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DOI

<https://doi.org/10.1016/j.jhevol.2018.10.001>

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The impact of hand proportions on tool grip abilities in humans, great apes and fossil hominins: a biomechanical analysis using musculoskeletal simulation

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Keywords: Hominoids; *Australopithecus*; *Homo*; Great apes; Manipulation; Dexterity

ABSTRACT

Differences in grip techniques used across primates are usually attributed to variation in thumb-finger proportions and muscular anatomy of the hand. However, this cause-effect relationship is not fully understood because little is known about the biomechanical functioning and mechanical loads (e.g., muscle or joint forces) of the non-human primate hand compared to that of humans during object manipulation. This study aims to understand the importance of hand proportions on the use of different grip strategies used by humans, extant great apes (bonobos, gorillas and orangutans) and, potentially, fossil hominins (*Homo naledi* and *Australopithecus sediba*) using a musculoskeletal model of the hand. Results show that certain grips are more challenging for some species, particularly orangutans, than others, such that they require stronger muscle forces for a given range of motion. Assuming a human-like range of motion at each hand joint, simulation results show that *H. naledi* and *A. sediba* had the biomechanical potential to use the grip techniques considered important for stone tool-related behaviors in humans. These musculoskeletal simulation results shed light on the functional consequences of the different hand proportions among extant and extinct hominids and the different manipulative abilities found in humans and great apes.

1. Introduction

In primates, and particularly humans, manipulating objects is a crucial skill for essential behaviors such as feeding, social interactions, tool-making and use (Boesch, 1993; Fragaszy, 1998; Byrne et al., 2001; Hopkins et al., 2007). However, non-human primates use their hands for both locomotion and manipulation and show bony and soft tissue morphology of the hands and forelimbs that reflect these diverse functional requirements (e.g., Straus, 1940; Schultz, 1956, 1969; Jouffroy et al., 1993; Zihlman et al., 2011; Myatt et al., 2012;

Kivell et al., 2016). In contrast, humans are distinct from other primates in typically only using their hands for manipulation and they show morphological features consistent with this more specialized function (e.g., Wood Jones, 1916; Napier, 1993; Marzke, 1997). In this context, the human hand is traditionally considered unique in the animal kingdom for its ability to use a variety of forceful precision grips, opposing the thumb to the pads of the fingers, and power squeeze grips (Napier, 1960; Marzke, 1997; Susman, 1998; Tocheri et al., 2008). This enhanced dexterity is usually linked to specific morphological features, such as a long, mobile and powerful thumb, short fingers with well-developed volar pads at the tips, and more stable radial carpometacarpal joints, which are thought to have evolved in response to tool-related behaviors (Napier, 1960; Marzke, 1997, Susman, 1998; Tocheri et al., 2008; Almécija et al., 2010, 2015; Feix et al., 2015; but see Rolian et al., 2010). Some grips are considered particularly important during stone tool-making and use in humans: the pinch grip between the thumb pad and the side of the index finger, the three-jaw chuck grip by the thumb pad and pad of the index and middle fingers, and the cradle grip, using the thumb and four finger pads, as well as the palm (Marzke and Shackley, 1986; Marzke, 1997).

The specific morphological features found in the human hand, and particularly intrinsic hand proportions (i.e., relative length of the thumb to the fingers), have been used in comparative morphological analyses to make inferences about the manipulative abilities of fossil hominins (e.g., Napier, 1962; Susman, 1988, 1994; Marzke, 1997; Alba et al., 2003; Niewoehner et al., 2003; Drapeau et al., 2005; Tocheri et al., 2008; Almécija et al., 2010, 2015; Kivell et al., 2011, 2015). For example, several researchers have estimated the intrinsic hand proportions of *Australopithecus afarensis*, suggesting they were capable of human-like pad-to-side and three-jaw chuck precision grips (Marzke, 1983) or pad-to-pad precision grasping (Alba et al., 2003; Almécija and Alba, 2014; but see Rolian and Gordon, 2014). Using 3D modeling based on hand bone geometry and range of motion, both australopiths

(Feix et al., 2015) and Neandertals (Niewoehner et al., 2003) were shown to be capable of human-like precision grasping. However, such manipulative abilities are not limited to humans and, potentially, fossil hominins. Recent research has shown that many non-human primates use hand grips that are comparable to those of humans, such as pinch grips and precision grips, and are capable of remarkable dexterity during, for example, food manipulation or tool use (Christel, 1993; Jones-Engels and Bard, 1996; Marzke and Wullstein, 1996; Christel et al., 1998; Byrne et al., 2001; Pouydebat et al., 2009, 2011; Bardo et al., 2016, 2017; Neufuss et al., 2017). Indeed, non-human primate manipulative abilities are largely unparalleled among mammals (Emery and Clayton, 2009; Bentley-Condit and Smith, 2010), and several species are efficient tool users such as macaques (Chiang, 1967; Malaivijitnond et al., 2007; Haslam et al., 2013), chimpanzees (Goodall, 1968; McGrew, 1992, 2010; Boesch, 2013), capuchin monkeys (Fragaszy et al., 2004; Ottoni and Izar, 2008; Visalberghi et al., 2007, 2013; Luncz et al., 2016), orangutans (van Schaik et al., 1996, 1999, 2003), and bonobos (Neufuss et al., 2017). Consequently, the relationship between morphology and potential dexterity remains unclear.

During object manipulation, including tool-related behaviors, humans and other primates are capable of a large diversity of grip strategies and hand movements (e.g., Fragaszy, 1998; Pouydebat et al., 2008, 2009; Crast et al., 2009; Reghem et al., 2013, 2014; Fragaszy and Crast, 2016; Bardo et al., 2016, 2017; Neufuss et al., 2017). Differences in grip strategies and abilities across primates are traditionally attributed to several factors, including variation in intrinsic hand proportions (Napier, 1960; Jouffroy et al., 1993; Marzke and Wullstein, 1996), differences in joint shape (Lewis, 1977, 1989; Tocheri, 2007; Marzke et al., 2010), in muscular anatomy (Day and Napier, 1963; Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012), or in social behaviors such as social learning (Whiten and Ham, 1992). For example, humans have the longest mean thumb length relative to the index finger

length (67%) compared to other apes (hylobatids, 52%; gorillas, 54%; chimpanzees, 47%; orangutans, 43%; Schultz, 1956). The short thumb and long, curved fingers of apes compared to humans (Schultz, 1956; Napier, 1960; Tuttle, 1969; Susman et al., 1984; Jouffroy et al., 1993) are thought to limit the pad-to-pad contact in thumb opposition (Napier and Napier, 1967; Marzke and Wullstein, 1996). In addition, there are interspecific differences in the range of motion across joints of the hand that are generally consistent with the typical hand postures used during locomotion (Napier, 1960; Tuttle, 1969; Rose, 1988). For example, great apes show greater flexion at the metacarpophalangeal joints of the fingers ($\sim 170^\circ$) than do humans ($\sim 90^\circ$), while extension is restricted in orangutans (19°) compared to that in African apes (50° ; Napier, 1960; Tuttle, 1969; Susman, 1979; Rose, 1988). The saddle-shaped morphology of the trapeziometacarpal joint allows for a large range of motion in all apes, including humans, although there is some interspecific variation with, for example, orangutans showing greater extension than African apes (Tuttle, 1969; Rose, 1992).

Great apes lack independent flexor pollicis longus (FPL; i.e., thumb flexor) and extensor pollicis brevis (EPB; i.e., thumb extensor) muscles, both of which are well-developed extrinsic thumb muscles present in humans (Straus, 1942; Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012). The EPB inserts on the pollical proximal phalanx to help maintain metacarpophalangeal joint extension simultaneously with the flexion of the distal phalanx by the FPL (Marzke et al., 1998; Diogo et al., 2012). Thus these two muscles are considered critical to the enhanced manipulative abilities in humans compared to great apes, particularly powerful flexion of the thumb (Straus, 1942; Tuttle, 1969; Susman, 1994, 1998; Tocheri et al., 2008; Almécija et al., 2010; Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012). However, bonobos have a stout tendon of the flexor digitorum profundus (FDP; i.e., extrinsic flexor muscle) attaching to the distal pollical phalanx (Miller, 1952; Myatt et al., 2012; Diogo et al., 2017; van Leeuwen et al., 2018) that functions similarly to the

FPL in flexing the thumb (as well as the index finger). This tendon is vestigial or absent in chimpanzees, orangutans and gorillas (Straus, 1942; Tuttle, 1969; Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012), it raises questions about how different muscles may function to perform similar manipulative tasks across great apes. There are few studies looking at the muscle activation/force involved during object manipulation in apes (hylobatids: Susman et al., 1982) compared to that during locomotor behaviors (gorillas: Tuttle et al., 1972; Tuttle and Basmajian, 1974; orangutans: Tuttle and Basmajian, 1978; chimpanzees: Susman and Stern, 1980; Tuttle et al., 1983; hylobatids: Jungers and Stern, 1981).

From a biomechanical point of view, performing a grip, such as a precision or power grip, and applying the appropriate grip force on an object requires, at least in part: (1) modifying joint angles to place the digits in contact with the object (which is related to joint morphology, soft tissue anatomy, and range of motion; Chan and Moran, 2006; Fleagle, 2013); (2) adapting muscle coordination to generate the appropriate force and balance at the joints (Johansson, 1996; Nowak and Hermsdörfer, 2005; Vigouroux et al., 2007; Fleagle, 2013); (3) having external and internal bone structures that can incur the mechanical loading (e.g., Napier, 1960; Tocheri et al., 2008; Almécija et al., 2010, 2015; Fleagle, 2013; Skinner et al., 2015a, b). Although the biomechanics of gripping in humans has been the focus of much clinical and biomedical engineering research (e.g., Cooney and Chao, 1977; An et al., 1985; Vigouroux et al., 2011; Goislard de Monsabert et al., 2012; Qiu and Kamper, 2014), comparatively little is known about joint angles, muscle forces and joint reaction forces during *in vivo* gripping in non-human primates (Brochier et al., 2004; Banks et al., 2007; Bury et al., 2009; Viaro et al., 2017). Consequently, it remains difficult to directly attribute specific anatomical characteristics (such as the size and shape of a bone, or absence of a muscle) to the use or non-use of a specific grip. In humans, these mechanical variables are

extensively studied using *in vivo* or biomechanical experiments combining kinematics, electromyography and force sensors, as well as using musculoskeletal modeling (Sancho-Bru et al., 2003; Vigouroux et al., 2011; Goislard de Monsabert et al., 2012). However, such *in vivo* experiments in non-human primates are not only logistically challenging (Chan and Moran, 2006; Oishi et al., 2008) but are often ethically impossible, and comparative studies across different species are hindered by discrepancies in muscle nomenclature and in methods used to quantify muscle architecture (Marzke et al., 1999; Myatt et al., 2011, 2012). Thus, biomechanical modeling of non-human primate or fossil hominin hands is most often by necessity founded upon a human hand model (e.g., Niewoehner et al., 2003; Feix et al., 2015; Liu et al., 2016; Domalain et al., 2017).

An understanding of human and non-human primate prehension requires clarification of the relationship between hand morphology and the grips used, which has several important practical implications. Muscle forces and joint loads may vary across hominids using the same grip due to variation in intrinsic hand proportions (Preuschoft, 1973, Thorpe et al., 1999) or differences in joint shape (Lewis, 1977, 1989; Tocheri, 2007; Marzke et al., 2010). Alternatively, the same articular shape may lead to different grip abilities related to variation in intrinsic hand proportions (Napier, 1960). For example, although great apes and humans all have a saddle-shaped trapeziometacarpal joint that permits mobility and opposition of the thumb (Napier, 1955; 1956; Rose, 1992; Marzke et al., 2010), the manipulative capabilities of the great ape hand are limited by the short length of their thumb relative to the length of the fingers (Schultz, 1956; Napier, 1960, 1993; Christel, 1993; Jouffroy et al., 1993; Marzke, 1997). This point is particularly relevant because variation in the trapeziometacarpal complex and thumb length often play a key role in inferences about manipulative abilities in extant primates and fossil hominins (Napier, 1955, 1961; Lewis, 1977, 1989; Susman, 1988; Trinkaus, 1989; Rafferty, 1990; Rose, 1992; Marzke, 1997; Niewoehner, 2001, 2003; 2005,

2006; Panger et al., 2002; Alba et al., 2003; Tocheri et al., 2003, 2005, 2008; Marzke et al., 2010; Marchi et al., 2017). Consequently, it is important to take into account the overall hand morphology and its potential influence on biomechanical loadings when inferring manipulative abilities in the past or explaining variation in manipulation in extant taxa.

