifying tools appropriately, usually before they started the tasks. When we observed tool manufacture, bonobos used the same specific behaviors as other captive bonobos (Boose et al., 2013) and as wild chimpanzees (McGrew, Tutin, & Baldwin, 1979): detachment of raw material, side-branch removal, bark peeling. In our study, bonobos accomplished these steps using one hand and the mouth or both hands. They used appropriate tools according to the task, in agreement with another study in captive bonobos (Boose et al., 2013). The tips of tools were modified especially for the food extraction with “brush” and “pointed” tips like in wild chimpanzees in the Goulougo Triangle who modify herb stems to fashion a brush tip for termite fishing (Sanz, Call, & Morgan, 2009). For the maze, bonobos used more curved tools than straight tools, and some subjects did so from the beginning of the task. This point is interesting in regard to anticipation and planning of the task by bonobos. This point has only been investigated to a limited extent study for bonobos (Bräuer & Call, 2015) compared to, for example, chimpanzees and orangutans (i.e., Osvath & Osvath, 2008). The fact that this group of bonobos had already experimented with tool manufacture and use in the context of their various enrichments may have impacted this. Alternatively, they may have immediately understood the future needs of the task. Boose et al. (2013) showed that bonobos rapidly became proficient in manufacturing tools and extracting bait from an artificial termite mound. Consequently, we could suppose that the group we studied was habituated to tool use and anticipated the choice of the tool according to the demands of the task. However, it may be a strategic choice to arrive directly with the tool already modified as we observed social pressure in this group. Thus, having a tool already modified could be a strategy developed by the males to save time before arriving on site. In females, the strategy may be to take the modified tool of the males, which we observed in some cases. In this context, males may have selected more appropriate tools than females. To test this, it would, however, be necessary to analyze a large sample of bonobos.

4.6 | Implications for the evolution of the human hand morphology

Our results indicated well developed manual abilities during tool use and manipulation in bonobos and a strong interindividual variability in the functional strategies used. As bonobos have a different hand morphology than humans, including a shorter thumb and different muscles like chimpanzees (Marzke et al., 1999; Diogo & Wood, 2011; Diogo et al., 2012; Myatt et al., 2012), our results may be interesting in regards to the evolution of manual abilities in primates in association with different locomotor modes.

Our findings in bonobos showed well developed abilities for tool manipulation with a wide variety of grasp types and in-hand movements. For our two tasks, bonobos also used one hand preferentially

(Bardo et al., 2015) and they used forceful grasp types with individual preferences. Hook grasps with an opposed thumb were particularly important during tool manipulation. Moreover, bonobos used the two-jaw chuck pad-to-side more often during food extraction. This point is interesting in connection with the use of this grasp for the flake tool-using behavior which involved higher forces on the human thumb than tool-making behavior (Williams, Gordon, & Richmond, 2012). Marzke (1983: 197) proposed that “this grip could have been exploited in the manipulation of small stone flakes and wood probes, and in the controlled manipulation of stone missiles.” Moreover, a bonobo named Kanzi removed flakes from stone cores with a hammer stone using a one hand technique (Schick & Toth, 1993) and created and selected appropriate flakes according to the task (Schick et al., 1999). These results could imply that a common ancestor to bonobos and humans with similar hand morphology to bonobos may have had similar functional capabilities. However, some authors consider the human hand more primitive than that of extant apes which have high levels of hand disparity explained by different evolutionary processes (Almécija, Smaers, & Jungers, 2015). Thus, the bonobo hand could be more derived. In this context bonobos are interesting because they use different locomotion modes such as knuckle-walking and bipedalism and use both terrestrial and arboreal substrates (see D’Août et al., 2004 for a review). Thus, they appear adapted for arboreal behavior and terrestrial locomotion. Our results showed a variety of grasp types and in-hand movements in bonobos which could be linked to these types of locomotion (Christel et al., 1998). According to Almécija et al. (2015) the morphology of the hand of bonobos may have evolved in conjunction with their different mode of locomotion, as extant apes. This hypothesis was consistent with Rolian, Lieberman, and Hallgrímsson (2010) which suggested that the evolution of the human hand is not linked to an adaptation for tool use or any other function, but rather that the hominin hand and feet coevolved. They suggested that the evolution of long robust big toes and short lateral toes for bipedalism led to changes in hominin fingers that may have facilitated the emergence of stone tool technology (Rolian et al., 2010).

No fossils of the last common ancestor of humans and apes have been discovered yet and the evolution of the human hand during the emergence of manual abilities to produce stone tool remains debated. Recent archeological and paleoanthropological discoveries showed that the earliest evidence of intentional stone tool production at 3.3 Ma (Harmand et al., 2015) predated the appearance of the genus *Homo* by at least 0.5 Ma (Skinner et al., 2015b), and that intensified manual manipulation could be linked to an arboreal lifestyle (Kivell, Kibii, Churchill, Schmid, & Berger, 2011; Kivell et al., 2015; Skinner et al., 2015a). These discoveries allow us to suggest that arboreal species could have the potential to produce and to use stone tools. Finally, following the studies conducted on Kanzi, who is able to manufacture and use various stone tools (Schick & Toth, 1993; Schick et al., 1999), the first tool maker could have been a bonobo.

Finally, bonobos do not appear to have one specific technique to perform a given task but show individual preferences. These individual differences could be due to inter-individual morphological variability in

bonobo hands. This strong variability quantified only in one small group of bonobos points out the extreme difficulty to infer the manual abilities of fossilized hand skeletons.

5 | CONCLUSION

Our results provide evidence that food retrieval from a maze is associated with a more dynamic manipulation compared to a food extraction task. The dynamic manipulation of tools could be an important factor in the evolution of morpho-functional abilities of the human hand. However, as suggested by Weiss (2012) and Marzke (2013), human hand morphology may not have directly evolved by natural selection in relation to tool use. Our results show the importance of quantifying dynamic object manipulation in different species for new and complex tasks, and with new methods to better understand the manual specificities of each species, essential for a better reconstruction of the evolution of primate manual ability. It is also important to investigate hand function and mechanics in this context. The next step focusing on manual abilities through an integrative approach involving biomechanics, comparative anatomy, and ethology is essential. Finally, our study suggests that inter-individual and intra-individual variability, and sex or gender differences need to be explored further.

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ANNEX B

Bardo A., Pouydebat E., Meunier H., **2015**. Do bimanual coordination, tool use, and body posture contribute equally to hand preferences in bonobos? *Journal of Human Evolution* **82**, 159-169.



Do bimanual coordination, tool use, and body posture contribute equally to hand preferences in bonobos?



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ABSTRACT

Approximately 90% of the human population is right-handed. The emergence of this hand preference in humans is thought to be linked to the ability to execute complex tasks and habitual bipedalism. In order to test these hypotheses, the present study explored, for the first time, hand preference in relation to both body posture (seated and bipedal) and task complexity (bimanual coordination and two tool use tasks of different complexity) in bonobos (*Pan paniscus*). Few studies have explored the effects of both posture and task complexity on handedness, and investigations with bonobos are scarce, particularly studies on tool use. Our study aims to overcome such a gap by addressing two main questions: 1) Does a bipedal posture increase the strength of hand preference and/or create a directional bias to the use of the right hand? 2) Independent of body posture, does task complexity increase the strength of the hand preference and/or create a directional bias to the use of the right hand? Our results show that independent of body posture, the more complex the task, the more lateralization occurred. Moreover, subjects tended to be right-handed for tasks involving tool use. However, posture had no significant effect on hand preference in the tasks tested here. Therefore, for a given task, bonobos were not more lateralized in a bipedal posture than in a seated one. Task complexity might thus have contributed more than bipedal posture to the emergence of human lateralization and the preponderance of right-handedness, although a larger sample size and more data are needed to be conclusive.

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Introduction

Laterality, defined as the functional dominance of one side of the body relative to the other, has been studied primarily in humans (*Homo sapiens*). Broca (1877) studied the relationships between language disorders and brain damage, and was the first to reveal hemispheric functional specialization of the human brain. Moreover, the link between cortical asymmetry and manual asymmetry was established very early in humans (e.g., Broca, 1877; Annett, 1972) and has been confirmed in other vertebrates (Marchant and Steklis, 1986; Bradshaw, 1991; Hopkins and Morris, 1993; Bisazza et al., 1996).

The human population is predominantly (i.e., ~90%) right-handed (Annett, 1985; Perelle and Ehrman, 1994), which would

correspond to a left hemisphere specialization for manual control. This phenomenon is thought to have played a prominent role in lateralization of human language (e.g., Warren, 1980; Ettliger, 1988; Corballis, 1998; Crow, 2004) and other cognitive functions such as tool use (e.g., Kimura, 1979; Gibson and Ingold, 1993; Preston, 1998), manual gestures (Kimura, 1973a; Hopkins and Leavens, 1998; Rizzolatti and Arbib, 1998; Corballis, 2003; Pollick and de Waal, 2007), and throwing (Calvin, 1983; Hopkins et al., 1993, 2005b; Colell et al., 1995). As nonhuman primates are genetically close to humans, they are often used as models to understand the origins of human brain asymmetry (MacNeilage et al., 1987; Fagot and Vauclair, 1991; McGrew and Marchant, 1997; Cashmore et al., 2008; for a review, see; Papademetriou et al., 2005). To date, such a bias of 90% for the right hand has never been observed in any other species of primate (Vallortigara and Rogers, 2005), and the origin of human hand preference remains unclear. However, several hypotheses have been proposed.

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MacNeilage et al. (2009) suggested that early primates evolved in an ecological context where it was necessary to undertake more difficult and more elaborate tasks than, for example, simple grasping in order to find food, which led to a concomitant increase in hand preference. Fagot and Vauclair (1991), according to their ‘theory of the complexity of the task,’ proposed that hand preference would depend on the demands of the task. They defined complexity “in terms of the movement precision, relative to the spatiotemporal dimension of the task” and classified tasks according to two broad categories: “high-level” tasks and “low-level” tasks (Fagot and Vauclair, 1991:77, 80). High-level tasks are more complex than low-level tasks in terms of postural, perceptual, and cognitive demands. For nonhuman primates, high-level tasks increase the strength of laterality and induce a preference for the right or the left hand (Fagot and Vauclair, 1991). A large number of studies in nonhuman primates also indicated that individuals were more strongly lateralized during a bimanual task considered as ‘complex’ than during a unimanual task considered as more ‘simple’ (gorilla: Byrne and Byrne, 1991; bonobo: Hopkins and de Waal, 1995; orangutan: Rogers and Kaplan, 1996; chimpanzee: Hopkins et al., 2007b; capuchin: Meunier and Vauclair, 2007). However, if the effect of the task on hand preference has been demonstrated in many studies, there is a lack of consensus around the definition of the complexity of the task. Indeed, each task has its own constraints, and each author identified various criteria depending on the task itself. This may be the reason why many definitions of task complexity are proposed in the literature. In addition, it is difficult to define exactly the various functional and cognitive requirements of a manual task, whereas it could help to define complexity and standardize the procedures and studies. We thus consider, in this study, the previous criteria mentioned in the literature, in addition to those we observed during the tasks in order to define complexity (see Methods). Complexity of the task was previously defined according to criteria such as: the use of one hand versus two hands in bimanual coordination (MacNeilage et al., 1987; Hopkins, 1995), the number of stages required to realize the task (Marchant and McGrew, 1991), the level of precision of the required motor acts (Healey et al., 1986; Morris et al., 1993), the use of visual guidance (MacNeilage et al., 1987; Fagot and Vauclair, 1988a,b) or tactile discrimination (Ettlinger, 1961), and, finally, any combination of these criteria (Fagot and Vauclair, 1991). Regarding the literature, tool use should be considered as a complex task since many of the criteria mentioned above are involved in tool use. Many definitions of tool use exist (reviewed in St. Amant and Horton, 2008), and here we use the widely accepted definition of Beck (1980:10): the use of an object to change “the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool.” If complex tasks increase laterality (Fagot and Vauclair, 1991), tool use tasks should induce a stronger hand preference than ‘simpler’ tasks, which has been already shown in apes (chimpanzees: Boesch, 1991; Sugiyama et al., 1993; orangutans: O’Malley and McGrew, 2006; gorillas: Pouydebat et al., 2010).

Another factor that might influence hand preference involves body posture. Bipedal or standing postures have been suggested to induce a stronger hand preference than other postures (e.g., chimpanzee and orangutan: Hopkins, 1993; bonobo: Hopkins et al., 1993). Moreover, a bipedal posture is also thought to influence the direction of laterality with a preference for the right hand (e.g., chimpanzee and orangutan: Hopkins, 1993; bonobo: Hopkins et al., 1993; macaque: Westergaard et al., 1998a; *Cercopithecus*: Chapelain et al., 2006; capuchin: Westergaard et al., 1997). This led Kimura (1979) to suggest that both tool use and bipedalism contributed to the emergence of the lateralization of the brain, particularly the

strong right hand preference in humans. This suggests the need to simultaneously evaluate the effects of tool use and bipedal posture on hand preference. To date, only two studies have examined hand preference when using tools in bipedal postures: one on chimpanzees (Braccini et al., 2010) and the other on capuchins (Westergaard et al., 1998b). In both species, authors showed that individuals were more lateralized while manipulating tools in a bipedal posture than in a quadrupedal one, with no significant group-level difference for hand preference. These results tend to validate the hypothesis linking the emergence of lateralization to tool use and bipedalism, but more investigations on other individuals of the same and other species are needed. Specifically, it remains unclear whether task complexity or bipedal posture has the greatest effect on laterality. Moreover, it is unclear if the effects of task complexity and bipedalism are independent, additive, or interactive. Finally, it remains unknown whether either parameter induces a right or a left hand preference. A combined approach would help us to understand the respective implication of both parameters in the evolution of laterality and the emergence of the right hand bias in humans.

Our main objective was to test the interaction between task complexity and body posture on hand preference simultaneously. To this end, we investigated the interaction of these two parameters in captive bonobos by quantifying, for the first time, hand preference in relation to both body posture (seated and bipedal) and task complexity: (i) bimanual coordination, (ii) food extraction with a tool, and (iii) food recovery in a maze with a tool through a wire netting. The last two tasks required the use of a tool that has never been tested in bonobos. We conducted this study on bonobos because they are, like chimpanzees (*Pan troglodytes*), close to humans with respect to phylogeny, sharing 98.4% of their coding DNA sequences (Wildman et al., 2003). However, behavioral data are scarce for bonobos, specifically concerning hand preference (around ten studies; e.g., Hopkins et al., 1993; De Vleeschouwer et al., 1995; Christel et al., 1998; Harrison and Nystrom, 2008; Chapelain et al., 2011), hand preference during tool use (Shafer, 1997; Harrison and Nystrom, 2008; Chapelain, 2010), and tool use in general (in the wild: Kano, 1982; Ingmanson, 1996; Hohmann and Fruth, 2003; in captivity: Jordan, 1982; Toth et al., 1993; Gold, 2002). Finally, bonobos are often bipedal, similar to chimpanzees, making them an excellent model (Doran, 1993; Videan and McGrew, 2001, 2002; D’Août et al., 2004).

Based on this existing literature, we thus suggested two main hypotheses (H): H1) bipedal posture increases the strength of hand preference and generates a directional bias to the use of the right hand; and H2) the complexity of the task increases the strength of hand preference, and tool use creates a directional bias to the use of the right hand.

Methods

Subjects

This study was conducted from 19 January to 27 April 2012 at the ‘Vallée des Singes’ (France, 86), on a small group of nine captive bonobos (five females and four males), ranging in age from four to 43 years (mean age of 15.88 years, SE = 4.12). One young female (four years old) had not yet included tool use in her behavioral repertoire and she was not included in the analyses. The bonobos were housed in an indoor building consisting of a network of eight cages from 30 to 98 m² with a height of up to 6 m (two main large cages and six smaller cages). Animals had access to a large wooded outdoor island. Water was available ad libitum in their pens and the food used for our protocol was part of the daily diet. All subjects were tested within their social group, in cages not visible to the

public. Before our study, this group received pipes and pierced logs that required tools to extract various foods on a weekly basis. Thus, the group was already used to, and experienced in, food extraction.

General procedure

Hand preference was documented in three tasks differing by their complexity and for each task, in a seated posture and a bipedal posture. We considered individuals to be in a bipedal posture when they were upright, that is to say when the angle between the trunk and the thigh was greater than 90° with the knee extended (thigh-leg angle $>90^\circ$). Only one task was imposed each day per session. A session lasted 30 min on average and lasted until the food was gone. Two cameras (Sanyo[®] Full HD) at 60 frames/second, one fixed and the other mobile, were used during the tests, thus optimizing the collection of data. The mobile camera was always filming the same cage, and the other camera was used to randomly film different cages every day. A focal sampling method of 5 min of filming on average for one individual was conducted until the food was eaten. Video analysis was performed with Windows Media Player[®] using a focal sampling protocol (Altmann, 1974).

Experimental tasks

Task 1: Coordinated bimanual task The first experiment was the ‘TUBE’ task (Hopkins, 1995). In this task, the individual held a tube containing food with one hand, and reached inside the tube with one or more fingers of the other hand (the dominant hand). The tubes presented to the bonobos were made of PVC (30 cm long, 40 mm diameter, 155 g empty, 400 g full). They were filled with sticky food on the inside edge of both extremities. According to the literature, the complexity of this task resides in the fact that the tube requires coordinated bimanual hand movements with different roles for each hand (e.g., Byrne and Byrne, 1991; Byrne et al., 2001). Two criteria of success were observed for this task: individuals had to grab and hold the tube with one hand and then extract the food with the other hand. We provided 14 tubes horizontally suspended by the center at a height necessitating a bipedal posture (Fig. 1a) and 14 tubes on the ground to induce a seated posture. Twenty-eight sessions were conducted with one session per day. On average, each subject was observed on 12.9 ± 1.2 days for the seated posture and 9.8 ± 1.4 days for the bipedal posture. The hand used to extract the food was noted with two different recording techniques: ‘frequencies’ and ‘bouts.’ For the frequencies, we counted each time the subject inserted one or more fingers into the tube and subsequently brought them to its mouth. This variable has been used in most other tube task

studies (e.g., Hopkins, 1995; Hopkins et al., 2003; Meunier and Vauclair, 2007), and we used the same technique in order to favor comparisons. However, this method has been criticized as lacking data independence (Marchant and McGrew, 1991; Palmer, 2003). So, to ensure data independence, we also recorded bouts, corresponding to a series of identical actions, by recording only the first pattern of each sequence (e.g., Marchant and McGrew, 1991). A bout was considered complete each time the subject performed an action allowing a change of the dominant hand. Hand preference was analyzed for each individual with a minimum of 10 bouts.

Task 2: The food extraction task In this task, hand preference was studied during a manipulative task involving tool use for food extraction. The task was comparable to the ‘termite-fishing’ task, well known in wild chimpanzees (Goodall, 1968) but still never observed in wild bonobos (McGrew et al., 2007). To accomplish this task, 12 logs (53.25 cm long, SE = 2.90 cm and diameter 9.17 cm, SE = 0.88 cm), pierced in their center, were hung vertically at different heights (six logs hung low and six high) so that individuals could perform this task in seated and bipedal postures (Fig. 1b) within each session. Sticky food was placed inside the holes. Branches (maximum length of 3 m) were provided to bonobos. The hand used to hold the branch was recorded each time a subject inserted a branch into a hole of a log, removed it from the hole, and brought it to its mouth with one hand. We considered this task more complex than the tube task because more criteria were required to succeed. Indeed, individuals had to use a tool with one hand to be able to extract the food and visual guidance was required to insert the tool into the holes. The other hand was placed on the log or on the mesh. As with the tube task, we used two recording techniques: ‘frequency’ and ‘bouts.’ Eleven test sessions were conducted with one session per day, and each subject was observed between five and nine days (mean = 6.875, SE = 0.58).

Task 3: The maze task This experimental setup represents a new task, specifically created for this study. The subject needed to recover walnuts positioned on a wooden maze (Fig. 1c) outside the cage (grid with a mesh size of 5×5 cm), with a stick. Nine mazes (45 cm wide by 60 cm long) differing in the shape, position, and size of the wooden obstacles (providing a different potential path of the walnut in each maze) were fixed outside the cages at different heights. In order to minimize as much as possible the social tensions in the group, the mazes were moved away from each other and the walnuts were placed in the mazes at the same moment. Four mazes were placed at 30 cm from the floor in the two main cages and five mazes at 60 cm height in the smaller cages so that individuals could choose to position themselves in a seated or bipedal posture. The walnuts were placed at the end of

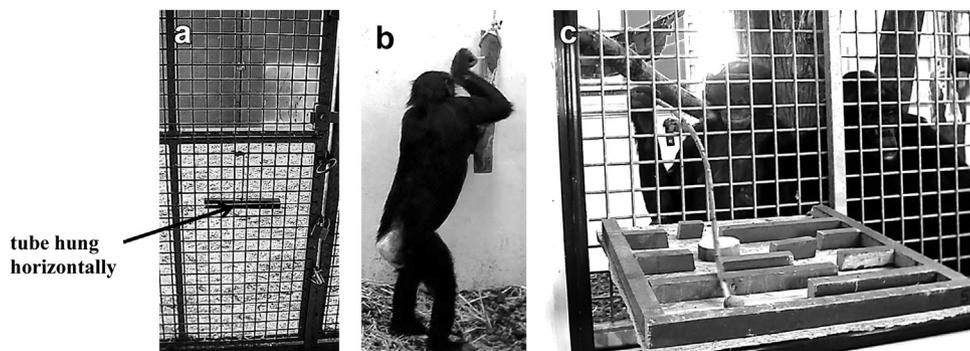


Figure 1. Pictures of the three tasks accomplished by bonobos: (a) the tube task, with a tube hung horizontally, (b) the extracting food task with tool, in a bipedal posture, and (c) the maze task with a tool, in a seated posture.

the maze (at 60 cm away from the individual). This task was considered the most complex one in this study because it required several steps to be performed. As in the food extraction task, individuals had to use a tool to succeed. However, the maze task required the use of a tool to recover the walnut by facing many obstacles: first, obstacles placed inside the maze in order to complicate the trajectory of the walnut and second, between the maze and the individual (wire netting). These obstacles involved several constraints in terms of forelimb coordination, body posture adjustments, manual skills, and vision. The behavior studied was the hand holding the branch. Fifteen sessions (each session comprising between two and eight walnuts by maze per day) were filmed. As for the two other tasks, we first planned to use 'frequency' and 'bouts' recording techniques, thinking that subjects would have alternated hand use or could leave their tool during the task. However, the individuals never changed hands nor left their tool during all of the maze sessions and we thus have recorded frequencies only. The hand holding the branch when recovering the walnut was thus recorded. Each subject was observed between nine and 14 days (mean = 11.85 and SE = 0.70), and only those who obtained a minimum of six successes for the maze were kept for the analyses. Among our nine subjects, one young male never succeeded in accessing the mazes and two other individuals (one male and one female) did not perform this task in a bipedal posture.