Recent studies have investigated the potential manipulative skills across anthropoid primates (monkeys, apes and humans) using a human-based kinematic model of the thumb and index finger adapted to the different hand segment proportions of each species (Feix et al., 2015; Liu et al., 2016). They have confirmed via biomechanical modeling the long-held assumption that, based on a long thumb, short fingers and a large range of motion, humans have the greatest manipulative potential among primates (e.g., Wood Jones, 1916; Napier, 1960; Marzke, 1997, Almécija et al., 2010, 2015). These studies have also demonstrated that non-human primate taxa, such as macaques, baboons and capuchin monkeys, have a manipulative potential that is equal to or greater than that of our closest living relatives, chimpanzees (Feix et al., 2015; Liu et al., 2016). However, both of these previous studies only looked at simulated precision grip between the thumb and index finger using a kinematic model, and neither took into account muscle action. Although there is a growing data set on muscle architecture in great apes (e.g., Tuttle, 1969; Thorpe et al., 1999; Diogo and Wood, 2011; Zihlman et al., 2011; Diogo et al., 2012; Myatt et al., 2012; van Leeuwen et al., 2018), in vivo muscle coordination and mechanical loading required for grips typically used by different non-human primates remain largely unquantified. This lack of in vivo data prevents a complete understanding of the reasons that lead different taxa to use or not use particular grips.

Musculoskeletal modeling is a practical way to investigate the biomechanical loadings of the hand in non-human primates when in vivo measurements are not possible (Orr, 2016). Moreover, musculoskeletal modeling can incorporate extinct taxa and, within this

comparative context, can help inform interpretations of the evolution of potential grip capabilities in hominins (Orr, 2016). The objective of this study is to clarify the relationship between intrinsic hand proportions and the different grips used by extant great apes, including humans, using musculoskeletal modeling. In particular, we focus on the influence of variation in the relative lengths of the digits and their segments (i.e., metacarpal and phalangeal lengths) on the biomechanical loadings (especially the muscle forces and resultant joint moments) associated with six different grips that were commonly used by humans, bonobos, gorillas and orangutans during the same complex tool use maze task (Bardo et al., 2016, 2017). We build upon previous studies that have focused only on the thumb and index finger (Niewoehner et al., 2003; Feix et al., 2015; Liu et al., 2016) in using a musculoskeletal model of the complete human hand, including the wrist, palm and all digits, which is then adapted to fit the hand proportions of each hominid species. Rather than estimating the potential workspace, like previous kinematic models (Feix et al. 2015; Liu et al. 2016), we focus on estimating the resultant muscle joint moments and the muscle forces that would be required in each species to perform each of the six grips. Finally, within this comparative hominid context, this musculoskeletal model is adapted to the hand proportions of two fossil hominin species that preserve relatively complete hand skeletons: *Homo naledi*, dated to approximately 250 Ka (Kivell et al., 2015; Dirks et al., 2017); and *Australopithecus sediba*, dated to 1.98 Ma (Kivell et al., 2011; Pickering et al., 2011). The hand of *A. sediba* presents a mosaic of primitive African ape-like features and derived human-like features (Kivell et al., 2011), while *H. naledi* shows a combination of a human-/Neanderthal-like wrist and palm with curved fingers, indicating potentially both intensified manual manipulation and a significant degree of climbing (Kivell et al., 2015). Thus, the musculoskeletal model is also used to simulate the biomechanical potential to use all six grips in *A. sediba* and *H. naledi*.

We investigate how variation in intrinsic hand proportions between humans, fossil hominins and great apes may invoke different biomechanical loadings during each grip action.

2. Material and methods

2.1. Identification of preferential grip techniques during tool use

The grips analyzed in the current study were selected from the observed grips used by humans (*Homo sapiens*) and captive bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla gorilla*) and orangutans (*Pongo pygmaeus*) while completing the same complex tool use task (Bardo et al., 2016, 2017). This task consisted of maneuvering a walnut through a wooden maze with a bamboo stick, the details of which are described by Bardo et al. (2016). The grips used during this task were selected for the current study because the complexity of the task generated the use of several different grips across species and the task was performed in the same unconstrained conditions for each taxon, allowing us to obtain a comparative functional context (Bardo et al., 2016, 2017). During this task, each species used a preferential grip technique and some techniques were not used by all the species. Therefore, we selected six grips that were commonly used among the four species: (1) the dynamic tripod grip used by humans (which is the common pencil grip; Wynn-Parry, 1966); (2) the interdigital 2/3 brace grip used by gorillas; (3) the power grip used by orangutans; (4) the hook grip used by bonobos; (5) the pinch grip, considered important in human stone tool making (Marzke and Shackley, 1986; Marzke, 1997) and observed in humans, bonobos, gorillas and orangutans; and (6) the scissor grip commonly used by apes but not humans (Fig. 1, Table 1). Each of these grips was functionally different (e.g., involvement of the thumb or not, use of the fingertips or the palm; see Table 1), allowing us to test a large variety of potential differences in muscle force and resultant joint moments.

2.2. Simulation of preferential grip techniques

The objective of the musculoskeletal simulations was to determine the resultant muscular moment at each joint and the global muscle coordination that is required by the six different grips for each species. Musculoskeletal modeling allows the investigation of variables that are either impossible or very challenging to measure directly on both humans and non-human primates and avoids the necessity for each species to perform each of the grips.

Musculoskeletal model A musculoskeletal model was previously developed and used for investigating human hand biomechanics (Chao et al., 1989; Vigouroux et al., 2006; Goislard de Monsabert et al., 2012). The model considered 16 articular joints (wrist, metacarpophalangeal joints [MCP], proximal interphalangeal joints [PIP], interphalangeal joint of the thumb [IP], distal interphalangeal joints [DIP] and the trapeziometacarpal joint [TMC]) with a total of 23 degrees of freedom (df; 1 df for flexion-extension at DIP, IP and PIP joints; 2 df for flexion-extension and adduction-abduction for MCP, TMC and wrist joints; Goislard de Monsabert et al., 2012). The equations held that these joints were equilibrated by the action of 42 muscles for which the forces were the unknown. This model uses an inverse approach to determine internal body forces that cannot be measured directly. Specifically, external finger force applied to hand segments and kinematics of hand segments are used as input data for equations derived from Newton's second law. The solutions to these equations allow estimation of the muscle forces acting during manual prehension. The model is thus a numerical representation of the mechanical equilibrium of hand segments and hand articulations, which states that external force moments about one joint are counterbalanced by muscle tendon tensions:

$$[R] \times \{t\} + \{m_F\} = \{0\} \quad (1)$$

where $[R]$ is a 23×42 matrix containing moment arms of the 42 muscles for the 23 df of the model. Moment arm values were dependent on joint angles and on hand length. $\{t\}$ is a 42×1 vector containing the unknown muscle tendon tensions. $\{m_F\}$ is a 42×1 vector containing moment of external forces at each df of the model. $\{m_F\}$ was determined based on hand segment lengths, hand joint angles and external applied force. The mechanical equation (1) was solved using an optimization process, which is necessary in the model since there are more muscle force unknowns ($n = 42$) than equations ($n = 23$). The process that minimized a muscle stress function was:

$$\min \sum_m \left(\frac{t_m}{PCSA_m} \right)^4 \quad (2)$$

where (t_m) is the muscle tendon tension of the m muscle. $PCSA_m$ is the physiological cross-sectional area of the m muscle. Muscle forces were constrained as follows to avoid negative values:

$$0 \leq t_m \quad (3)$$

To reach our objective, we solved equation 1 with the optimization process for each species with each identified grip technique. These simulations thus needed to i) adapt the model parameters to each species, especially hand segment lengths and ii) receive input data of joint angles and grip forces. These two points were developed below. Computing was performed with Matlab (The MathWorks, Natick, USA).

Musculoskeletal model adaptation to each species The initial human musculoskeletal model resulted from anthropometric measurements of the human hand (Chao et al., 1989; Buchholz, 1992). This initial model was further adapted for each great ape species by replacing the length of each segment with the species mean values derived from morphometric data from osteological collections (see Supplementary Online Material [SOM] Table S1). Two

additional versions of the musculoskeletal model were developed by using the segment lengths of *A. sediba* MH2 (Kivell et al., 2011) and *H. naledi* Hand 1 (Kivell et al., 2015). The non-pollical distal phalanges (DP) of the *A. sediba* MH2 hand are not preserved and thus we used the estimated length of the DP2 reported in Feix et al. (2015), and estimated the length of the other DPs using a similar ratio (see method in SOM Table S1).

One limitation of our simulation study is that the muscle anatomy and the muscle moment arms ($[R]$) of the great ape models were not modified from the initial human model. Moment arms were only scaled according to the segment lengths as in the human hand model (Chao et al., 1989). We kept these initial muscle parameters because some of the necessary comparable data are currently lacking the specific muscle anatomy of each great ape species (e.g., specific dimensions, specific attachment sites of each muscle, muscle moment arms) and those of *A. sediba* and *H. naledi*. Therefore, because the real muscular architecture is not identical across the tested species, the resulting simulated variables cannot be considered as an estimation of the muscle force magnitude generated by each great ape hand muscle in itself but are rather an estimation of the global muscle strength/capacities required to perform the tested grips (e.g., required finger flexor strength). To cope with this limitation, we carefully analyzed the obtained results in two ways: first we considered the net joint moments ($\{m_F\}$ expressed in N·cm) which represent the summed muscular efforts applied on the joints during the grip and are not dependent on muscle moment arms. Secondly, we are interested in muscle forces in each of the eight main muscle groups of the hand (i.e., sum of individual muscles showing the same function) rather than individual muscle forces. The muscle groups, for which the details are presented in SOM Table S2, are the following (Fig. 2): fingers flexors (FF); fingers extensors (FE); intrinsics of the fingers (FI); thumb flexors (TF); thumb extensors (TE); intrinsics of the thumb (TI); wrist flexors (WF); and wrist extensors (WE).

Input model data To determine m_F and $[R]$ before solving equation 1 with the optimization process, input data of joint angles were obtained. Thus, a set of joint angles for each grip technique should be provided for each species. Unfortunately, the kinematic angle data could be collected experimentally only for humans and not for great apes for two reasons. First, it was not possible to collect kinematic data on the captive great apes due to the practicalities of using kinematic equipment in a zoo environment and attaching kinematic markers to animals was not permitted. Secondly, it is challenging, if not impossible, to prompt each great ape species to perform all of the six tested grip techniques and this is obviously not possible for the extinct species. To circumvent these limitations, an initial set of data was collected, during each grip, from one human participant with no pathology or notable anatomical specificity (age = 37 years; size = 177 cm; body mass = 72 kg; hand length = 19.4 cm). A set of 32 markers was positioned on the hand segments to record the 3D hand joint posture using an optoelectronic system (Vicon Motion System, Oxford Metrics, UK). The participant was asked to manipulate a bamboo stick using the six grips described above. The joint angles were computed in 3D using the method described in Chao et al. (1989) and Cooney et al. (1981), which consisted of attaching a coordinate system to each finger and hand segment. For each joint, the angles allowing the rotation from the distal coordinate system to the proximal one were then extracted from an Euler rotation matrix using a Z-Y-X sequence (flexion-extension; adduction-abduction, axial rotation) with fixed axes (Fig. 3). Results of net joint moment and muscle forces for the initial human model were obtained using this set of joint angles. For the other species (great apes, *A. sediba* MH2 and *H. naledi* Hand 1), kinematic data were calculated by modifying the initial sets of 3D joint angles obtained with the human participant. To do this, the 3D joint angles of the great ape models (Table 2) were adjusted to best fit the postures observed in the videos. A 3D representation of the primate hand models was used to compare video postures and model representation (Fig. 4). The estimated joint

posture was considered reliable when (1) the model posture appeared similar to the posture observed in the video, and (2) the shortest distance between finger segments and the bamboo were on average 0.5 mm, which represents a reasonable estimation of the width of the skin and soft tissues. The latter method was used for both fossils, *A. sediba* and *H. naledi*, with the initial set of joint angles modified to reproduce at best the observed grip we know in great apes and humans.

The grip forces applied to the bamboo were distributed over the fingers that were in contact with the bamboo and were equal to a summed magnitude of 40 N. As no force data exist on the force applied while manipulating bamboo, either in humans or non-human primates, simulations were run with the same force intensity of 40 N for each species. This force represents approximately 30% of the maximal pinch grip force in humans (Goislard de Monsabert, 2014) and is representative of the intensity used by humans during manipulative activities (Domalain et al., 2008). The same intensity of force was applied to all the grips and all species, to standardize the grip force conditions and comparisons.