Data analysis

The data obtained in this study were analyzed using the methods proposed by Hopkins (1999). For each subject the binomial z-scores were calculated based on frequency (Table 1) and

bouts. The z-scores allowed us to categorize the bonobos individually as right-handed ($z \geq 1.96$), left-handed ($z \leq -1.96$), or without hand preference ($-1.96 < z < 1.96$). Next, the individual hand preference index (Handedness Index, denoted by HI) was calculated using the formula: $HI = (R - L)/(R + L)$. The HI varies from -1 to 1, with negative values indicating a left-hand bias and positive values indicating a right-hand bias. Thanks to these individual HI, we evaluated hand preference at group level using a Wilcoxon signed-rank test for one sample. Finally, for each subject we calculated the absolute value of HI (denoted ABS-HI), which indicates the strength of hand preference. The stronger the laterality, the closer the ABS-HI is to 1. We evaluated if the hand preference based on z-score changed for each subject between the postures and tasks with a chi-square goodness of fit test (e.g., Bogart et al., 2012). For pairwise comparisons, we considered only the individuals who were represented in both compared tasks. We compared only tasks performed by a minimum of six individuals. All statistical tests were performed with the software R (R Development Core Team, 2013; exact method) and were two-tailed with a level of significance set at $p < 0.05$.

Results

Bouts versus frequency

Regarding the z-scores, we found differences between frequency and bout data for the tube task in bipedal posture where two bonobos previously classified as left-handed were classified with no preference (Table 1). To test data independence (Marchant and McGrew, 1991), we compared the HI values found between the two recording techniques (see Methods) for the two postures in the

Table 1
Raw data and statistical results with frequencies for the three tasks and the two postural conditions (seated and bipedal).^a

	Individuals	Seated						Bipedal					
		Bout R/L	Freq R/L	HI	ABS-HI	z	Category	Bout R/L	Freq R/L	HI	ABS-HI	z	Category
Tube task	Diwani	1/65	1/161	-0.988	0.988	-12.57	LH	1/26	4/57	-0.869	0.869	-6.786	LH
	Kirembo	51/2	132/4	0.941	0.941	10.976	RH	62/0	110/0	1	1	10.488	RH
	Daniela	46/8	185/24	0.77	0.77	11.137	RH	35/12	93/16	0.70	0.70	7.3753	RH
	Ukela	8/42	15/197	-0.858	0.858	-12.5	LH	3/7	4/22	-0.692	0.692	-3.5301	LH A
	Khaya	6/49	12/156	-0.857	0.857	-11.11	LH	6/16	14/35	-0.428	0.428	-3	LH
	Lingala	18/38	35/91	-0.444	0.444	-4.9889	LH	26/29	42/64	-0.207	0.207	-2.1368	LH A
	David	28/28	90/86	0.023	0.023	0.03015	A	7/3	12/5	0.412	0.412	1.6977	A
	Kelele	40/14	91/31	0.492	0.492	5.4321	RH	51/16	101/23	0.629	0.629	7.0046	RH
	Means	55.5	163.88	-0.115	0.672			37.5	75.25	0.068	0.618		
	Standard error	1.647	12.309	0.276	0.116			8.161	14.868	0.249	0.091		
Extracting food task	Diwani	70/0	129/0	1	1	11.3578	RH	23/0	25/0	1	1	5	RH
	Kirembo	68/0	86/0	1	1	9.2736	RH	27/0	33/0	1	1	5.7446	RH
	Daniela	54/13	69/28	0.423	0.423	4.1629	RH	37/18	59/22	0.457	0.457	4.1111	RH
	Ukela	0/38	3/67	-0.914	0.914	-7.6495	LH	0/12	0/20	-1	1	-4.4721	LH
	Khaya	57/0	101/0	1	1	10.05	RH	60/0	172/0	1	1	13.115	RH
	Lingala	70/0	163/0	1	1	12.767	RH	60/0	155/0	1	1	12.45	RH
	David	70/0	112/0	1	1	10.583	RH	21/0	26/0	1	1	5.099	RH
	Kelele	44/17	54/23	0.403	0.403	3.5328	RH	22/0	22/0	1	1	4.6904	RH
	Means	62.625	104.38	0.614	0.842			35	66.75	0.719	0.932		
	Standard error	3.677	10.107	0.238	0.094			6.322	22.449	0.249	0.068		
Maze task	Diwani		35/0	1	1	5.916	RH		9/0	1	1	3	RH
	Kirembo		30/0	1	1	5.477	RH		33/0	1	1	5.745	RH
	Daniela		33/0	1	1	5.744	RH		26/0	1	1	5.099	RH
	Ukela		0/23	-1	1	-4.796	LH		0				
	Khaya		23/0	1	1	4.796	RH		21/0	1	1	4.582	RH
	Lingala		30/0	1	1	5.477	RH		33/0	1	1	5.744	RH
	David		18/0	1	1	4.242	RH		0				
	Means		27.429	0.714	1				20.333	1	1		
Standard error		2.338	0.285	0				4.467	0	0			

^a R = Number of right-hand responses. L = Number of left-hand responses. HI = Handedness Index. ABS-HI = Absolute value of HI. z = z-scores. Category (based on the z-scores): LH = left-handed individuals, RH = right-handed individuals, A = ambiguously-handed individuals and in italics the differences based on bout data.

tube task and the food extraction task. For all conditions we found a significant positive correlation between HI measured with frequencies and HI measured using bouts (Spearman correlation, $n = 8$: tube task seated $r = 0.97$, $p = 0.001$; tube task bipedal $r = 0.95$, $p = 0.01$; food extraction task seated $r = 1$, $p = 0.01$; food extraction task bipedal $r = 1$, $p = 0.05$), indicating that these two approaches are similarly sensitive to individual hand preferences (Bogart et al., 2012; Hopkins, 2013). Thus, all analyses only used frequency data for determining individual hand preference, as has been proposed in other studies (e.g., Bogart et al., 2012).

Quantification of hand preference and influence of posture

Task 1: The coordinated bimanual task Three bonobos were classified as right-handed, one was classified with no preference, and four were classified as left-handed for both postures. At the group level, we had no differences on the HI values for the seated posture (One-sample Wilcoxon signed-rank test; $n = 8$, $z = 15$, $p = 0.74$) or for the bipedal one (One-sample Wilcoxon signed-rank test; $n = 8$, $z = 20$, $p = 0.84$), indicating individualistic hand preferences. A significant difference in the HI values was found between the seated and bipedal postures (Wilcoxon signed-rank test; $n = 8$, $z = 2$, $p = 0.02$), indicating a trend that bonobos were more lateralized in the seated posture over that of the bipedal posture. When we considered hand preferences based on z-scores for the two postures, a chi-square goodness of fit test revealed that the distribution of hand preference was random [$\chi^2(2, n = 8) = 0$, $p = 1$], indicating that there was no difference in the hand used between the postures. Concerning the ABS-HI values, no difference appeared between seated and bipedal postures (Wilcoxon signed-rank test; $n = 8$, $z = 24$, $p = 0.46$), indicating that individuals were not significantly more strongly lateralized in seated than bipedal posture.

Task 2: The food extraction task All of the individuals were lateralized in the food extraction task for both postures. Seven bonobos were classified as right-handed and one as left-handed. At the group level, a preference for the right hand appeared for seated posture (One-sample Wilcoxon signed-rank test; $n = 8$, $z = 36$, $p = 0.01$), and in bipedal posture individuals also seemed to have a preference for the right hand (One-sample Wilcoxon signed-rank test; $n = 8$, $z = 31$, $p = 0.05$). When we considered hand preferences based on z scores for the two postures, a chi-square goodness of fit test revealed that the distribution of hand preference was not random [$\chi^2(2, n = 8) = 10.75$, $p = 0.01$]. For both postures, there were significantly more right than left-handed subjects [$\chi^2(1, n = 8) = 4.5$, $p = 0.05$]. No significant difference in HI values (Wilcoxon signed-rank test; $n = 8$, $z = 2$, $p = 0.59$), nor in ABS-HI values (Wilcoxon signed-rank test; $n = 8$, $z = 0$, $p = 0.11$), was observed between bipedal and seated postures.

Task 3: The maze task Individuals were exclusively right- or left-handed, and they never changed hands between the nine different mazes, suggesting that manual preference was not affected by the structure of the mazes. Thus, we added the data of each maze to consider hand preference in the seated ($n = 7$) and the bipedal ($n = 5$) postures. Individuals never changed their body posture (from seated to quadrupedal and conversely) during the maze task. Considering hand preference, we showed that in the seated posture six bonobos demonstrated an exclusive use of the right hand and one individual an exclusive use of its left hand. Among the six right-handed individuals in seated posture, only five performed the task in bipedal posture and remained all right-handed in that case. At the group level, a preference for the right hand seemed to appear in both seated (One-sample Wilcoxon signed-rank test; $n = 7$, $z = 24$, $p = 0.06$) and bipedal

postures (only right-handed individuals). For both postures, the strength of lateralization was maximal for all of the individuals (ABS-HI = 1).

Influence of the complexity of the task and body posture

In both seated (Fig. 2a) and bipedal postures (Fig. 2b), individuals classified as left handed or no preference during the tube task inverted to the right-hand during the food extraction and the maze task, except one. One individual remained left-handed throughout the study (Table 1).

In the seated posture, the HI values were significantly higher for the maze task than during the tube task (Wilcoxon signed-rank test; $n = 7$, $z = 26$, $p = 0.05$), indicating a preference for the right hand during the maze task. Between the HI values of the tube task and the food extraction task we did not find differences in seated posture (Wilcoxon signed-rank test; $n = 8$, $z = 8$, $p = 0.19$), and in bipedal posture we observed a trend for a greater preference for the right hand during food extraction than for the tube task (Wilcoxon signed-rank test; $n = 8$, $z = 3$, $p = 0.06$). When we considered hand preference categories for the three tasks in seated posture, a chi-square goodness of fit test revealed that the distribution of hand preference was random [$\chi^2(4, n = 7) = 7.2857$, $p = 0.12$], indicating that there was actually no difference in the actual hand used between tasks. When only the right-handed and left-handed categories are examined, we observed a trend for a preference for the right hand over the left hand [$\chi^2(2, n = 7) = 5.4875$, $p = 0.06$]. Between the tube and food extraction tasks in bipedal posture, the distribution of hand preference was random [$\chi^2(2, n = 8) = 4.4$, $p = 0.11$], indicating that there was actually no difference in the actual hand used between the two tasks. Considering ABS-HI

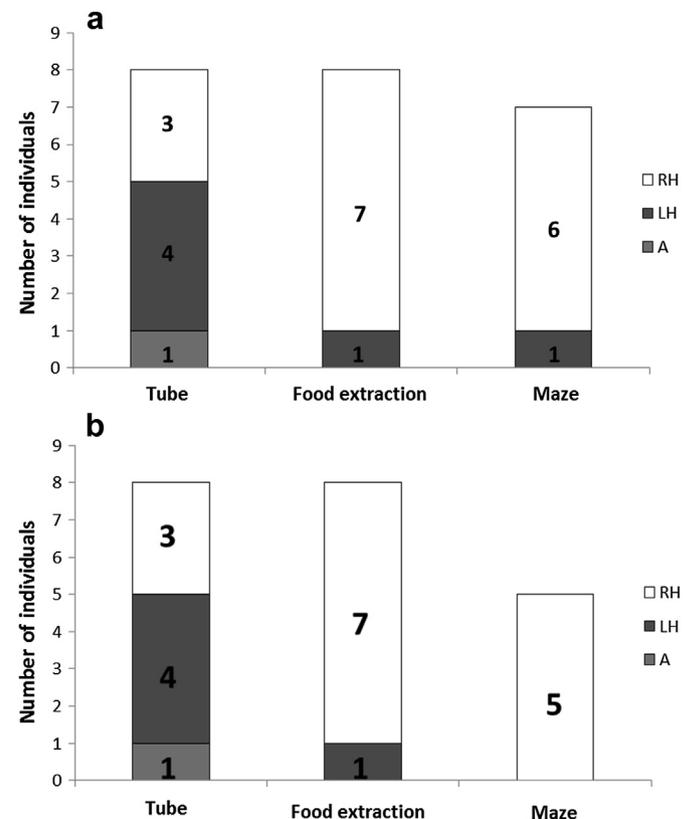


Figure 2. Number of right-handed (RH); left-handed (LH), and ambiguously-handed (A) subjects by task and by posture: (a) seated and (b) bipedal, with frequencies data.

values, individuals were significantly more strongly lateralized in a seated posture during the maze task compared with the tube task (Wilcoxon signed-rank test; $n = 7$, $z = 0$, $p = 0.05$). Moreover, individuals were significantly more strongly lateralized in a bipedal posture during the food extraction task compared with the tube task (Wilcoxon signed-rank test; $n = 8$, $z = 2$, $p = 0.05$; Fig. 3).

Discussion

This study is the first to simultaneously analyze the effect of both complexity and body posture on hand preference in bonobos. Our main result indicated that, independent of body posture, task complexity resulted in a greater lateralization for the two tool use tasks, with a tendency to preferentially use the right hand. In addition, one tool task was new and more complex than the other one, and specifically created for this study. Moreover, little research has been conducted on laterality in bonobos (with around 10 studies; e.g., Hopkins et al., 1993; De Vleeschouwer et al., 1995; Christel et al., 1998; Harrison and Nystrom, 2008; Chapelain et al., 2011), and very few studies have discussed the effects of both posture and complexity of a tool task on hand preference (e.g., Westergaard et al., 1998b; Braccini et al., 2010). As a result, this research is useful and compelling in spite of our small sample size. Indeed, even though we analyzed ‘only’ eight individuals, the large number of independent data points suggests robust results.

Contributions to the theory of task complexity

We observed a significant increase in the strength of laterality according to task complexity, with a stronger hand preference in both tasks involving tool use. Moreover, four bonobos who were left-handed or with no preference in the tube task were right-handed for both the food extraction task with a tool and the maze task. Our results were in agreement with our hypotheses, based on the task complexity hypothesis (Fagot and Vauclair, 1991) and the tool use hypothesis (Kimura, 1979; Frost, 1980). In the course of evolution, complex behaviors might have increased and demanded greater time and energy costs (Mutha et al., 2013). It has been hypothesized that these costs may have been counter-balanced by the hemispheric specialization that emerged to accommodate increasing motor complexity during hominoid evolution (Mutha et al., 2013). There are probably other correlations

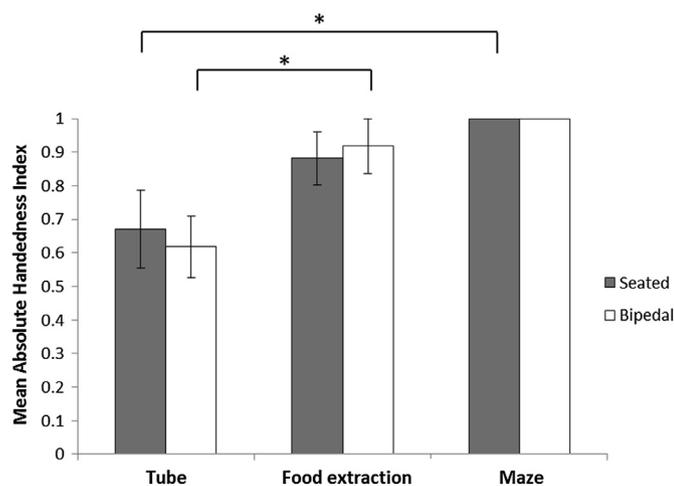


Figure 3. Mean absolute values of individual handedness index (ABS-HI), with frequencies, for the tube task ($n = 8$), the food extraction task ($n = 8$), and the maze task ($n = 7$ for the seated posture and $n = 5$ for the bipedal posture) depending on the posture. Bars = standard errors. * = $p < 0.05$.

with hemispheric specialization, such as the evolution of the size of the brain in primates. The evolution of larger brain size in primates would be accompanied by diminished interhemispheric connectivity and augmented intrahemispheric connectivity that might accompany the emergence of cerebral lateralization (Rilling and Insel, 1999). Moreover, increased motor complexity might lead to larger, more gyrified brains, which would then lead to hemispheric specialization (e.g., Aboitiz et al., 1992; Rilling and Insel, 1999). Thus, complex behaviors such as tool use would be strongly lateralized and could be managed in a specific hemisphere in bonobos such as the left hemisphere, as in humans (reviewed in Johnson-Frey, 2004) and chimpanzees (Hopkins et al., 2007a). The tool use tasks conducted in this study might demand higher and more costly cognitive abilities than the bimanual coordinated task, and, as such, might promote the specialization of a cerebral hemisphere—particularly the left hemisphere, which controls the right hand. This could explain why our bonobos tended to preferentially use their right hand during our tool use tasks.

Concerning the tube task in the seated posture, we observed individual preference but no bias at the group level, which contrasts with results obtained for the same task in other species (e.g., chimpanzees: Hopkins, 1995; Hopkins et al., 2003; orangutans: Hopkins et al., 2003; baboons: Vauclair et al., 2005) that showed a bias in hand preference at the group level. One explanation might be our small sample size compared with other studies (e.g., Hopkins, 1995 with 110 chimpanzees; Vauclair et al., 2005 with 104 baboons). However, our results converged with a similar study on bonobos (Chapelain et al., 2011), which showed no bias in hand preference at the group level with a sample of 77 bonobos but did show a pronounced individual hand preference. We have no explanation for this difference within this species (Chapelain et al., 2011). Studies on hand preference for bonobos are scarce (e.g., Hopkins et al., 1993; De Vleeschouwer et al., 1995; Christel et al., 1998; Harrison and Nystrom, 2008; Chapelain et al., 2011), and the ecology of bonobos in their natural environment is poorly known (e.g., McGrew et al., 2007). More studies should be conducted to explore if bonobos use bimanual coordination more or less than other species do both in captivity and in the wild. Subsequently one may try to better understand the potential role of bimanual coordination from an evolutionary point of view.

Concerning the tool use tasks tested in this study, our results showed that the hand preference of bonobos was very strong, and even exclusive (i.e., individuals always used the same hand), for the maze task. Thus, even though bonobos have not appeared to use tools to obtain food in their natural environment (Ingmanson, 1996), they successfully completed these tool use tasks in this study. Chapelain (2010) studied tool use with 19 bonobos in a task (‘termite fishing’) similar to our food extraction task, and she observed 11 individuals that were lateralized (four left-handed and seven right-handed). Harrison and Nystrom (2008) examined hand preference for tool use actions that occurred in the daily activities with 12 bonobos. They observed seven lateralized individuals (three left-handed, four right-handed). These results differ from ours, as all of our subjects were lateralized and we found one left-handed and six right-handed individuals for the food extraction task. This difference could be explained by the fact that during observations in previous studies, many parameters might have affected hand preference. In fact, in both studies they quantified the hand preference without taking into account the potential influence of the body posture and the potential influence of the variability of the type of tool used, in spite of their potential complexity differences. Regarding the findings in wild chimpanzees for ‘termite fishing,’ a significant group level left bias was reported by Lonsdorf and Hopkins (2005) and recently by Bogart et al. (2012), who combined their data with those obtained by McGrew and

Marchant (1992, 1996) and Lonsdorf and Hopkins (2005) and based on this combined data set showed a left-hand bias for wild chimpanzees. In captivity, the same left bias was found by Fletcher and Weghorst (2005), but no bias was detected in the study by Hopkins and Rabinowitz (1997). In wild chimpanzees, most individuals were lateralized and showed an almost exclusive use of one hand (Nishida and Hiraiwa, 1982; McGrew and Marchant, 1992, 1999; Marchant and McGrew, 1996; Lonsdorf and Hopkins, 2005; Bogart et al., 2012), which was more consistent with our results (all individuals lateralized and 66% exclusively lateralized). Finally, because ‘termite-fishing’ behavior has never been observed in wild bonobos (McGrew et al., 2007), comparison between natural and artificial habitat is still not possible for this task.

The results of the maze task must be considered as preliminary because we had only a limited number of individuals to compare (seated posture $n = 7$ and bipedal posture $n = 5$). Yet, for both seated and bipedal postures, all individuals showed a strong hand preference with a tendency for the use of the right hand. Moreover, in this novel task we observed an exclusive hand preference, whereas only 66% were exclusively lateralized for the food extraction task with a tool. One explanation might be the task novelty. Indeed, novel tasks are known to elicit higher hand preferences than highly familiar tasks (Fagot and Vauclair, 1991). In fact, bonobos were supplied weekly with pipes and pierced logs requiring tools to extract various foods, and thus all of them were already experienced in food extraction before our experiments. However, the maze task was novel for the bonobos we studied, which could explain the greater strength in hand preference compared with the familiar actions of food extraction. Moreover, we considered the maze task more complex (regarding the definitions of literature and the presence of more criteria) than the food extraction task, which could explain why we observed an exclusive hand preference for all individuals in the maze task.