Analyzed results Although the musculoskeletal model is of the entire hand and results incorporate muscle force from all digits, we focus on the results of the thumb and index finger (Fig. 2) only, as the opposition of these two digits is involved in most human manipulative behaviors (Taylor and Schwarz, 1955; Marzke et al., 2010). Moreover, as mentioned above, the individual muscle forces were summed in their respective groups to be representative of the muscle involvement in the eight main muscle groups. Analyzed output results consisted of i) joint angles of the thumb and index finger during each of the six grips (Table 2, Fig. 3), ii) the net joint moments of thumb and index finger, and iii) the involvement of the muscle groups during the grip (Fig. 2). We considered that a group of muscles was significantly recruited during a grip when its intensity exceeded 5% of their capacity (estimated in humans). Although the muscle capacities of great apes may be higher than those of humans,

this threshold is used to set a minimal tension under which we consider the muscle involvement negligible. The number of muscle groups involved during each grip provided an index of muscle coordination complexity for each specific grip, allowing us to judge the neuromuscular complexity of a grip (information not provided by net joint moments or strength of each muscle group looked at individually).

3. Results

3.1 Joint angles

Humans and fossil hominins present the same, or very similar, required joint angles for all of the grips, but there are several differences found between humans and great apes (detailed results in Table 2). Overall, the joint angles required during grips involving the thumb (i.e., dynamic tripod, pinch, interdigital 2/3 brace, and power grip) are particularly pronounced for great apes, especially for orangutans, but these joint angles appear to stay within the range of motion known for each species (Napier, 1960; Rose, 1988). For example, the pinch grip requires higher flexion of the index finger for all the great apes compared with humans: flexion of the MCP joint ranging from 101–90° in great apes to 55° in humans and 67° in fossil hominins, and flexion of the PIP joint ranging from 81–92° in great apes to 75° in humans and fossil hominins. Orangutans show particularly high flexion of the fingers during pinch grip, with the MCP joint flexed at 101° compared to 55° for humans, and the PIP joint flexed at 92° compared to 75° in humans. Different joint angles are observed across all the species to realize the dynamic tripod grip: great apes need 28° of flexion of the TMC joint compared to 17° in humans and fossil hominins, and need higher flexion of the index PIP joint compared to humans and fossil hominins, with gorillas needing especially high flexion at 90° compared to 36° for humans. At the index MCP joint, bonobos and orangutans require

higher flexion (both $\sim 83^\circ$) compared with humans and gorillas (both $\sim 63^\circ$). The interdigital 2/3 brace grip requires extension of the TMC joint for humans (51°) and orangutans (11°), while the other species require flexion (13°). Humans need higher adduction of the TMC joint (50°) than in great apes and fossil hominins ($20\text{--}33^\circ$), and need higher flexion of the thumb MCP joint (61°) compared to orangutans (11°), while the other species require extension (15°). Orangutans need 68° flexion of the index PIP joint compared to 41° in all other species. During the interdigital 2/3 brace grip, thumb joint angles differ substantially between hominins and humans (e.g., IP and MCP joints are flexed for humans compared to in extended in both fossils, and TMC joint is extended in humans compared to flexed in both fossils). The power grip requires 42° adduction of the TMC joint for humans and fossil hominins compared to 14° in great apes, and orangutans show 103° of flexion of the MCP joint compared to 86° for all other species.

3.2. Net joint moments

Musculoskeletal simulation results for net joint moments are depicted in Figure 5 for each of the six grips and each extant and extinct species. Here we summarize the joints that experience the highest net joint moments and/or show the most dramatic differences across taxa and grip type (for all of the raw results, see SOM Table S3). The dynamic tripod grip, most commonly used by humans (Bardo et al. 2016, 2017), generates distinctly different thumb loadings for gorillas compared to the other species (Fig. 5a). Gorillas require more muscular effort to stabilize the thumb TMC and MCP joints in adduction; the gorilla TMC and MCP joint abduction requires $106.6\text{ N}\cdot\text{cm}$ and $50.4\text{ N}\cdot\text{cm}$, respectively, compared to a mean of $46.2 \pm 2.8\text{ N}\cdot\text{cm}$ and $19.2 \pm 1.9\text{ N}\cdot\text{cm}$, respectively, in all other extant and fossil taxa. In contrast, the gorilla TMC and MCP joints require less net joint moments in extension: -

52.0 N·cm and -20.0 N·cm, respectively compared with -104.6 ± 8.5 N·cm and -50.0 ± 4.9 N·cm, respectively, in other taxa. For the index finger, humans need the highest moments in extension at the PIP joints at -36.3 N·cm, while gorillas need the lowest moments (-3.9 N·cm), compared with a mean of -16.0 N·cm for all other taxa. Orangutans (-83.0 N·cm) and humans (-75.9 N·cm) require the highest joint moments in the MCP joint in extension, while *H. naledi* (-52.0 N·cm) and *A. sediba* (-48.7 N·cm) require the least.

During the pinch grip, used by all the species except gorillas (Bardo et al., 2016, 2017; Fig. 5b), all extant hominoids, including humans, share a similar pattern of requiring higher net joint moments at the TMC joint in extension (mean -153.0 ± 5.1 N·cm), while fossil hominins *A. sediba* (-109.0 N·cm) and *H. naledi* (-106.7 N·cm) require less moments. For the index finger, all great apes, and especially orangutans (95.2 N·cm), experience high net joint moments in abduction, while *H. naledi* (-11.0 N·cm), *A. sediba* (-11.3 N·cm) and, especially, humans (-34.8 N·cm) experience moments in adduction.

During the interdigital 2/3 brace grip, most commonly used by gorillas (Bardo et al., 2016, 2017), humans (-29.6 N·cm) require the lowest net joint moments at the TMC joint in extension, and orangutans (-85.1 N·cm) require the highest, while all other taxa have a mean of -44.5 ± 2.9 N·cm (Fig. 5c). Orangutans (-5.6 N·cm) and, especially, humans (-27.9 N·cm) are unique within the sample in requiring moments in adduction at the TMC joint, while the other species require muscular moments in abduction (mean 9.8 ± 5.1 N·cm). Humans require the highest net joint moments at the thumb's MCP joint in extension (-46.6 N·cm), while *H. naledi* (-26.8 N·cm) and *A. sediba* (-26.2 N·cm) require the lowest. For the index finger, *H. naledi* (-32.5 N·cm) and *A. sediba* (-31.0 N·cm) require the lowest joint moments at the MCP joint in extension (-31.7 ± 0.7 N·cm), while gorillas (-62.8 N·cm) and orangutans (-59.1 N·cm) need the highest. Similarly, *H. naledi* (-8.9 N·cm) and *A. sediba* (-8.2 N·cm) require

the lowest moments at the PIP joint in extension, while orangutans require the highest (-34.6 N·cm).

The power grip, most commonly used by orangutans (Bardo et al., 2016, 2017), involves the lower net joint moments at the TMC joint in extension for *H. naledi* (-25.3 N·cm), *A. sediba* (-25.7 N·cm) and humans (-37.1 N·cm) compared with great apes (mean -65.0 ± 2.9 N·cm; Fig. 5d). For the index finger, joint moments at the PIP and MCP joints in extension are lowest in *H. naledi* (-19.5 and -21.3 N·cm, respectively) and *A. sediba* (-18.1 and -19.8 N·cm), while moments are highest in orangutans (-56.5 and -56.2 N·cm).

The hook grip, most commonly used by bonobos (Bardo et al., 2016, 2017), requires relatively small moments at the DIP, PIP and MCP joints of the index finger in extension that are relatively similar across all sample species (the thumb is not used; Fig. 5e). At all joints, *A. sediba* (-2.6, -6.4 and -1.7 N·cm, respectively) and *H. naledi* (-2.8, -7.1 and -2.7) require the lowest moments, while orangutans require the highest (-7.6, -15.8 and -10.7 N·cm).

The scissor grip, only used by great apes (Bardo et al., 2016, 2017), requires only joint moments at the MCP joint, primarily in abduction and less so in extension for all species. Again, *A. sediba* (50.7 and -2.3 N·cm, respectively) and *H. naledi* (52.4 and -2.5 N·cm) have the lowest moments and orangutans require the highest (103.1 and -11.3 N·cm), while all other taxa have a mean of 83.1 ± 6.9 and -4.6 ± 0.5 N·cm (Fig. 5f).

3.3. Muscle coordination

Muscle coordination is assessed with regard to the mean muscle force magnitude in the thumb, fingers, and wrist for each of the six grips across all species (Table 3) and muscle force magnitude for each species and each grip type (Fig. 6; SOM Table S4). The most

complex set of muscle coordination is observed for the dynamic tripod grip, pinch grip, interdigital 2/3 brace grip and the power grip, each of which requires the involvement of five to seven muscle groups (Table 3). In contrast, the muscle coordination needed for the scissor grip and hook grip is less complex, involving the simultaneous action of only three muscle groups.

The dynamic tripod grip is the most complex, requiring the coordinated action of seven muscle groups and generally requiring strong muscle force magnitude across all species. Among the seven muscle groups involved, the highest muscle force magnitude is required by the intrinsic muscles of the fingers, ranging from 86.6 N in humans to 136.0 N in bonobos and 172.4 N in orangutans. The finger extensors average 69.2 ± 0.7 N in humans, fossil hominins and gorillas, while they amount to 105.1 N in bonobos and 139.0 N in orangutans. The intrinsic thumb muscles range from a mean of 121.6 ± 1.9 N in humans, both fossil hominins and bonobos to a mean of 147.2 ± 2.5 N in gorillas and orangutans. On average, orangutans show higher required muscle force magnitude of all the muscle groups needed for the dynamic tripod grip than any of the other species, particularly humans (Fig. 6a).

The pinch grip requires muscle coordination of six muscle groups, and higher muscle force magnitude across all species than any of the other grips. The highest muscle force magnitude occurs in the intrinsic thumb muscles, ranging from a mean of 158.6 ± 3.3 N in humans and fossil hominins to a mean of 188.3 ± 1.95 N in gorillas and orangutans. The thumb flexor muscles also showed strong magnitudes ranging from 51.6 in *H. naledi* to 74.5 ± 1.6 N in the remaining species, while the wrist extensors ranged from 23.4 N in orangutans to 109.2 N in humans. Orangutans stand out in requiring higher muscle force magnitude of the intrinsic muscles of the finger and the finger extensors compared with all the other species

(Fig. 6b), while *H. naledi* is the only taxon to require no action of thumb extensors during the pinch grip.

The interdigital 2/3 brace grip requires coordinated action of six muscle groups, for which the highest muscle force magnitude is needed for the finger extensor muscles, ranging from 90 N in *A. sediba* to a mean of 113 ± 1.38 N in humans, *H. naledi*, and bonobos, and the intrinsic muscles of the thumb, ranging from a mean of 52.19 ± 2.34 N in fossil hominins, bonobos, and gorillas to 113.9 N in orangutans and 130.1 N in humans. Humans stand out in requiring the lowest muscle force magnitude for the thumb flexor muscles (15.3 N) across the sample, while orangutans require the highest (49.7 N). Humans and bonobos are the only taxa to not require action of the thumb extensors, while both these species and *H. naledi* require higher muscle force magnitude of the wrist flexors (mean 39.0 ± 3.5 N) compared to the rest of the sample (mean 15.9 ± 0.6 N).

The power grip requires coordinated action of five muscle groups, for which the highest muscle force magnitude occurs in the intrinsic muscles of the thumb, ranging from 66.9 ± 2.1 N in humans and fossil hominins to 107.0 N in orangutans, the wrist extensors, ranging from 63.2 ± 2.9 N in humans and fossil hominins to 93.9 N in orangutans, and the finger flexor muscles, ranging from a mean of 67.7 ± 0.2 N in bonobos and gorillas to 84.2 N in orangutans. Orangutans require higher muscle force magnitude for all of the muscle groups compared with the other species, while humans and fossil hominins require the lowest magnitude (Fig. 6d).

The scissor grip requires coordinated action of only three muscle groups and generally only high muscle force magnitude is required for the intrinsic muscles of the finger and the finger extensors across all the species (mean of 161.7 ± 3.6 N and 187.7 ± 7.6 N, respectively; Fig. 6f). The hook grip also requires coordinated action of three muscle groups—all in the

fingers—and the muscle force magnitude was the lowest across all of the grip types for all species. Across all taxa and finger muscle groups, the muscle force magnitude is relatively similar: a mean of 37.6 ± 0.3 N for the intrinsic finger muscles, 39.4 ± 3.0 N for the finger extensors and 39.1 ± 2.3 N for the finger flexors. For the hook grip, orangutans stand out in requiring lower muscle force magnitude of the finger extensor muscles (25.9 N) compared with all other species (42.1 ± 1.7 N; Figure 6e).