Our results contribute additional reflections on hand preference and supplied task complexity data in bonobos. Indeed, the maze task was interesting in terms of complexity because it required several cognitive processes such as using a tool and moving around obstacles to retrieve walnuts. Bonobos might be exclusively lateralized for this task because it demanded many abilities, which were managed by one hemisphere to optimize manipulation, and specifically by the left one linked to calculation abilities in humans (Popper et al., 1977). However, some authors inferred that there was likely to be right hemisphere specialization for trajectory perception in humans (Boulinguez et al., 2003). In addition, the right hemisphere seems to be used to process geometrical and global spatial cues in many species (humans: Wendt and Risberg, 1994; rats: Cowell et al., 1997; chicks: Tommasi and Vallortigara, 2004). Finally, some authors have suggested that preferred directions of arm movements are independent of visual perception of spatial directions (Dounskaia et al., 2014) and that hemispheric specialization emerged to accommodate increasing motor complexity during evolution in humans (Mutha et al., 2013). In particular, some studies suggested an enhanced role for the left hemisphere during the learning of new sequences and skills and that this specialization emerged from a left hemisphere specialization for predictive control (the ability to plan and coordinate motor actions; Mutha et al., 2012). This last idea is in agreement with our results, but neurological studies in primates during different manipulation tasks would be needed to better understand the hemispheric specialization for the hand preference.

Effect of posture on hand preference

Our results did not indicate posture (seated or bipedal) as an influencing factor on the direction of hand preference, nor on the

strength of lateralization during the three tasks. Thus, our hypotheses that a bipedal posture should increase the strength of manual preference and generate a directional bias for the right hand were not supported by our data. According to these hypotheses, individuals in a bipedal posture should have been more strongly lateralized and should have had a directional bias in favor of the right hand. Other studies in bonobos showed an increase in the strength of hand preference and a right hand preference for a reaching task, when individuals shifted from a quadrupedal posture to a bipedal one (Hopkins et al., 1993). On the contrary, De Vleeschouwer et al. (1995) showed, in a group of five bonobos, a preference for using the left hand while the animals shifted from a seated to a bipedal posture. Still, most of these studies considered simple reaching tasks (Fagot and Vauclair, 1991). In our study we examined complex tasks for which individuals were already strongly lateralized in a seated posture, with a tendency to be right-handed. Thus, this could explain the lack of increase in right hand preference in a bipedal posture. However, as previously discussed, because complexity differences elicited differences in direction and strength of hand preference, our results also suggest that the complexity of the task has a greater effect on hand preference than posture. This idea is supported by a study of capuchins involving a bimanual coordination similar to the tube task (vertically hung tubes) and taking into account the body posture (crouched and upright; Spinozzi et al., 1998). The results showed that individuals had no significant difference in either the direction of hand preference or in the strength of lateralization between the two postures. These results are in accordance with ours in that capuchins and bonobos were already lateralized in crouched and seated posture (respectively for the two species), and their hand preference and strength of laterality did not change when they performed the task in an upright posture. This suggests both that a bimanual coordinated task (that requires a precise bimanual coordination while manipulating a tube) is a high level, complex task (Fagot and Vauclair, 1991) and that bipedal posture might not provide any supplementary bias in laterality. However, the postural effect on bimanual coordination tasks should be studied in many other species of nonhuman primates to confirm this hypothesis.

Our study is the first one involving bipedal tool use in bonobos, and, to date, only two studies have been conducted on bipedal tool use in nonhuman primates: one in chimpanzees (Braccini et al., 2010) and the other in capuchins (Westergaard et al., 1998b). Our two tasks involving tool use showed no significant difference in direction of hand preference between a seated and a bipedal posture, which is in agreement with these two previous studies. However, these authors showed that chimpanzees and capuchins were more strongly lateralized when using tools in a bipedal posture, in contrast to our results showing that bonobos were strongly lateralized for both postures. This suggests three possible explanations: (1) our sample size was too small to show a significant effect of the posture, (2) the difference between laterality patterns found in other studies and our results could be due to an effect of the task (as suggested above), and (3) bonobos may be less sensitive to the effect of bipedalism compared with chimpanzees. Indeed, bonobos seem more adept at maintaining balance in a bipedal posture and might therefore be less susceptible to the effect thereof on hand preference than other species. For instance, Braccini et al. (2010:238) noted that: “the bipedal posture appeared to be difficult for the chimpanzee.” These authors noticed that in a bipedal posture the legs of chimpanzees were shaking and some individuals did not want to perform the task in this posture. We did not observe this phenomenon during our observations in bonobos. However, one can note that two individuals did not use a bipedal posture for the maze task and one, the youngest subordinate male, never had access to mazes for the two postures. We could explain

this observation by a problem of access opportunity related to the hierarchy. Indeed, the young subordinate male avoided the small cages that housed the mazes, most likely due to the higher amount of competition and his low ranking status. The second individual was the dominant female who only used the maze of the main cage that necessitated a seated posture. This could be explained by the fact that the dominant female often occupied the large cages in order to keep a close watch on group members. It would be interesting to conduct the maze task with isolated individuals, in the same cage, and/or by proposing only mazes necessitating bipedal posture in order to better understand the influence of comfort and hierarchy.

'Bouts' versus 'frequency'

Concerning the two different recording techniques ('bouts' versus 'frequency'), our measurements for HI values were significantly and strongly correlated. Thus, using HI values based on frequency or bouts provided similar results in agreement with other studies (Westergaard and Suomi, 1996; Hopkins et al., 2001, 2004, 2005a; Palmer, 2002, 2003; Hopkins and Cantalupo, 2003; Bogart et al., 2012; Hopkins, 2013). However, regarding the z-scores, we found differences between frequency and bout data for the tube task in bipedal posture. In this case, the number of data points had an effect on our estimate of laterality. Some authors suggested that the use of frequencies may influence laterality estimates and may thus introduce sampling biases (McGrew and Marchant, 1997; Palmer, 2002, 2003; Hopkins and Cantalupo, 2003). However, in a recent article, Hopkins (2013) suggested that the use of the z-score with bout data might bias data towards the null hypothesis (no significant hand preference) because the z-score is sensitive to sample size and with bout data we typically have fewer numbers of right and left hand use for bouts than frequencies. Moreover, Hopkins (2013) suggested that there is no statistical justification for claims that the independence of data points introduces biases in the measurement of hand preference in nonhuman primates. Thus, as suggested by Hopkins (2013), it appears opportune to continue to record and report bouts and frequencies in behavioral asymmetry studies in order to resolve the disagreement about these two recording techniques.

Contributions to human evolution: link between hand preference, tool use, locomotion, and language

Task complexity had a greater effect than posture on hand preference in our subjects. Our results have interesting implications for theories on the emergence of human lateralization in relation with tool use and bipedalism. Even if our data cannot by themselves explain the preponderance of right-handers in the human species, they support the tool use hypothesis (Kimura, 1979; Frost, 1980), which proposed that the preference for the right hand might have emerged in humans as an adaptation for complex tool use and manufacture.

Bonobos do not often use tools in the wild for feeding (Ingmanson, 1996), but in this study they used tools in this context with preferentially the right hand. Moreover, it seemed to require little effort for them to remain in a bipedal posture. Kimura (1979) suggested that tool use and bipedalism are linked to the emergence of the lateralization of the brain and particularly to the strong right hand preference in humans. In accordance with this hypothesis several studies suggested that hand preference in great apes might be linked to posture and/or tool use (Olson et al., 1990; Hopkins, 1993; Hopkins et al., 2007a; Cantalupo et al., 2008; Braccini et al., 2010). However, the bonobos we studied here often preferentially used the right hand in seated posture and bipedal posture did not

have a supplementary effect on hand preference during tool use tasks. Moreover, several studies showed a preference for the right hand when individuals manipulated in bipedal postures but not in other postures such as seated or tripod ones (e.g., chimpanzees and orangutans: Hopkins, 1993; bonobos: Hopkins et al., 1993; macaques: Westergaard et al., 1998a; *Cercopithecus*: Chapelain et al., 2006; capuchins: Westergaard et al., 1997). However, only one study directly examined bipedal tool use (Braccini et al., 2010) and did not report a preference for the right hand when chimpanzees used tools in this posture.

It is unlikely that bipedalism had such an important role in the elaboration of tool use and in the preponderance of the right hand preference in humans. Indeed, a recent neurological study conducted by Hashimoto et al. (2013:1) suggested "that adaptations underlying tool use evolved independently of those required for human bipedality." Hand preference might be older than bipedalism in origin and rather linked to an arboreal lifestyle that requires complex body postures and manipulation. In fact, arboreal locomotion requires fine motor control, and the anatomical specializations of the forelimbs of arboreal species are probably associated with a well-developed grasping ability (Fabre et al., 2013). In addition, there might have existed a link between the mode of locomotion and manipulative abilities, with a tendency for the adaptation of manipulation for arboreal species (Sustaita et al., 2013). In this context, the capacity to grasp has been proposed as a "critical adaptive innovation" for arboreal primates (Kivell et al., 2010:1549) and a "key feature" of primate evolution (Ravosa and Dagosto, 2007:18). An arboreal lifestyle could have led to the elaboration of manual skills and tool use in primates, and hand preference could have emerged from arboreal ancestors coming down to the ground to use tools like some apes today.

Finally, the present work shows that the link between bipedalism and hand preference is far from being established and that the link between bipedalism and the capacity to use and manufacture tools is far from being obvious. It thus remains to be demonstrated, and more studies are needed to explore the link between arboreal lifestyle and manual preference. In this framework, species such as gibbons, gorillas, orangutans, and bonobos are of particular interest.

Another factor often invoked in the emergence of the strong hand preference for the right hand in humans is language. A predominance of right hand use has been reported in gestures occurring while humans are talking (Kimura, 1973a,b), including the communication between deaf people (Grossi et al., 1996). These asymmetrical gestures reflect the dominance of the left hemisphere for the perception and production of speech (Knecht et al., 2000). Moreover, studies in humans showed that brain regions implicated in the perception and production of speech (Broca's area and Wernicke's area) were also implicated with tool use behavior (Hopkins et al., 2007b). Some authors suggest that the neuronal substrates of tool use may have served as a preadaptation for the evolution of language and speech in modern humans (e.g., Greenfield, 1991; Bradshaw and Rogers, 1993). Hopkins et al. (2007b) reported asymmetries in chimpanzees in the homologs to Broca's and Wernicke's areas associated with hand preference for tool use. Consequently, these authors suggested that control of complex motor tool use action may have served as a preadaptation for the emergence of neural capacities required for language in humans (Hopkins et al., 2007b). Our results in bonobos showed a tendency to preferentially use the right hand for tool use tasks, which reflects the dominance of the left hemisphere for these actions. Moreover, Kanzi, a bonobo, was thought to have rudimentary language comprehension skills comparable to a 2.5 year-old child and also displayed impressive symbolic communicative skills (e.g., Savage-Rumbaugh et al., 1977, 1985, 1986; Savage-Rumbaugh,

1987). So, it appears interesting to apply in bonobos the same neurological study of Hopkins et al. (2007b) to confirm the link between tool use and language. This could bring us more information about the emergence of language regarding hypotheses that propose a relationship between language and hand preference (Hewes, 1973; Corballis, 2003; Vauclair, 2004), in that the emergence of right hand preference would be a preadaptation to language. However, more studies are needed to test the hypothesis that lateralization based on tool use preceded that for language (e.g., Steele and Uomini, 2009).