4. Discussion

Using an analysis of internal biomechanical loadings, this study helps to clarify the interaction between variation in intrinsic hand proportions and the performance of specific grips during tool use. We found that interspecific variation in hand proportions has a strong biomechanical effect on the six grips analyzed. In particular, our results show clear interspecific differences in joint angles, joint moments, and/or muscular effort required to perform each grip, all of which directly drive the magnitude of bone loadings (i.e., intra-articular stress, magnitude and direction of the bone to bone contact force) while manipulating tools. In other words, the same grip can generate different bone loadings according to variation in hand proportions and, vice versa, a similar bone loading does not necessarily mean the use of the same grip. This study highlights the importance of analyzing the entire chain of biomechanical loadings from the object grip force to the mechanical efforts exerted by the anatomical structures of the hand. These results also highlight the challenges of inferring manipulative abilities in fossil taxa, particularly for incomplete hand skeletons when hand proportions remain unknown.

That being said, it is important to acknowledge that although the musculoskeletal simulation used here is useful to investigate the potential ‘efficiency’ of certain grips across

multiple species, it cannot be used as a predictor of actual behavior. For example, the results show that orangutans appear to have the highest biomechanical loadings across the different taxa for the pinch grip and the power grip, but experimental behavioral research shows that they commonly use both of these grips during object manipulation (and locomotion; Christel, 1993; Pouydebat et al., 2009; Bardo et al., 2017). Thus, the current simulation method is an additional tool for clarifying potential biomechanical factors of specific grips, but should be used in addition to other explanatory factors (e.g., locomotor behavior/constraints, and other morphological adaptations such as phalangeal curvature) and need to be interpreted within the context of real manipulative (and locomotor) behaviors and actual musculature and bone morphology of each species. Considering these caveats, we discuss the implication of the simulation results for tool use grip abilities in humans, great apes and fossil hominins.

4.1 Interaction between hand proportions and grip technique in extant species

Results from the musculoskeletal simulations show that variation in hand proportions affects the joint angles, net joint moments and muscular coordination in all six grip techniques. Moreover, the amplitude of this effect differs according to the grip. The hook and the scissor grips require less ‘complex’ muscle group coordination and low muscle force magnitude in all of the studied species. This is not surprising, as neither of these grips involve the thumb, and thus the mechanical requirements are not affected by variation in thumb-finger proportions across species (Schultz, 1956; Napier, 1960; Tuttle, 1969; Susman et al., 1984; Jouffroy et al., 1993; Marzke and Wullstein, 1996). In contrast, the dynamic tripod grip, pinch grip, interdigital 2/3 brace and power grips required more complex muscle coordination and higher net joint moments in all species.

The dynamic tripod grip was the only grip used exclusively by humans during the maze task (Bardo et al., 2016, 2017). This is the common ‘pencil grip’, in which the pencil is stabilized against the radial side of the third finger by the thumb pad with the pad of the finger on top of the pencil (Wynn-Parry, 1966). Compared to the other grips, it requires the most complex muscle coordination, including seven muscle groups, high muscle force magnitude (e.g., humans and gorillas respectively need 23% and 18% higher total muscle force to use a tripod grip vs. a power grip, which is the next highest grip), the highest joint moments (e.g., humans and orangutans need respectively 58% and 32% higher total joint moments to use a tripod grip vs. a power grip), and shows the greatest differences across species. These differences can be explained by the strong interspecific variation in intrinsic hand proportions, such that great apes with a short thumb/long index finger required higher flexion of the fingers than in humans with a long thumb/short index finger (Napier, 1960; Rose, 1988). Bonobos and orangutans, with relatively longer fingers than gorillas (Schultz, 1930, 1956; Almécija et al., 2015), were unusual in requiring 25% higher flexion angle of the MCP joint and 37% and 42% higher force, respectively, of intrinsic and extensors muscles of the fingers compared with both humans and gorillas. Although gorillas have thumb/finger proportions that are most similar to humans in this study (Schultz, 1930; Almécija et al., 2015), their hand proportions required different positioning (i.e., joint angles) of the digits to perform this grip compared with humans, resulting in higher net joint moments in the thumb MCP and TMC joints and lower net joint moments in the index finger. Even though great apes required higher flexion of their joints, the degree of flexion was still within the range of motion reported for the MCP joints of the index finger (maximum 170°) and TMC joint ($32.8 \pm 5.3^\circ$; Napier, 1960; Rose, 1988).

With regards to muscle forces when performing the dynamic tripod grip, all great apes required on average 20% higher total muscle force (range 11% to 32%) compared to that of

humans. These muscle loadings may be too high to be balanced by their musculature and/or could generate greater muscle fatigue. In particular, great apes lack an independent flexor pollicis longus (FPL) muscle, which is a powerful flexor of the distal thumb in humans (Hamrick et al., 1998; Marzke et al., 1998; Diogo and Wood, 2011; Diogo et al., 2012) that is required for the pencil grip. Although the FPL was nevertheless included in the musculoskeletal model of all species for our simulations, the lack of this muscle action for the dynamic tripod grip in great apes suggests that such a grip would not be easy for great apes to perform. As discussed above, although bonobos have a well-developed stout tendon of the FDP that acts to flex the distal phalanx of the thumb (Miller, 1952; Myatt et al., 2012; Diogo et al., 2017; van Leeuwen et al., 2018), van Leeuwen et al. (2018) suggested that differences in muscle architecture between humans and bonobos, rather than relative muscle development, explained the enhanced dexterity of humans. Finally, the complex coordination of several muscle groups requires accurate neurological control to perform the dynamic tripod grip (Bizzi et al., 1992; Hepp-Reymond et al., 1996; Kuhtz-Buschbeck et al., 2001; Nowak and Hermsdörfer, 2005; Li et al., 2016) and advanced social learning (Selin, 2003), both of which may be different in humans, extant great apes and fossil hominins (Verendeev et al., 2016; Bardo et al., 2016, 2017). For example, the pencil grip is not learned by children until between four and six years of age (Schneck and Henderson, 1990).

Compared with great apes, the anatomy of the human thumb is generally considered to facilitate contact between the thumb and the index finger, particularly during pinch grips (Susman, 1988, 1994; Marzke, 1992). Our results show that during the pinch grip the thumb of all species incurs high biomechanical loadings (i.e., require the highest total muscle force compared to other grips, and the highest joint moments after the dynamic tripod grip), while the interspecific variation in hand proportions has a greater influence on the biomechanical loadings of the index finger. For example, the great apes require a 38–45% higher flexion of

the MCP joint of the index finger than humans, while joint angles within the thumb are relatively similar across all taxa. This high degree of flexion in the great ape index finger contributes to a high net joint moment in abduction at the MCP joint to stabilize against the force of the thumb during the pinch grip, while the human MCP joint experiences lower moments in adduction. Moreover, the pinch grip requires the extension of the MCP joint and the flexion of the PIP joint of the thumb in all species, an action which involves activation of the extensor pollicis brevis (EPB) in humans (Marzke et al., 1998; Diogo et al., 2012). This muscle is also lacking in great apes (Straus, 1942; Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012) but was included in the musculoskeletal model of all species for our simulations. Our results did not show great differences in thumb extensor force across species but the lack of this muscle action for the pinch grip in great apes suggests that the force applied by thumb extensors could be lower in great apes compared to humans. Behavioral data show that all great apes use a pinch grip during manipulative activities in captive and natural environments (Christel, 1993; Marzke and Wullstein, 1996; Byrne et al., 2001; Pouydebat et al., 2011; Lesnik et al., 2015; Marzke et al., 2015; Bardo et al., 2016, 2017). Furthermore, wild gorillas and chimpanzees (with similar hand proportions to bonobos) use pinch grips during seemingly forceful food processing (Byrne et al., 2001; Marzke et al., 2015), while this has not been reported for orangutans. It may be that in orangutans, use of the pinch grip may be more difficult when engaging in manipulative activities that require higher grip force. However, further research on force production during pinch grips with the specific morphology of the orangutan hand could offer interesting insights into their hand function. Detailed study of the grips used by orangutans in their natural environment is also needed to understand their manipulative capabilities and limitations.

The interdigital 2/3 brace grip was preferentially used by gorillas during the maze task, and less so by bonobos, humans and, especially, orangutans (Bardo et al., 2016, 2017; Fig. 1).

Moreover, wild chimpanzees have also been shown to use this grip during tool use (Lesnik et al., 2015). The simulations showed much higher mechanical loadings in orangutans when using this grip compared with all other species, including 38–65% higher net joint moment to stabilize the TMC joint in extension, and 28–69% higher muscular magnitude of the thumb flexors. In contrast, bonobos and gorillas require on average lower muscular force for all the muscular groups compared to orangutans and humans. These differences may reflect the interspecific differences in the length of the thumb relative to that of the index finger, with the longest thumb in humans (72%; this study) and the shortest in orangutans (43%; Schultz, 1956), that would result in different joint angles compared to bonobos' and gorillas' hand proportions. Humans rarely used an interdigital 2/3 brace grip because it is an inefficient variant of pencil grip (Selin, 2003). Compared to the dynamic tripod grip, use of the interdigital 2/3 brace grip in humans requires 10% higher muscular magnitude at the intrinsic muscles of the thumb, 38% higher muscular magnitude at the extensors muscles of the fingers, and the recruitment of the flexor muscles of the wrist (while the tripod grip does not).

The power grip was used by all the species during the maze task, but most frequently by orangutans (Fig. 1; Bardo et al., 2016, 2017). Simulation results show that during this grip the intrinsic muscles of the thumb, the flexors of the fingers and the extensors of the wrist are strongly recruited in all species, but different muscle force magnitudes are required across species. In particular, the great apes need on average 53% higher net joint moments to flex the TMC joint than do humans. Within the index finger, there are greater interspecific differences. For example, compared to humans, orangutans require 33% higher net joint moments at the MCP joint, and 48% higher net joint moments at the PIP joint during index finger flexion. Moreover, orangutans require on average 20% higher muscle force magnitude in all the muscle groups to use a power grip compared to all other taxa. However, orangutans use power grips frequently during both manipulation and locomotion (Christel, 1993;

Pouydebat et al., 2009; Bardo et al., 2017) and seemingly endure these biomechanical constraints without difficulty. Thus, we emphasize that the current simulation is an additional tool for helping to understand the potential biomechanical factors of grip use. This biomechanical insight should be interpreted within the context of real manipulative abilities of the species and other associated factors influencing grip use (e.g., social, psychological, neural factors, morphological adaptation). For example, dorsopalmarly curved phalanges have been shown to experience less strain during grasping a branch with flexed PIP and MCP joints than straight phalanges (Preuschoft, 1973; Richmond, 1998, 2007; Jungers et al., 2002; Nguyen et al., 2014). The current musculoskeletal model assumes the phalanges are straight and thus the greater phalangeal curvature of orangutans (60° of curvature for orangutans compared to 42° for chimpanzees, Susman et al., 1984; see also Stern et al., 1995; Deane and Begun, 2008; Matarazzo, 2008; Rein, 2011; Patel and Maiolino, 2016) could alter joint angles and decrease the muscular loading during this grip.

Simulation results show that orangutans are distinguished from the other species in experiencing higher muscle loading for all six grips. This result reflects the fact that orangutans have the shortest thumb relative to the fingers among hominids (Schultz, 1930; Napier, 1993; Alméjida et al., 2015). This also highlights a limitation of the method in which orangutans show the greatest discrepancy from human hand proportions, which form the basis of the musculoskeletal model, leading to more constrained joint postures (e.g., highly flexed index finger to oppose the thumb), and thus higher biomechanical loadings (i.e., joint moments and muscular force). Incorporation of orangutan bone and joint morphology, range of motion, and soft tissue structures would obviously result in more biologically realistic results that are more consistent with actual orangutan hand use (Napier, 1960; Rose, 1988; Christel, 1993; Pouydebat et al., 2009; Bardo et al., 2017). Despite these limitations, it is interesting to note that orangutans showed the greatest intraspecific variability in grip use

during the maze task, such that they modified their grip more often than the other hominids (Bardo et al., 2016, 2017). This variability may in part be a result of the higher muscular loadings demonstrated here, such that changing grips more frequently could limit muscle fatigue and discomfort (Wells et al., 2010).

4.2 Implications for fossil hominins

Based on the preserved postcranial morphology of the two hominins, it is likely that *H. naledi* and *A. sediba* used their hands for both manipulation and locomotion (Berger et al., 2010, 2015; Churchill et al., 2013; Feuerriegel et al., 2017). Simulation results suggest that both hominins had the biomechanical potential to use all six grips with a similar, if not better, efficiency (i.e., low muscular demands) to that of humans. This result can be explained by the relatively long thumb of *H. naledi* (66% of second digit length) and *A. sediba* (70%), which is similar to the average in recent humans (72%). Like humans, *A. sediba* and *H. naledi* also require high muscular force of the wrist extensors during the pinch grip, which were, respectively, 47% and 36% higher than the mean of great apes. This result is interesting with regards to the importance of wrist extension in humans during knapping, providing “an important role in this increased mechanical work by positioning the hand for effective flexor muscle recruitment and rapid flexion immediately prior to strike” (Williams et al., 2010:143). Moreover, previous quantification of muscle coordination during object grip tasks in humans showed that the wrist extensors are crucial for maintaining an appropriate wrist joint equilibrium while manipulating an object (Snijders et al., 1987; Rossi et al., 2014; Vigouroux et al., 2017). Our results show that *A. sediba* and *H. naledi* may have a greater advantage than great apes in the wrist extension during pinch grip. Since it is hypothesized that complex upper limb activities such as stone tool production could have had important evolutionary

implications in the specific reorganization of the human wrist (e.g., Marzke, 1997; Tocheri, 2007; Williams et al., 2010), hominins may, in comparison to great apes, have developed better control of wrist equilibrium to favor activities that require forceful grips.