To conclude, although our sample size does not allow us to generalize at the group level, and even less at the population level, our large number of independent data points suggests robust results. It appears therefore essential to replicate our study in more groups of bonobos and to compare the maze task between different species of primates, including humans, in order to provide additional leads on the evolution of hand preference. Comparing this task among different primates would be of particular interest regarding the hypothesis proposing tool use as a selective pressure for hand preference (Kimura, 1979; Frost, 1980). It would also be essential to quantify hand preference in several primate species during natural activities varying in complexity in their natural habitat and on the ground, but also in trees.

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ANNEX C

Bardo A., Pouydebat E., 2015. Stratégies de manipulation d'outils lors de la tâche du labyrinthe chez les gorilles et les orangs-outans. *Revue de primatologie* (6) document 54. XXVIIIe Conference of the French Society Of Primatology in Strasbourg, 14-16 October 2015.

Résumé

La manipulation et les mouvements intra-manuels ont largement été décrits dans la littérature chez les humains. Les primates non-humains présentent également de grandes capacités de manipulation (fruits, proies, substrats, outils, congénères...) qui diffèrent selon les espèces. Cependant, les études dynamiques chez ces derniers sont rares et portent essentiellement sur les chimpanzés (*Pan troglodytes*). Il apparaît nécessaire d'explorer les capacités manuelles chez différentes espèces de primates non-humains afin de mieux comprendre les spécificités de chaque espèce et l'évolution des capacités de manipulation d'objets ainsi que de discuter sous un nouvel angle l'émergence des éventuelles spécificités humaines. L'objectif de cette étude était de comparer les capacités de manipulations chez deux espèces de grands singes, les gorilles (*Gorilla gorilla gorilla*) et les orangs-outans (*Pongo abelii*), lors d'une même tâche de manipulation et d'utilisation d'outils. Cette tâche a été testée afin de mettre en évidence leurs capacités à saisir, à manipuler à l'intérieur de la main (identification de mouvements intramanuels) et à utiliser des outils dans le but de récupérer une noix placée dans un labyrinthe en bois et ceci à travers un grillage. Six sessions par individu, une session correspondant à 1 noix récupérée, ont été menées chez les gorilles (N = 5) comme chez les orangs-outans (N = 7). Différents paramètres ont été quantifiés comme le type de saisie (par ex. uni-manuelle, bouche) ou de postures manuelles (par ex. puissance, précision). Afin de décrire les stratégies intra et interspécifiques adoptées, des analyses à composantes principales (ACPs) ont été réalisées en intégrant différents paramètres tels que le nombre de mouvements de la main, le nombre d'obstacles touchés, de mouvements intra-manuels utilisés, de postures manuelles différentes et le temps total passé à récupérer la noix. Une ACP a été réalisée sur l'ensemble des sessions ainsi qu'une ACP sur la session considérée comme la plus performante pour chaque individu, c'est-à-dire celle au cours de laquelle l'individu a effectué le moins de mouvements de la main. Les résultats montrent des différences inter et intra-spécifiques. Les stratégies de manipulation chez les orangs-outans étaient néanmoins plus variées que chez les gorilles. Par exemple, pour saisir l'outil, les orangs-outans ont utilisé leurs mains, leur bouche ou encore leurs pieds tandis que les gorilles ont employé systématiquement une main. Les différences de stratégies observées entre les deux espèces et la forte variabilité chez les orangs-outans pourraient s'expliquer par leur différent mode de vie. En effet, les orangs-outans qui sont arboricoles sont connus pour manipuler dans les arbres ce

qui n'a pas été observé chez les gorilles qui semblent manipuler davantage au sol. Les deux espèces pourraient donc avoir développé des stratégies qui leur sont propres en rapport avec leur écologie. Il serait intéressant de comparer la morphologie des mains de ces deux espèces afin de mettre en évidence un potentiel lien entre forme et fonction, les orangs-outangs étant, parmi les grands singes, ceux qui ont proportionnellement à leur main le pouce le plus court. L'ensemble des résultats montre la nécessité de quantifier la manipulation d'objets chez différentes espèces, avec de nouvelles tâches et méthodes, pour mieux comprendre les réelles capacités manuelles spécifiques à chaque espèce en fonction de leur écologie. Merci au zoo d'Amnéville, La Vallée des Singes, le zoo de La Palmyre ainsi que la Ménagerie à Paris pour leur accueil et leur aide lors de nos expérimentations. Nous tenons aussi à remercier la SFDP, les ATM Formes et Collections Vivantes du MNHN pour leur aide financière.

Mots-clés : labyrinthe, manipulation, mouvements intra-manuels, outil, postures manuelles

ANNEX D

Bardo A., Borel A., Guéry J.P., Lemaire M., Lempereur E., Pouydebat E., **2015**. Manipulative abilities during the same tool use task in different species of primates. *Folia Primatologica* **86** (4): 243. 6th Congress of the European Federation for Primatology Meeting in Rome, August 25-28 2015.

Abstract

Primates have highly developed abilities for grasping and manipulation that differ between species. In this context, the human hand is considered unique, based on its functional characteristics. However, the real dynamic manual abilities of primates remain poorly known. The purpose of this study is to compare the manipulative strategies in different species of primates (humans, chimpanzees, gorillas, orangutans, capuchins), during the same tool use task. This task requires the use of a tool to recover a static food item in a wooden maze while facing many obstacles; the wire netting between the subject and the maze, and the obstacles inside the maze. All species were in the same experimental conditions allowing us to compare across species. We here focus on the functional strategies used during this task by the different species and quantify the grip types and the in-hand movements involved to reposition the tool in the hand. We found common strategies despite the differences in hand morphology but also strategies specific to some species. We discuss the results in the context of the evolution of manipulative behaviours and highlight the importance of novel methods to understand better the manual specificities of each species. This study complies with the ethical guidelines by the CNRS and French governmental animal care committees and with the IPS Guidelines for the Use of Nonhuman Primates in Research.

ANNEX E

Bardo A., Borel A., Pouydebat E. Functional strategies during tool use tasks in captive bonobos. The Anthropology of Hands conference in University of Kent (UK), 24-26 June 2015.

Abstract

Primates have highly developed capacities for gripping and manipulating that differ between species. In this context, the human hand is considered as unique based on its functional characteristics. However, the real dynamic manual abilities of primates remain poorly known. The aim of the present study was to quantify the functional strategies (manual postures and in-hand movements) used by 8 captive adult bonobos during a new complex tool use task, consisting of recovering food in a wooden maze placed outside the cage. We found 1) that each individual presented his own manipulations techniques and 2) a difference between males and females with a greater variability in manual postures for males and more in-hand movements for females. Bonobos had individual specificities that could reflect the specialization of their manipulation strategies, especially here for a complex task. They were able of in-hand movements similar to humans and chimpanzees. The observed sex effect could reflect the hierarchy with females taking/having more time to perform a task. These preliminary results show the necessity to pursue the quantification of object manipulation in different species for new tasks and with new methods to better understand the manual specificities of each species.

ANNEX F

Bardo A., Borel A., Pouydebat E. Tool making and use by captive bonobos: functional & behavioral strategies. 21st Benelux Congress of Zoology in Liège (Belgium), 11-12 December 2014.

Abstract

Primates have highly developed capacities for gripping and manipulating that differ between species. In this context, the human hand is considered as unique based on its functional characteristics. However, the real dynamic manual abilities of primates remain poorly known. The aim of the present study was to quantify the behavioral strategies (tool selectivity and modification) and functional strategies (manual postures and in-hand movements) used by 8 captive adult bonobos (*Pan paniscus*) during two tool use tasks: food extraction and a new, more complex task consisting of recovering food in a wooden maze placed outside the cage. We found that 1) bonobos were able to plan, chose and modify their tools according to the task; 2) that each individual presented his own manipulation techniques with more variability for the maze task than extractive food tasks; 3) more in-hand movements for the maze task than extractive food task; 4) a difference between males and females with a greater variability in manual postures for males for both tasks, and more in-hand movements for females. Bonobos had individual specificities that could reflect the specialization of their manipulation strategies, especially for the more complex task. They were able of in-hand movements similar to humans and chimpanzees. The observed sex effect could reflect an effect of the hierarchy with females taking more their time to perform a task. These preliminary results show the necessity to pursue the quantification of object manipulation in different species for new tasks and with new methods to better understand the manual specificities of each species.

ANNEX G

Bardo A., Borel A., Meunier H., Lemaire M., Lempereur E., Guery J.P., Pouydebat E., 2015. Stratégies de manipulation d'outil chez les humains et les bonobos. *Revue de primatologie* (6) document 8. XXVII Conference of the French Society Of Primatology in Poitiers, 4-7 November 2014.

Résumé

La main humaine est considérée comme unique au travers certaines spécificités fonctionnelles comme l'individualisation des doigts et la capacité de saisir avec puissance un outil entre le pouce et le côté latéral de l'index. Cependant, les primates non-humains présentent de grandes capacités de manipulations. Ainsi, peut-on réellement affirmer que ces caractéristiques fonctionnelles humaines ne sont pas partagées par d'autres primates ? L'étude préliminaire menée ici a pour objectif d'analyser les stratégies de manipulation chez des humains, adultes (N = 10 hommes, âge = $28 \pm 5,92$ ans) comme enfants (N = 10 garçons, âge = $5,3 \pm 0,48$) et des bonobos (*Pan paniscus*) captifs (N = 6 dont 4 femelles et 2 mâles, âge = $20,33 \pm 5,31$) au cours d'une même tâche nécessitant la manipulation d'un outil. Cette nouvelle tâche consiste à récupérer une noix placée dans un labyrinthe en bois et ceci à travers un grillage. Les deux espèces disposaient d'un choix varié de branches (divers tailles et diamètres). Trois sessions par individu, une session correspondant à 1 noix récupérée, ont été menées chez les bonobos comme les humains. Différents paramètres ont été quantifiés comme le type de saisie (uni-manuelle versus bi-manuelle), de postures manuelles (e.g. puissance, précision) et la performance (basée sur les nombres de mouvements et d'obstacles touchés). Les résultats montrent des différences inter et intra-spécifiques et un effet de l'âge chez les humains pour certains paramètres. Tout d'abord, les bonobos ont utilisé un seul outil avec une seule main alors que les humains (adultes et enfants) ont employé en majorité des stratégies bi-manuelles (65 %) et les adultes se sont parfois servis de deux outils (30 %). Concernant les saisies uni-manuelles, les bonobos ont utilisé 32 formes de postures manuelles contre 26 pour les humains adultes et 125 pour les enfants. Au cours des saisies bi-manuelles, 4 fois plus de postures ont été quantifiées. Par ailleurs, les enfants ont davantage utilisé des saisies de puissance que les adultes qui ont principalement employé une saisie de précision à 3 doigts (e.g. tenue du stylo) pendant que les bonobos ont présenté des préférences différenciées au niveau individuel. Pour finir, les adultes humains se sont montrés plus performants que les bonobos, eux-mêmes plus performants que les enfants. L'utilisation des deux mains chez les humains pourrait s'expliquer par une saisie plus stable et puissante de l'outil pendant que l'utilisation de deux outils chez les adultes, plus complexe sur le plan de la coordination, pourrait apporter à certains individus une optimisation du trajet de la noix par dissociation des actions de la main droite versus de la main gauche (pousser vs contrôler). La plus grande

variabilité des types de saisies chez les enfants pourrait s'expliquer par le manque d'expérience et d'apprentissage dans les stratégies de manipulation. Les bonobos présentent quant à eux des spécificités individuelles pouvant traduire la spécialisation de leurs stratégies de manipulations. L'ensemble des résultats montre qu'il est nécessaire d'approfondir les manipulations d'objets afin de mieux comprendre les spécificités de chaque espèce, et pas seulement humaines, et les causes des convergences parfois partagées. Seule une approche détaillée et comparative (inter et intra-spécifique) nous permettra de discuter sous un nouvel angle l'émergence des éventuelles spécificités humaines.