Although both *A. sediba* and *H. naledi* have human-like hand proportions, both hominins show, on average, lower joint moments in the thumb and index finger during the dynamic tripod grip and the interdigital 2/3 brace grip compared with that of humans. Moreover, hominins show a low degree of flexion at the TMC joint while humans show, instead, a high degree of extension during the use of the interdigital 2/3 brace grip. These differences may reflect the slightly shorter thumb relative to index finger length in *A. sediba* and *H. naledi* compared with humans. For all of the six grips simulated in this study, hominins appear to have fewer mechanical demands when using many of these grips than humans. However, as discussed above, the musculoskeletal model does not consider variation in joint morphology, range of motion, phalangeal curvature and various other subtle and not-so-subtle differences among *H. naledi*, *A. sediba* and recent humans (Kivell et al., 2011, 2015). Nevertheless, both fossil hominins have a broad distal pollical phalanx with a well-developed gable suggesting the presence of an independent and well-developed FPL (Almécija et al., 2010; Kivell et al., 2011, 2015), which is included in the simulation. In *H. naledi*, the thumb bones also have particularly robust muscle attachments, and the radial carpal bones show morphology found only in committed tool-using *Homo neanderthalensis* and *H. sapiens*, suggesting powerful opposition of the thumb during manipulation (Kivell et al., 2015).

4.3 Limitations

This study has several important limitations. First, we consider only six grips used during a single maze task by all four species, while there was substantial intra- and interspecific variability in grip use observed during this task (Bardo et al., 2016, 2017) and, indeed, each species is capable of wide range of gripping abilities (e.g., Christel, 1993; Marzke and Wullstein, 1996; Christel et al., 1998; Byrne et al., 2001; Pouydebat et al., 2009, 2011). It is possible that the kinematic variability in humans, as well as in great apes, led to an overlap between species. Additional experimental studies, such as those conducted by Lesnik et al. (2015) or Bardo et al. (2016, 2017), may determine a greater range of kinematics used by each species and future musculoskeletal modeling could investigate additional grips, such as pad-to-pad precision grips considered distinct to humans (Napier, 1960; Marzke, 1997; Susman, 1998; Tocheri et al., 2008; but see Macfarlane and Graziano, 2009 in macaques), or the ‘V-pocket’ grip used by wild chimpanzees (Marzke et al., 2015). It could also be interesting to explore the results of the other digits as well.

Second, we used a simulation approach in which only a representative (or a simulated) behavior and a representative anatomy of each species were tested in six grip types. The simulations are based by necessity on a human hand model for which only the segment lengths have been changed for great apes and fossil hominins. Interspecific variation in bony morphology (e.g., phalangeal curvature; Susman et al., 1984; Stern et al., 1995; Deane and Begun, 2008; Patel et al., 2016) and range of motion according to specific joint morphology (Napier, 1962; Tuttle, 1969; Lewis, 1989; Marzke, 1992, 1997; Tocheri et al., 2008; Marzke et al., 2010; Orr et al., 2010) will certainly affect the results of the model. Furthermore, no adaptations of muscle trajectories and moment arms were implemented in the models, which can lead to errors in estimating the force of each muscle. Such muscular data are sparse for great apes and data that are published (e.g., Tuttle, 1969; Thorpe et al., 1999; Diogo and Wood, 2011; Zihlman et al., 2011; Myatt et al., 2012; Diogo et al., 2012; van Leeuwen et al.,

2018) are not reported in sufficient detail for each species. Furthermore, muscular data are unknown for fossil hominins. We aimed to cope with the limitation by considering muscle groups, rather than individual muscular forces. Given that, for example, great apes lack the independent FPL or EPB muscles found in humans (Straus, 1942; Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012), it would be necessary to create a specific model for each species with the specific dimension/position of each muscle, force of each muscle, and muscle moment arms. Although future models could be adapted to incorporate such data, recent studies have highlighted strong intraspecific variability in hand anatomy within great apes (Diogo et al., 2012; van Leeuwen et al., 2018), which adds further challenges.

Third, we assumed a loading condition of 40 N was applied to the bamboo in all species. It is currently unclear how relatively larger forelimb muscle mass in great apes (Tuttle, 1969; Alexander et al., 1981; Zihlman, 1992; Thorpe et al., 1999) versus relatively larger thumb muscle mass in humans (Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012; van Leeuwen et al., 2018) might translate into differences in potential grip force. Without *in vivo* data on grip force in great apes, we constrained the model to use the same loading for each species based on human *in vivo* data. Additional studies are needed to detail muscle morphology in the same way, and to quantify muscle moment arms, range of joint motion and grip force in non-human primates that can be used to create more biologically realistic musculoskeletal models.

5. Conclusions

We found that variation in intrinsic hand proportions modify the joint angles required in each grip and thus have a strong effect on biomechanical loading, especially for muscle forces. These biomechanical loadings, related to direct behavioral observations of the grips

used by great apes and humans, appear to be one important factor in selecting an appropriate grip for use, especially for orangutans and for the pencil grip. We also suggest that other factors, such as social learning, are of at least equal importance. Since the muscle forces directly manage the bone to bone force on contact during a grip, our simulations show that it is important to take into account hand proportions and their potential influence on the entire mechanical chain for a better understanding of potential grip techniques used in hominin fossils. To conclude, musculoskeletal modeling can be an informative tool for better understanding variability in manipulation in extant and extinct species.

Acknowledgements

This research was supported by the Doctoral School FdV, the Foundation Bettencourt-Schueller, Paris Descartes University, and a Fyssen Foundation Research Fellowship to A.B. E.P. thanks the Action Transversale of the National Museum of Natural History (Paris, France). T.L.K.'s research is supported by a European Research Council Starting Grant (#336301). Finally, we thank the Editor Dr. David Alba, the Associate Editor Dr. Evie Vereecke, and two anonymous reviewers for their thoughtful comments, which greatly improved this article.

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Figures and Tables

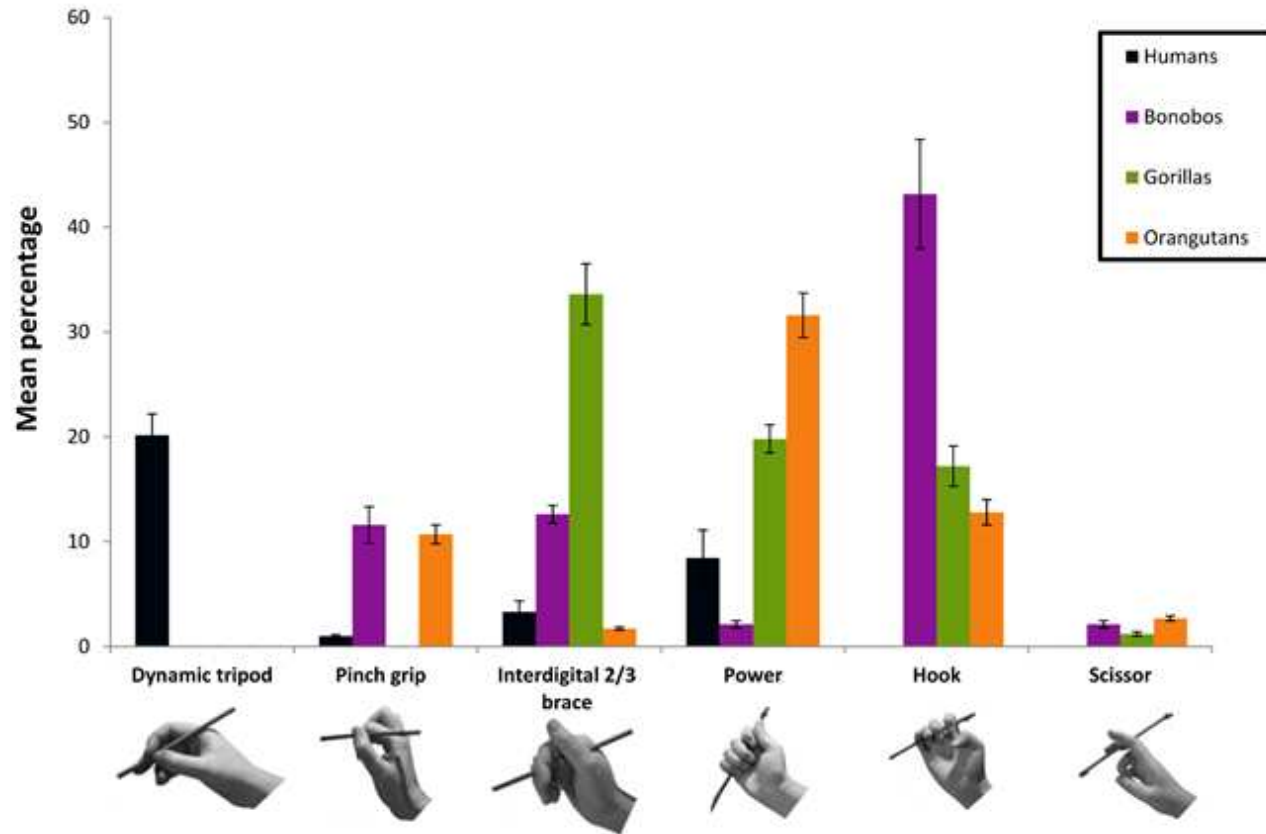


Figure 1. Mean percentage of the preferential grip techniques (defined in Table 1) used by each species during the maze task (Bardo et al., 2016, 2017).

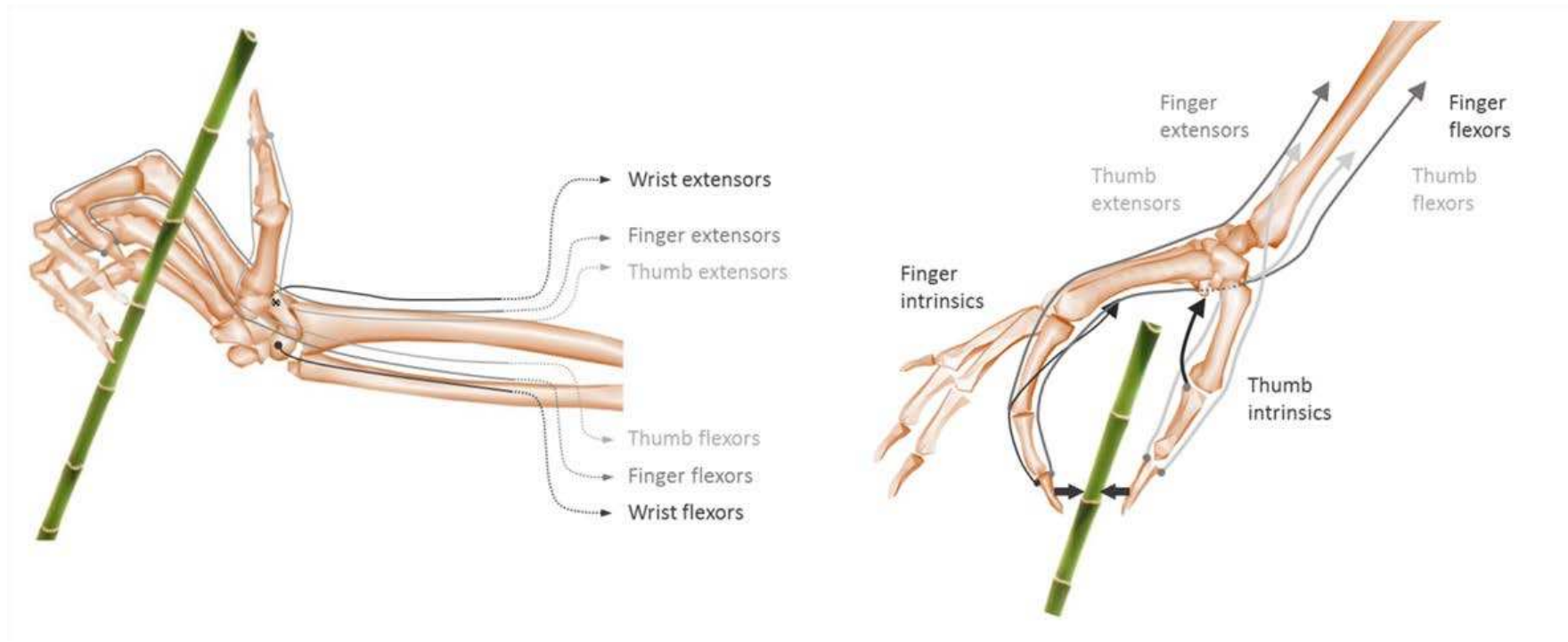


Figure 2. Representation of the musculoskeletal models with the six main muscles groups used in the study for the index finger and the thumb during the grip of the bamboo (in green).