Mots-clés : bonobos, humains, manipulation, outil, performance

ANNEX H

Bardo A., Meunier H., Pouydebat E. Tool making and use by captive bonobos: behavioral strategies, efficiency and tool selectivity. 25th Congress of the International Primatological Society, Hanoi (Vietnam), 11-16 August **2014**.

Abstract

The bonobos do not appear to use tools in the context of food acquisition in their natural environment but primarily in social functions (e.g. communication, play, cleaning). However, captive studies indicate that they use a variety of tools for food acquisition and comparative detailed data on the strategies they can set up are lacking. The aim of the present study is to test how captive bonobos deal with tasks necessitating the use and manufacture of tools to acquire static food. We studied a task of extracting food, close to the “termite-fishing” task known in wild chimpanzees but still never observed in wild bonobos, and a new task of recovering food in wooden mazes placed outside the cage. During these two tool use tasks, we quantified the behavioral strategies (e.g. body posture, hand preference, manipulation techniques), efficiency and tools selectivity in a captive group of 8 adult bonobos (a 4-year-old bonobo never used tools). We found that all adult bonobos (1) were able to succeed these both tool use tasks, (2) all chose their tools and some modified them and (3) each individual presented his own manipulations techniques. Further experiment would be necessary and interesting to develop in other groups of bonobos, to assess intraspecific variability or the learning processes. This study complies with the ethical guidelines by the CNRS and French governmental animal care committees.

Keywords: bonobo, manipulation, strategies, tool use

ANNEX I

Bardo A., Pouydebat E., Cornette R. Morphological variability of the trapeziometacarpal joint among Hominids and functional involvements. IX national Symposium of Morphometric and Forms Evolution in Paris, 1-2 June **2016**.

MORPHOLOGICAL VARIABILITY OF THE TRAPEZIOMETACARPAL JOINT AMONG HOMINIDS AND FUNCTIONAL INVOLVEMENTS

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Introduction

Humans demonstrate high dexterity in daily tasks and are known to possess more complex manual abilities than non-human primates. The humans' manipulative skills are mainly justified by functional hand characteristics and the presence of unique morphological features considered to be linked to stone tool-making (Napier, 1960; Marzke, 1997; Susman, 1998; Tocheri et al., 2008). The trapeziometacarpal joint (Fig.1), with its saddle-shape, permits opposition of the thumb with other fingers (Napier, 1952) and is considered the most important articulation during human's manipulative activities. As we quantified manipulative inter and intraspecific variability across species during the same tool use task (Fig.2), we wonder if it could be explained by a shape variability of the trapeziometacarpal joint across species and individuals.

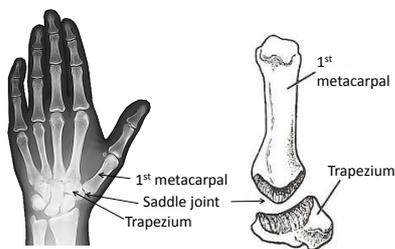


Fig. 1 Humans hand bones with the trapeziometacarpal joint called, according to its form, saddle joint.

Objectives

The purpose of this study is to detail 1) the shape variability of the trapeziometacarpal joint in humans (modern and fossil) and great apes, using 3D geometric morphometric analyses and 2) its functional implications. In addition, the quantified manipulative abilities used by the species during the tool use task will be compared to the morpho-functional variability.

Material & Methods

In order to precisely describe the complex shape of the trapezium and the metacarpal, we chose 3D surfacic geometric morphometric approaches. To begin, 3D acquisitions of each bone were performed using photogrammetry (Fig.3). This method allows to create high quality 3D models using pictures.



Fig. 3 3D acquisitions. From left to right: Illustration of one step of photogrammetry workflow; 3D model of trapezium and first Metacarpal obtained thanks to photogrammetry.

Then, in order to compare all bones in an homologous way, two templates were created using anatomical landmarks and sliding semi-landmarks of curves and surfaces (Fig.4). After superposition and sliding step (minimizing the bending energy), Principal Component Analyses (PCA) and 3D visualizations of the axes were performed. Shape co-variation analyzes will also be realized.

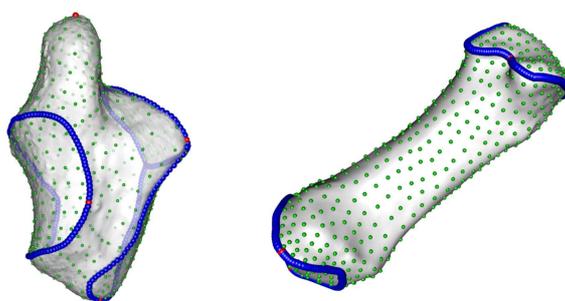


Fig. 4 Templates used for this study. Left: trapezium, right: first metacarpal. Red points= anatomical landmarks, blue=3D sliding-landmarks of curves, green=3D sliding-landmarks of surfaces.

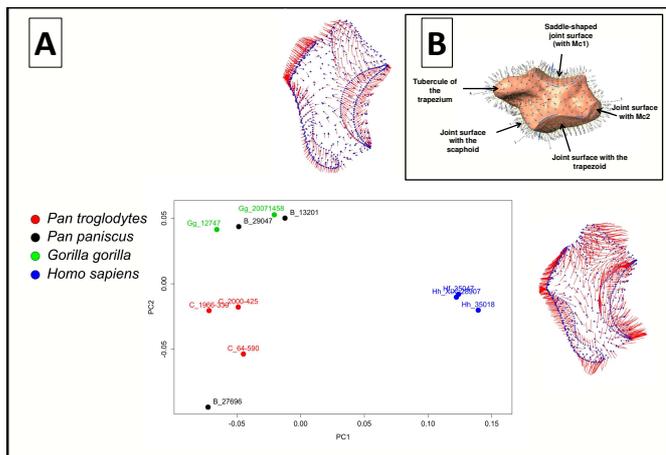


Fig. 5. Preliminary results. (A) Two first principal axes of PCA performed on trapezium (43 % and 14 % of variance respectively) for four species. Shape visualisations along axes shows (I) shape of the consensus in blue points and (II) red arrows for shape visualisations for the positive part of the axis. (B) Shape variation is directly interpreted regarding functional consequences on joint surfaces.

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Results and discussion

Preliminary results on the trapezium performed on eleven specimens from four species, *Pan troglodytes* (N=3), *Pan paniscus* (N=3), *Gorilla gorilla* (N=2) and *Homo sapiens* (N=2) show promising results (Fig. 5 A) : (I) a specific shape structure (II) a clear opposition between humans and the rest of the species and (III) a high shape variability in bonobos (*Pan paniscus*).

Shape differences are mainly situated on highly functional areas such as surface joints or muscular attachments (Fig. 5 B) involving different manual abilities.

This morpho-functional variability will be discussed in connection with the behavioral data.

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ANNEX J

Bardo A., Pouydebat E. How to objectively assess the complexity of a task? 25th Congress of the International Primatological Society, Hanoi (Vietnam), 11-16 August **2014**.



HOW TO OBJECTIVELY ASSESS THE COMPLEXITY OF A TASK?



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Introduction

Despite the fact that the effect of task complexity on hand preference has been considered for a long time, a lack of consensus around the definition of the complexity of a task still exist. It is difficult to define exactly the various functional and cognitive requirements of a manual task, yet it appears crucial to precisely define the complexity in order to standardize experimental protocols.

→ So, how to objectively assess the complexity of a task?

In our study we compared hand preference in nine captive bonobos during three “complex” tasks (one bimanual coordinated task and two different tool use tasks) in seated and bipedal postures. Our aims are to (1) assess the complexity of the tasks by identifying the criteria necessary to accomplish a task and (2) quantify the presence of these criteria in our three tasks. We hypothesized that the more criteria required to perform a task, the more functional and cognitive abilities are called upon, and thus the more “complex” the task will be.



Fig. 1 Tube task (N=9), requires coordinated bimanual hand movements involving different roles for each hand.



Fig.2 Extractive food task (N=8), needs the use a tool with one hand to be able to extract the food and visual guidance to insert the tool into the holes.

Material & Methods

First, we listed and qualified 16 existing cognitive and functional criteria (Table 1) present in the three tasks (Fig. 1, 2 and 3). Secondly, we quantified the presence of these criteria for all individuals and by task. Wilcoxon signed rank tests were used to test if there was a significant difference in the number of criteria involved in the task (with bonferroni correction, p').

Table 1 Criteria involved in the three tasks. Criteria were defined by the viewing of videos taken during the experiments concerning hand preference in bonobos (Fig. 1, 2 and 3).

Criteria linked to the :				
Generality of the task	Manipulation	Body posture	Tool	Movements to recover the food
Novelty of the task ¹	Requires the implication of both hands ³	Control of the body balance ¹	The task requires a tool to be successful	The action requires « precision » ⁵
Constraints related to the age of individuals (e.g. the age at which individuals would be interested and/or able to performing a behavior)	To complete the task and to manipulate it, the object must be stabilized by subordinate hand (opposite to the one which manipulates) ³	= posture different from that adopted spontaneously by the subject e.g. bipedal vs. seated	Complex tool use manipulation : tool use that includes more than one element ⁴ e.g. the need to manufacture the tool for recover embedded food ⁵	The shoulder is involved
Visual constraints ² (e.g. eyes fixed all the time on the object during the task)	Requires more than one step (element) to complete the task ^{1,3,4} e.g. manipulation of one detached object relative to another involving subsequent change of state of one or both of the objects ³	Need for body posture adjustments e.g. to realize the maze task, adjustments of body posture are needed		The elbow is involved
	Or to use a tool to recover the food by facing many obstacles such as a wire netting and obstacles placed inside the maze (Fig. 3)	Need for postural support or not		Wrist and fingers are involved
				The movements are executed in more than one plane



Fig. 3 Maze task (N=7), requires to use a tool to recover the nut by facing many obstacles: first, obstacles placed inside the maze in order to complicate the itinerary of the walnut, and second, between the maze and the individual (wire netting).

Results

The bimanual coordinated task involved significantly fewer criteria than tool use tasks (Fig. 4). The extractive task involved also significantly fewer criteria than the maze task (Fig. 4).