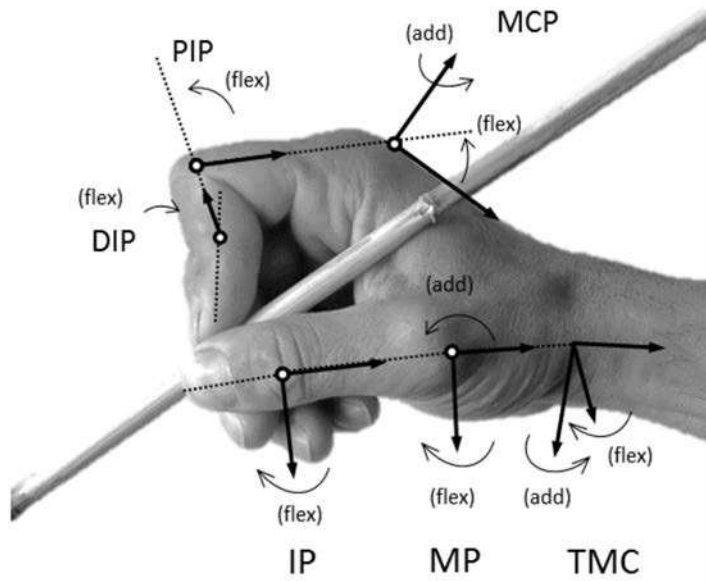


Figure 3. Representation of the method to calculate the joint angles of the thumb and the index finger. Abbreviations: add = adduction; CMC = carpometacarpal; DIP = distal interphalangeal joint; flex = flexion; IP = interphalangeal joint; MCP = metacarpophalangeal joint; PIP = proximal interphalangeal joint; TMC = trapeziometacarpal (first CMC).

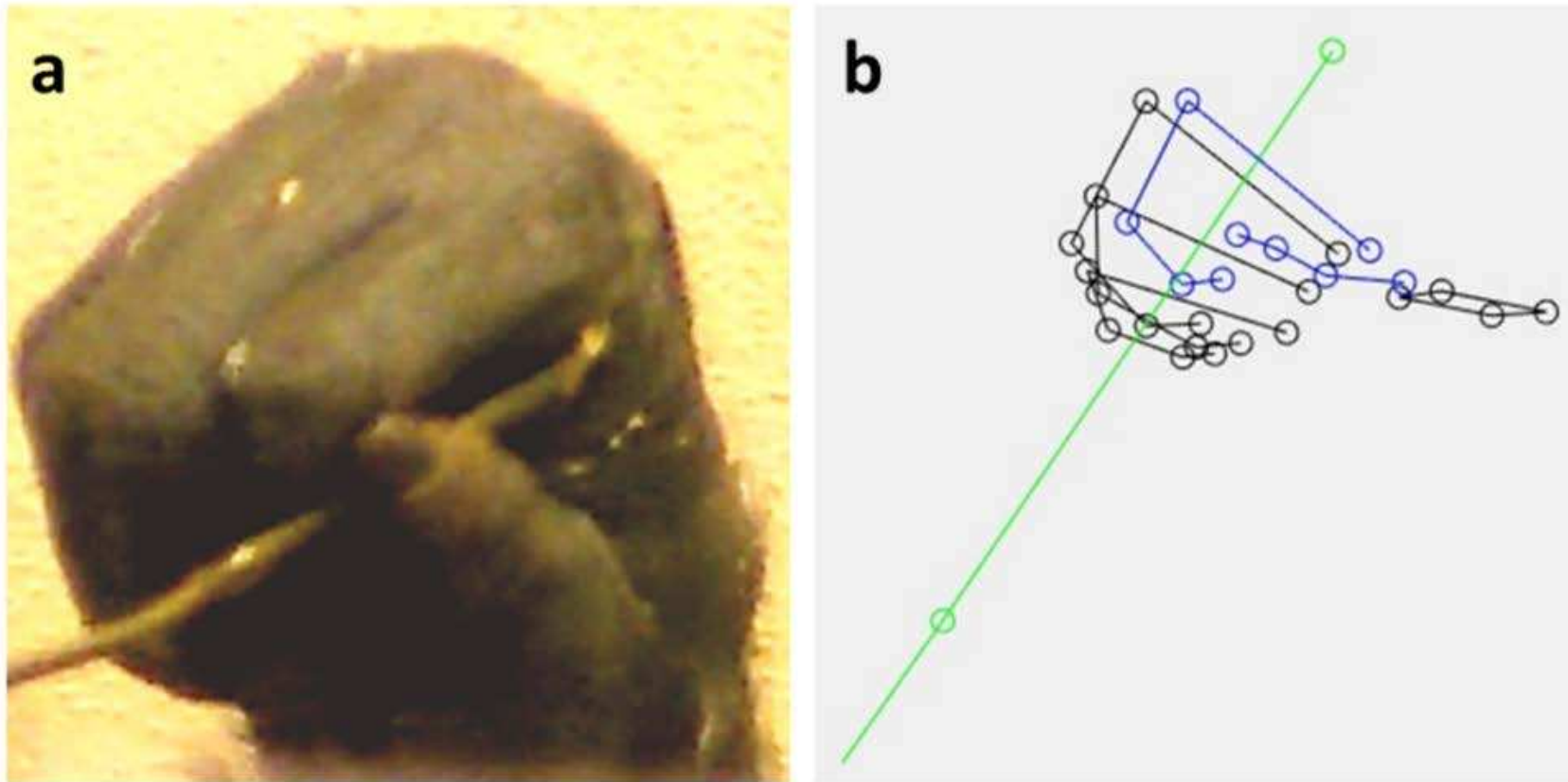


Figure 4. Example of a video posture used (a; pinch grip use by a bonobo) to adapt the 3D representation of the primate hand models (b; bonobo hand 3D model during pinch grip). The segments of the thumb and index fingers are in blue, the other fingers and the wrist in black, and the bamboo is in green.

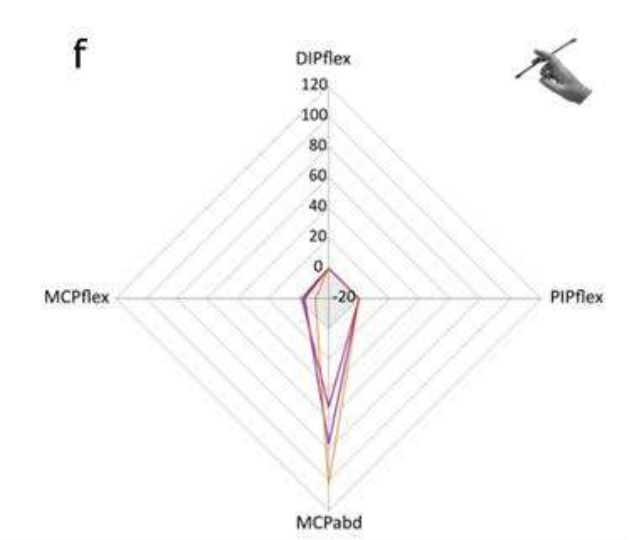
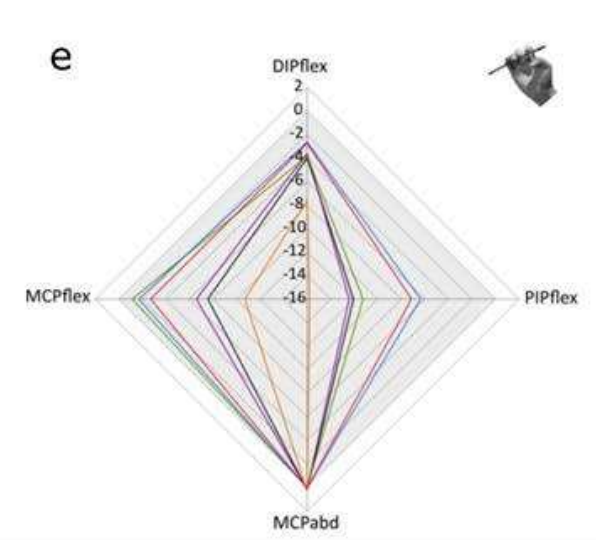
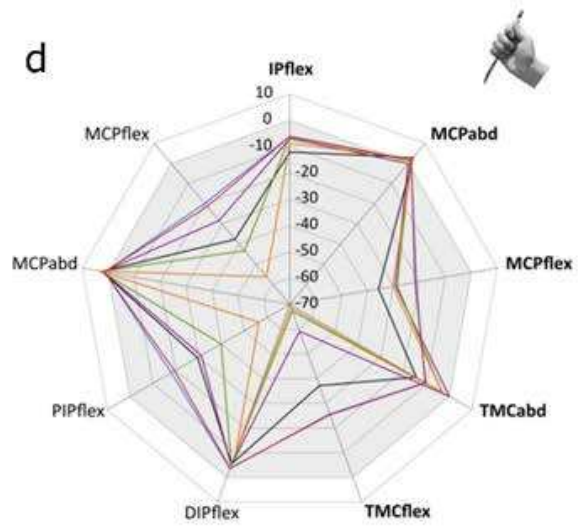
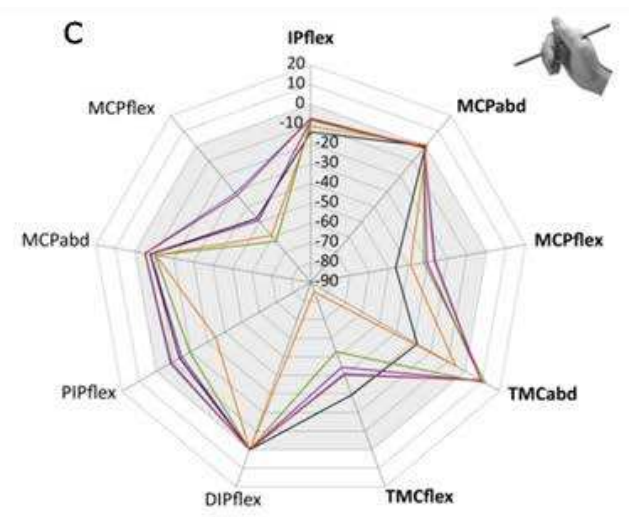
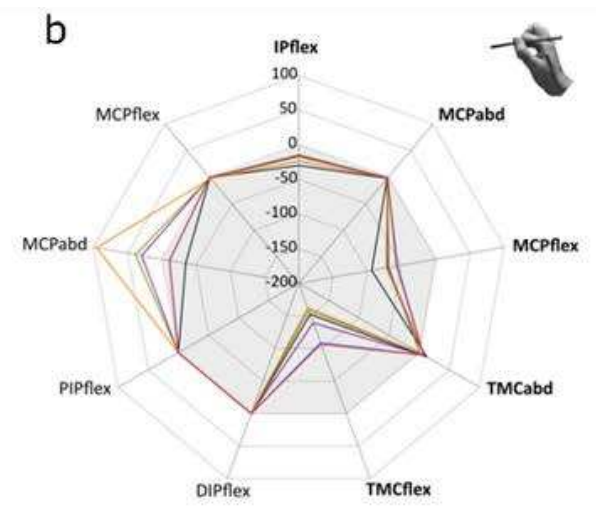
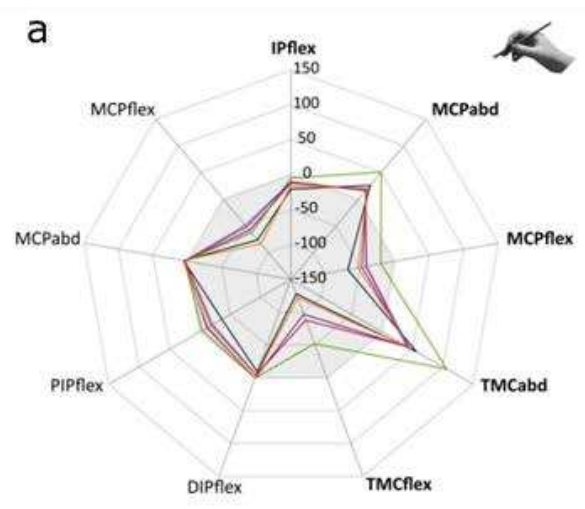


Figure 5. Radar plot of net joint moments (in N·cm) exerted on the thumb (in bold at right) and index fingers (left) during the simulation for humans (black), *Homo naledi* (red), *Australopithecus sediba* (blue), bonobos (purple), gorillas (green), and orangutans (orange), during: a) the dynamic tripod grip; b) the pinch grip; c) the interdigital 2/3 brace; d) the power grip technique; e) the hook grip; f) the scissor grip. Abbreviations: abd = abduction; DIP = distal interphalangeal joint; flex = flexion; IP = interphalangeal joint; MCP = metacarpophalangeal joint; PIP = proximal interphalangeal joint; TMC = trapeziometacarpal joint. Negative values are in the gray part of the radar plot and corresponded to extension and adduction.

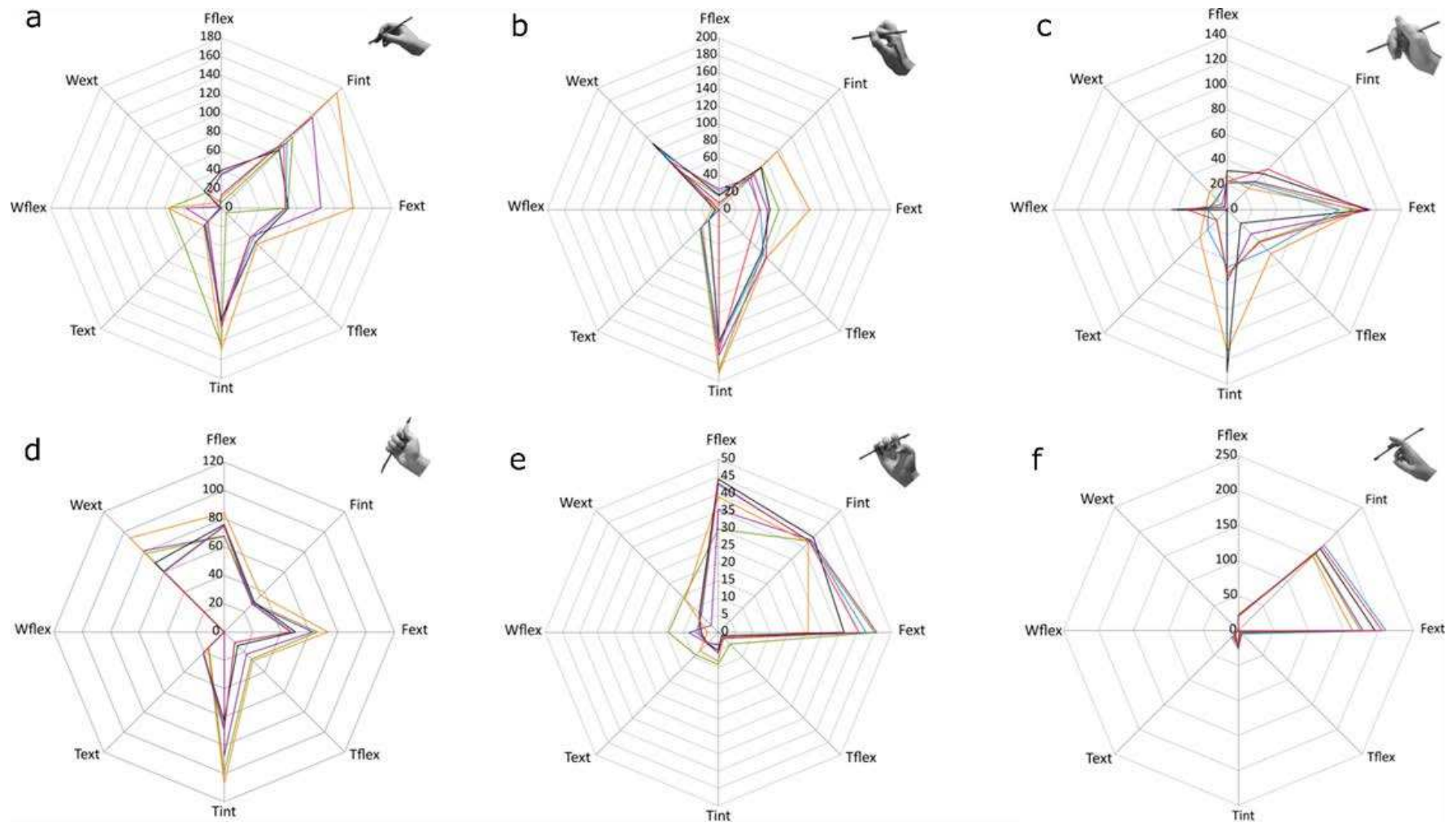


Figure 6. Radar plot of muscle coordination and force magnitude (in N) during the simulation for humans (black), *Homo naledi* (red), *Australopithecus sediba* (blue), bonobos (purple), gorillas (green), orangutans (orange), during: a) the dynamic tripod grip; b) the pinch grip; c)

the interdigital 2/3 brace; d) the power grip technique; e) the hook grip; f) the scissor grip. Abbreviations: Fext = fingers extensors; Fflex = fingers flexors; Fint = fingers intrinsics; Text = thumb extensors; Tflex = thumb flexors; Tint = thumb intrinsics; Wext = wrist extensors; Wflex = wrist flexors.

Table 1 Description of the grip techniques simulated in this study.

Grip techniques	Description
Dynamic tripod	<p>The tool is stabilized against the radial side of the third finger by the thumb pulp with the index finger pulp on top of the tool</p> <p>Defined in human studies as the common pencil grip (Wynn-Parry, 1966)</p>
Interdigital 2/3 brace	<p>The tool is held by flexed index finger and exits the hand between the proximal or middle phalanges of the index and third fingers.</p> <p>Defined in human studies as an inefficient variant of the pencil grip (Selin, 2003)</p>
Power	<p>The tool is held in opposition between the palm and flexed fingers with pressure possibly applied by the thumb</p>
Hook	<p>The tool is held transversally by flexed fingers and without the thumb</p>
Pinch	<p>The tool is held between the thumb pad and the side of the index finger</p> <p>Considered particularly important during stone tool making and use in humans (Marzke and Shackley, 1986; Marzke, 1997)</p>
Scissor	<p>The tool is held between two fingers excluding the thumb</p>

Table 2

Joint angles (in degrees) of the thumb and the index finger input in the model for each grip techniques and each species.

	Thumb					Index finger			
	IP_F-E	MCP_F-E	MCP_A-A	TMC_F-E	TMC_A-A	DIP_F-E	PIP_F-E	MCP_F-E	MCP_A-A
Dynamic tripod									
Human	19.11	10.73	11.41	17.25	-13.08	-4.97	36.28	62.76	-4.45
Bonobo	19.11	10.73	11.41	28.65	-13.08	22.92	68.75	80.21	-4.45
Gorilla	19.11	10.73	11.41	28.65	-13.08	5.73	90.00	63.03	-4.45
Orangutan	15.41	10.73	11.41	28.71	-7.35	17.95	64.93	85.67	-4.45
<i>A. sediba</i>	19.11	10.73	11.41	17.25	-18.81	12.22	42.01	62.76	-4.45
<i>H. naledi</i>	19.11	10.73	11.41	17.25	-13.08	23.68	36.28	62.76	-4.45
Pinch grip									
Human	27.22	-5.92	-13.76	13.91	-26.93	36.35	75.27	55.62	2.07
Bonobo	11.46	-5.92	-13.76	13.91	-15.47	47.81	81.00	90.00	2.07
Gorilla	27.22	-5.92	-13.76	13.91	-14.32	36.35	81.00	90.00	2.07
Orangutan	27.22	-5.92	-13.76	19.64	-14.32	42.08	92.46	101.45	2.07
<i>A. sediba</i>	27.22	-5.92	-13.76	13.91	-26.93	36.35	75.27	67.08	2.07
<i>H. naledi</i>	27.22	-5.92	-13.76	13.91	-26.93	36.35	75.27	67.08	2.07
Interdigital 2/3 brace									
Human	51.31	61.46	0.00	-51.57	-50.35	14.64	41.38	56.93	10.97
Bonobo	-12.83	-15.36	-7.36	13.08	-33.57	14.64	41.38	56.93	10.97
Gorilla	-12.83	-15.36	-7.36	13.08	-33.57	14.64	41.38	58.20	10.97
Orangutan	17.19	11.46	-7.36	-11.46	-20.05	14.64	68.75	68.75	10.97
<i>A. sediba</i>	-12.83	-15.36	-7.36	13.08	-33.57	43.28	41.38	56.93	10.97
<i>H. naledi</i>	-12.83	-15.36	-7.36	13.08	-33.57	14.64	41.38	56.93	10.97
Power									
Human	34.51	22.2	-12.42	-17.22	-42.35	-4.13	83.54	86.36	-3.76
Bonobo	0	0	0	0	-14.32	7.33	89.27	86.36	-3.76

Gorilla	5.73	11.46	-12.42	-17.22	-14.32	-4.13	89.27	86.36	-3.76
Orangutan	11.46	22.2	-12.42	-17.22	-14.32	1.6	89.27	103.55	-3.76
<i>A. sediba</i>	34.51	22.2	-12.42	-17.22	-42.35	7.33	83.54	86.36	-3.76
<i>H. naledi</i>	34.51	22.2	-12.42	-17.22	-42.35	7.33	83.54	86.36	-3.76
Hook									
Human						47.02	89.06	23.47	-4.29
Bonobo						47.02	94.79	23.47	-4.29
Gorilla						64.21	89.06	23.47	-4.29
Orangutan						64.21	100.52	23.47	-4.29
<i>A. sediba</i>						58.48	89.06	17.74	-4.29
<i>H. naledi</i>						55.62	89.06	17.74	-4.29
Scissor									
Human						-0.72	49.34	37.30	-10.79
Bonobo						-0.72	49.34	37.30	-10.79
Gorilla						-0.72	49.34	37.30	-10.79
Orangutan						16.47	60.80	37.30	-10.79
<i>A. sediba</i>						-0.72	49.34	37.30	-10.79
<i>H. naledi</i>						-0.72	49.34	37.30	-10.79

Abbreviations: A-A = abduction/adduction; DIP = distal interphalangeal joint; F-E = flexion/extension; IP = interphalangeal joint; MCP = metacarpophalangeal joint; PIP = proximal interphalangeal joint; TMC = trapeziometacarpal.

Table 3

Summary of muscle coordination assessed in regards to the mean muscle force magnitude in the thumb, fingers, and wrist for each of the six grips across all species.

	Dynamic tripod	Pinch	Interdigital 2/3 brace	Power	Hook	Scissor
Number of involved muscle groups	7 (TI, TF, TE, FE, FI, FF, WF)	6 (TI, TF, TE, FE, FI, WE)	6 (TI, TF, FE, FI, FF WF)	5 (TI, FE, FI, FF, WE)	3 (FF, FI, FE)	3 (FF, FI, FE)
Thumb	TI +++++ ^a TF ++ TE +	TI +++++ TF+++ TE +	TI +++ TF + TE -	TI +++ TF - TE -		
Fingers	FE +++ FI ++++ FF +	FE ++ FI ++ FF -	FE ++++ FI + FF +	FE ++ FI + FF +++	FE + FI + FF +	FE +++++ FI +++++ FF +
Wrist	WE - WF +	WE +++ WF -	WE - WF +	WE +++ WF 0	WE - WF -	WE 0 WF 0

Abbreviations: FF = fingers flexors; FI = fingers intrinsics; FE = fingers extensors; TF = thumb flexors; TI = thumb intrinsics; TE = thumb extensors; WF = wrist flexors; WE = wrist extensors.

^a Muscle force magnitude requires: -, < 20 N; +, magnitude > 20 N; ++, magnitude > 40 N; +++, magnitude > 70 N; +++++, magnitude > 100 N; ++++++, magnitude > 130 N; 0 = absent.

Supplementary Online Material

The impact of hand proportions on tool grip abilities in humans, great apes and fossil hominins: a biomechanical analysis using musculoskeletal simulation

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SOM Table S1

Mean values of the length of each segment (in cm) used for each great ape model. The lengths were derived from morphometric data on osteological collections.