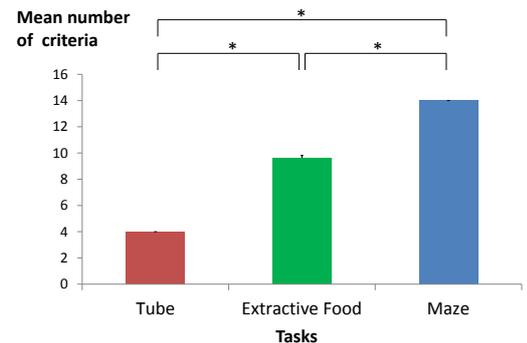


Fig. 4 Means number of criteria by task. Friedman rank sum test, F = 12.06, df = 2, p = 0.002. * = Wilcoxon signed rank test, p' < 0.05.

Discussion

- According to this method, our preliminary results show that a task involving the use of a tool to recover a food in a maze, and requiring several criteria to solve the problem, is more "complex" than an extractive food task with a tool involving fewer criteria, and than a bimanual coordination task.
- However, for the next step we need to improve the method by distinguishing the functional from the cognitive criteria in order to better discuss the link between both. Some manipulative task may have been underestimated compared with some tool use tasks.
- Finally, it is important to standardize the procedures and to describe and quantify the most objectively as possible the different degrees of the "complexity" of the task if we want to better understand the evolution of manipulative abilities in association with the many parameters involved (i.e. motor control, hand preference, diet, locomotion).

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ANNEX K

Pouydebat E., **Bardo A.**, Canteloup C., Borel A. Preliminary observation of coconut cracking open among capuchins monkeys and humans: proto tool-use costs and benefits. 25th Congress of the International Primatological Society , Hanoi (Vietnam), 11-16 August **2014**.

PRELIMINARY OBSERVATION OF COCONUT CRACKING BEHAVIOR IN CAPUCHINS: COSTS & BENEFITS



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Photo: Bardo A.

Figure 1. Capuchin cracking a coconut

Introduction

In semi-captivity, capuchins (*Sapajus sp.*) open coconuts (Fig. 1) by pounding it against hard substrates. The difficulty of this task consists in opening the coconut without losing the coconut milk. Individuals need to strike the coconut with a lot of power to open it but they also need to control their movement to avoid blowing up the nut and loose the coconut milk. Here, we aim at understanding which behavioral and functional strategies are developed by capuchins to be efficient in this task.

Material & Methods

We analyzed the contribution of behavioral and functional parameters (repositioning, number of strikes, hand posture on the coconut, joint amplitudes) on the efficiency of coconut cracking among adults and juveniles capuchins. This experiment involved 7 adult females and 7 juveniles capuchins (*Sapajus sp.*) and focused on the opening of 10 coconuts per individual.



A: Low inferior limb amplitude & left hand on the top of the coconut

B: High inferior limb amplitude & both hands on the top of the coconut

Photo: Pouydebat E.

Figure 2. Example of different functional strategies

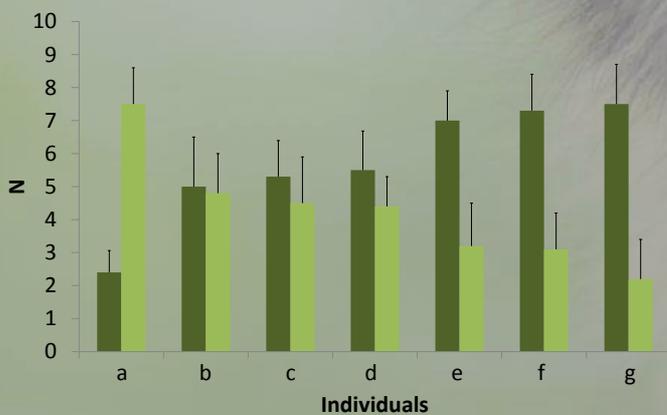


Figure 3. Number of repositioning (light green) and number of strikes (dark green) per individual (a to g)

Results

The juveniles never succeeded to open the coconut even after several attempts and after having observed the adults. Among adults, various functional strategies were used (Fig. 2) and different repositioning strategies were observed. The most efficient capuchin needed 2,4 strikes per coconut and the least efficient 7,5 strikes per coconut. Repositioning strategies predicted whether a capuchin would crack a coconut with efficiency. Indeed, the most efficient individuals were those who repositioned the most the coconut.

Discussion

Coconut cracking in capuchins involves several strategies and costs varying across individuals. As juveniles did not succeed, we can suppose that this non tool using task need several years to be successfully accomplished. In addition, these results are consistent with the strategies of stone tool making in humans (Fig. 4) for which the number of repositioning is higher among experts than among beginners, allowing them to reduce the number of strikes and then the cost of the task (Geribàs et al., 2010). However, the contrary could be found during tool use among capuchin (Fragaszy, personal observation) as in human. For example, preliminary results show that human expert performs less repositioning of the tool in the hand than beginners (Borel et al., in prep.). So, does the variability of the used strategies is a specificity of tool using versus manipulation or could we expect inter and even intraspecific variability for the same task ? In future studies on capuchin monkeys, we will quantify the functional parameters involved in coconut cracking behavior in order to test the correlation between the benefit and the functional strategies (i.e. hand positioning, body motion). This could help us to discuss the evolution of manipulation and the emergence of tool use in primates.



Photo: Borel A.

Figure 4. Tool making by percussion

ANNEX L

Bardo A., Meunier H., Pouydebat E., **2013**. Differential manipulative strategies in great apes during a new complex tool use task. 5th Congress of the European Federation for Primatology. *Folia Primatologica* **84**, 246-247.



Differential manipulative strategies in great apes during a new complex tool use task

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Introduction

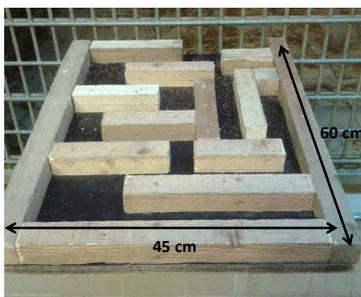
High level of manual function and dexterity is a crucial adaptation in primates. All primates use their hand for feeding, moving and during social interaction, and show a great variety of grips and hand movements. Some authors suggest that the emergence of bipedalism enabled the liberation of hands (e.g., Jablonski and Chaplin, 1993), and thus favored bimanual coordination and tool use in primates (Videan and Mc Grew, 2002). Lateralization and particularly the emergence of right hand preference in humans could thus be linked to the emergence of bipedalism and tool use. In order to understand the origins and evolution of manual object manipulation in primates, we need a detailed description of manual function. For that purpose, we provided a new complex tool use task to bonobos, chimpanzees, orangutans and gorillas. In this preliminary study, we created a specific tool-using task consisting in recovering nuts with a stick (branches) in a wooden maze placed outside along their cage. We investigated and compared between species their manipulative strategies, success rates, hand preferences and grip postures. We expected that chimpanzees and bonobos show both the greatest manipulative strategies and best success rates and that individuals using tools have a preference for the right hand.

Material and methods

- 8 bonobos (4♀4♂, 7 to 43 years) → 6 sessions/individuals
- 7 chimpanzees (5♀2♂, 5 to 25 years) → 15 sessions for the group
- 3 orangutans (2♀1♂, 19 to 36 years) → 10 sessions/individuals
- 3 gorillas (2♀1♂, 14 to 22 years) → 10 sessions /individuals

→ 1 session= 30 minutes

Wooden maze



We recorded for each individuals :

- Tool use, modification of tool
- Success rates
- Hand preferences
- Grip postures

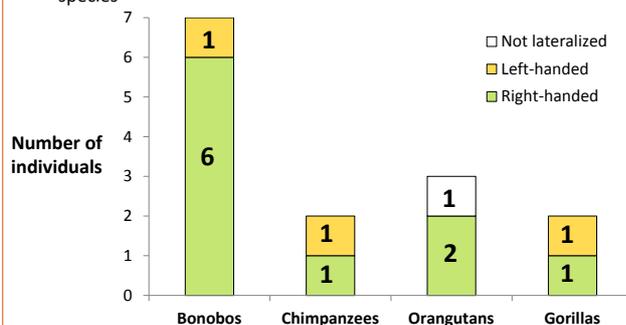
- Individual hand preferences were calculated using a binomial *z-score* for individual having performed at least six sequences.

Results

1) Percentages of individuals that used tool, modified tool and who succeeded the task by species

	Bonobos (N=8)	Chimpanzees (N=7)	Orangutans (N=3)	Gorillas (N=3)
Tool use	100 %	71 %	100 %	100 %
Modification of the tool	87.5 %	0 %	100 %	33 %
Success	87.5 %	0 %	33 %	0 %

2) Number of right-handed, left-handed, and not lateralized subjects by species



3) Percentages of grip postures used by species

	Bonobos	Chimpanzees	Orangutans	Gorillas
Power	41 %	74 %	62 %	33 %
Precision	53 %	0 %	2 %	12 %
Other	6 %	26 %	36 %	55 %

Discussion

- Bonobos and orangutans had the greatest interest in mazes. Moreover they modified their tool (branch) during the experiment. In addition, six bonobos (out of seven) and two orangutans (out of three) show a right-hand preference. These data support the tool-use hypothesis (Frost, 1980; Kimura, 1979) predicting a right-hand preference for tool-use.

- Current hypotheses suggest a link between the mode of locomotion and manipulation in primates, with a tendency for exaptation of manipulation for arboreal species, which is the case in our experiment.

- Bonobos showed the greatest diversity of grips. In humans and non-human primates, several studies have shown that the object properties such as size or form influence grasp patterns (e.g. Pouydebat *et al.*, 2011). In our case, bonobos had a greater choice of branches than the other three species, and the diversity in branches availability between species could thus explain both the fact that some species used more power grip than others and the interspecies differences in task success. This preliminary experiment should thus be redone with identical tools between species. We plan to test more subjects of these species but also capuchin monkeys with more standardized tools to try to better understand the evolution of dexterity and its neuromuscular and morphological requirements.

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ABSTRACT

Humans are considered to have unique manual abilities in the animal kingdom. However, we still do not know what the real manual abilities of primates are, nor how they evolved. Are humans really unique? This dissertation aims to investigate the manipulative abilities in Hominids related to their hand anatomy and function, using an interdisciplinary framework combining behavioral, morphological, functional, and biomechanical approaches. To quantify the behavioral strategies and manipulative abilities in Hominids, I have conducted an ethological study on different captive great apes and on humans during the same complex tool use task. I used 3D geometric morphometrics and comparative approaches on the trapeziometacarpal complex combined with a musculo-skeletal model to better interpret the behavioral results and to test the link between hand morphometric and biomechanical constraints during tool use in Hominids. The results of this PhD show that great apes demonstrate dynamic manipulative abilities but that each species has its own specificities. More complex dynamic abilities, such as in-hand movements, are observed for bonobos and gorillas than for orangutans. The different lifestyles of the species may explain this variability. Moreover, during the complex tool use task, humans perform better than great apes and show specificities. The new integrative approach also clearly shows that the different manipulative abilities of Hominids cannot only be a consequence of the different morphologies of the trapeziometacarpal joint but also of the different mechanical constraints related to the overall hand morphometric. These results highlight the difficulty to infer manual abilities in fossils from some bone shape information, without taking into account the overall morphometric of the hand and its possible link with biomechanical constraints. This PhD thesis provides new information on the manual abilities of Hominids, on the different constraints surrounding these abilities, and new information to better understand the evolution of manual abilities in primates.