Species	Thumb			Index				Middle finger				Ring finger			Little finger				Ratio thumb/index length	
	Mc1	PP1	DP2	Mc2	PP2	IP2	DP2	Mc3	PP3	IP3	DP3	Mc4	PP4	IP4	DP4	Mc5	PP5	IP5		DP5
<i>Homo sapiens</i> ^a	4.82	3.76	3.03	6.79	4.70	2.74	1.86	5.66	5.11	3.26	2.07	5.09	4.68	3.17	2.05	4.98	3.92	2.25	1.79	0.72
<i>Pan paniscus</i> ^b	3.97	2.80	1.72	8.80	4.68	2.98	1.66	8.70	5.46	3.85	2.07	7.80	5.08	3.65	2.04	6.97	4.17	2.58	1.63	0.46
<i>Gorilla gorilla</i>																				
<i>gorilla</i> ^b	5.33	3.00	1.70	10.12	5.92	3.92	1.77	9.77	6.34	4.36	2.05	9.37	5.82	3.79	1.94	9.13	5.11	3.26	1.59	0.46
<i>Pongo</i>																				
<i>pygmaeus</i> ^b	5.38	2.83	1.49	11.55	7.05	4.33	2.19	11.26	8.01	5.35	2.48	10.93	7.91	5.39	2.23	10.09	6.65	4.36	2.09	0.39
<i>Homo naledi</i> ^c	3.74	2.45	1.52	5.37	3.22	1.78	1.27	4.90	3.59	2.26	1.44	4.27	3.31	2.21	1.41	4.07	2.65	1.56	1.24	0.66
<i>Australopithecus</i>																				
<i>sediba</i> ^d	3.94	2.38	1.51	5.28	3.12	1.64	1.21 ^e	4.83	3.47	2.16	1.39 ^d	4.4	3.34	2.04	1.37 ^d	4.16	2.72	1.68	1.25 ^f	0.70

Abbreviations: DPf = distal phalanx of the f finger with f = {1 for thumb, 2 for index finger, 3 for middle, 4 for ring, 5 for little}; IPf = intermediate phalanx of the f finger; Mcf = metacarpal of the f finger; PPf = proximal phalanx of the f finger.

^a Bucholz et al. (1992).

^b T.L.K. data set.

^c Kivell et al. (2015).

^d Kivell et al. (2011) and Feix et al. (2015).

^c *Australopithecus sediba* (MH2) DP2 length was estimated by Feix et al. (2015).

^e MH2 is missing the distal phalanx of the middle finger (DP3) and the ring finger (DP4). We estimated the length of DP3 and DP4 based on a ratio of the overall length of the fingers 2–4 in *Australopithecus sediba* multiplied by, respectively, the DP3 and DP4 length in *H. naledi*.

^f The length of DP5 in *A. sediba* that we used (1.25 cm) is probably from ray four or five in MH2 left hand (Kivell et al. 2011).

SOM Table S2

Muscles groups used in the simulations for all the species.

Muscles groups	Muscles
FF – Finger flexors	FDP II, FDP III, FDP IV, FDP V, FDS II, FDS III, FDS IV, FDS V
FE – Finger extensors	EDC II, EDC III, EDC IV, EDC V, EI, EDQ
FI – Finger intrinsics	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 intrinsics	OPP, APB, ADPt, ADPo
WF – Wrist flexors	FCR, FCU, PL
WE – Wrist extensors	ECRL, ECRB, ECU

Abbreviations: ADPo = adductor pollicis oblique head; ADPt = adductor pollicis transverse head; ADQ = abductor digiti quinti; APB = abductor pollicis brevis; APL = abductor pollicis longus; DIO_n = nth dorsal interosseous; ECRB = extensor carpi radialis brevis; ECRL = extensor carpi radialis longus; ECU = extensor carpi ulnaris; EDC_f = extensor digitorum communis of the f finger with f = {II for index finger, III for middle, IV for ring, V for little}; EDQ = extensor digiti quinti; EI = extensor indicis; EPB = extensor pollicis brevis; EPL = extensor pollicis longus; FCU = flexor carpi ulnaris; FCR = flexor carpi radialis; FDP_f = flexor digitorum profundus of the f finger; FDS_f = flexor digitorum superficialis of the f finger; FPB = flexor pollicis brevis; FPL = flexor pollicis longus; LUn = nth lumbrical; OPP = opponens pollicis ; PION = nth palmar interosseous; PL = palmaris longus.

SOM Table S3

Raw results of net joint moments (in N·cm) for the thumb and index finger joints for each of the six grip types and each extant and fossil hominins. ^a

	Thumb					Index finger			
	IPflex	MCPabd	MCPflex	TMCabd	TMCflex	DIPflex	PIPflex	MCPabd	MCPflex
Dynamic tripod									
Human	-20.8	25.9	-67.7	56.7	-127.8	-9.2	-36.3	5.2	-75.9
Bonobo	-11.9	18.3	-47.3	42.2	-96.8	0	-11.6	4.5	-58.2
Gorilla	-4.9	50.3	-19.9	106.6	-52	0	-3.9	4.3	-62.6
Orangutan	-16.5	20.1	-52.9	47.2	-122.2	0	-13.3	6.4	-83
<i>A. sediba</i>	-10.5	15.6	-40.5	44.4	-88.2	-4.3	-18.1	3.4	-48.7
<i>H. naledi</i>	-10.5	16	-41.5	40.7	-87.9	-4.5	-21.1	3.6	-52
Pinch									
Human	-30	-2.4	-93.6	12.4	-152.3	0	0	-34.8	-1
Bonobo	-17.2	-1.7	-70	8.1	-139	0	0	29.4	-1.1
Gorilla	-17	-1.7	-68.4	0.9	-158.2	0	0	38.7	-1.4
Orangutan	-23.8	-1.8	-72	7.3	-162.5	0	0	95.2	-2.5
<i>A. sediba</i>	-15.1	-1.4	-55.8	7.3	-108.9	0	0	-11.3	-0.6
<i>H. naledi</i>	-15.2	-1.4	-57.1	7.5	-106.6	0	0	-11	-0.6
Interdigital 2/3 brace									
Human	-13.9	0	-46.5	-27.9	-29.6	0	-13.6	-7.7	-47.7
Bonobo	-7.9	-1	-30.5	9.5	-44.3	0	-14.9	-7.9	-49.1
Gorilla	-7.8	-1.1	-32.1	11.8	-52.7	0	-19.6	-10.4	-62.8
Orangutan	-11	1	-38.9	-5.6	-85.1	0	-34.6	-10.7	-59.1
<i>A. sediba</i>	-6.9	-1	-26.2	8.9	-40.8	0	-8.2	-5	-31
<i>H. naledi</i>	-7	-1	-26.8	8.8	-40.3	0	-8.9	-5.3	-32.4
Power									
	IPflex	MCPabd	MCPflex	TMCabd	TMCflex	DIPflex	PIPflex	MCPabd	MCPflex

Human	-12	2.9	-35.7	-14.5	-37.1	-5.5	-29.6	2.5	-37.7
Bonobo	-6.9	0	-29.3	0	-59.1	-4.9	-31.2	1.9	-28.3
Gorilla	-6.3	1.2	-28.6	-3.2	-67.3	-5.2	-39.9	2.8	-43.3
Orangutan	-8.8	2.5	-30.3	-2.9	-68.7	-10.4	-56.5	3.6	-56.3
<i>A. sediba</i>	-6	1.8	-21.2	-10.6	-25.7	-3.6	-18.1	1.3	-19.8
<i>H. naledi</i>	-6.1	1.8	-21.7	-10.4	-25.3	-3.8	-19.5	1.4	-21.3
Hook	IPflex	MCPabd	MCPflex	TMCabd	TMCflex	DIPflex	PIPflex	MCPabd	MCPflex
Human	-	-	-	-	-	-4	-12.1	0	-7.6
Bonobo	-	-	-	-	-	-3.6	-12.4	0	-6.6
Gorilla	-	-	-	-	-	-3.8	-11.2	0	-1.1
Orangutan	-	-	-	-	-	-7.6	-15.8	0	-10.7
<i>A. sediba</i>	-	-	-	-	-	-2.6	-6.4	0	-1.7
<i>H. naledi</i>	-	-	-	-	-	-2.8	-7.1	0	-2.7
Scissor	IPflex	MCPabd	MCPflex	TMCabd	TMCflex	DIPflex	PIPflex	MCPabd	MCPflex
Human	-	-	-	-	-	0	0	75.9	-3.9
Bonobo	-	-	-	-	-	0	0	76.4	-4.2
Gorilla	-	-	-	-	-	0	0	96.8	-5.6
Orangutan	-	-	-	-	-	0	0	103.1	-11.3
<i>A. sediba</i>	-	-	-	-	-	0	0	50.7	-2.3
<i>H. naledi</i>	-	-	-	-	-	0	0	52.4	-2.5

Abbreviations: TMC = trapeziometacarpal joint; IP, interphalangeal joint; MCP, metacarpophalangeal joint; PIP, proximal interphalangeal joint; DIP, distal interphalangeal joint; flex, flexion; abd, abduction.

^a Negative values corresponded to extension and adduction.

SOM Table S4

Raw results of muscle force intensities (in N) for each muscle groups, for each of the six grip types, and each extant and fossils hominins. ^a

Dynamic tripod	Fflex	Fint	Fext	Tflex	Tint	Text	Wflex	Wext
Human	39.9	86.6	70.8	51.2	117.8	24.9	0	25.7
Bonobo	13.9	136	105.9	43.3	118.9	20.1	37.3	2.5
Gorilla	5.9	106.5	69.9	7.1	144.7	55	55.6	22.7
Orangutan	10.5	172.4	139	53.7	149.6	26.3	56.2	8.1
<i>A. sediba</i>	35	97.9	68.3	46.4	124.1	23.1	2	18.8
<i>H. naledi</i>	36.5	93.3	67.6	43.5	125.1	20.2	0	18.4
Pinch	Fflex	Fint	Fext	Tflex	Tint	Text	Wflex	Wext
Human	17.1	69.6	59.1	70.4	153.8	16.6	4.2	109.2
Bonobo	7.9	57.7	56.3	77.9	169.8	29.8	0	66.7
Gorilla	16.3	70.1	69.9	72	186.4	31.2	0	61.3
Orangutan	4.7	96.1	105.9	78.9	190.3	26.5	8.2	23.4
<i>A. sediba</i>	21.6	48.7	48.4	73.3	157.1	29.5	0	95.6
<i>H. naledi</i>	24.4	52.6	47.3	51.6	164.9	0	0	78.4
Interdigital 2/3 brace	Fflex	Fint	Fext	Tflex	Tint	Text	Wflex	Wext
Human	31.4	40.9	113.5	15.2	130.1	0	44.6	2.9
Bonobo	21.4	32.1	115.2	27.2	57.5	0	40	0
Gorilla	21.3	30.9	101.4	36	53.5	11.9	15.5	12.5
Orangutan	27.6	24.2	106.8	49.8	113.9	30.8	17.2	20.2
<i>Au. sediba</i>	23.3	28.6	90.1	45.7	46.2	22.2	15.1	11.2
<i>H. naledi</i>	22.9	46	110.4	36.8	51.5	11.6	32.4	5.9

Power	Fflex	Fint	Fext	Tflex	Tint	Text	Wflex	Wext
Human	75.9	29.8	50.2	13.4	62.8	20.8	0	69
Bonobo	67.8	28.1	62.5	22.1	87.5	0	0	81.1
Gorilla	67.5	29.2	65.8	27.1	99.3	15.3	0	78.3
Orangutan	84.2	36.3	73.2	28.7	106.9	16.1	0	93.8
<i>A. sediba</i>	75.2	28.9	47.4	10.6	69.9	21.1	0	60.7
<i>H. naledi</i>	74.6	27.8	46.6	10.3	67.8	20.5	0	60
Hook	Fflex	Fint	Fext	Tflex	Tint	Text	Wflex	Wext
Human	44.3	38.9	36.3	1.3	5.2	4.4	4.9	7.7
Bonobo	35.5	37.8	45.7	1.9	6	4.4	8.5	2.9
Gorilla	29.9	37.3	45.1	4.7	9.2	9.2	14.4	14.1
Orangutan	39.2	36.8	25.9	2.1	8.3	7.5	3.1	13.4
<i>A. sediba</i>	42.7	37.4	42.7	2.4	3.6	4.3	6.5	6.9
<i>H. naledi</i>	43.1	37.2	40.7	2.3	3.4	4.3	5.7	7.2
Scissor	Fflex	Fint	Fext	Tflex	Tint	Text	Wflex	Wext
Human	21.5	165.4	195	2.1	24.8	7.4	0	0
Bonobo	20.8	156.4	177.9	5.4	21.8	11.8	0	0
Gorilla	21.3	155.6	174.2	4.4	17.8	9.7	0	0
Orangutan	23.3	150.7	162.9	1.6	19.2	5.5	0	0
<i>A. sediba</i>	20.9	173.2	210.6	6.6	26.3	14.3	0	0
<i>H. naledi</i>	20.5	168.9	205.2	2.2	26	7.9	0	0

Abbreviations: Fext = fingers extensors; Fflex = fingers flexors; Fint = fingers intrinsics; Text = thumb extensors; Tflex = thumb flexors; Tint = thumb intrinsics; Wext = wrist extensors; Wflex = wrist flexors.

^a Negative values corresponded to extension and to adduction.