Finite element analysis of the proximal phalanx of the thumb in Hominoidea during simulated stone tool use

Ana BUCCHI, Thomas A. PÜSCHEL, Carlos LORENZO & Jordi MARCÉ-NOGUÉ

art. 19 (2) — Published on 10 August 2020
www.cr-palevol.fr
Finite element analysis of the proximal phalanx of the thumb in Hominoidea during simulated stone tool use

ABSTRACT

Finite element analysis was applied to analyze six individuals from different primate species (Homo sapiens Linnaeus, 1758, Homo neanderthalensis King, 1864, Pan troglodytes Blumenbach, 1779, Gorilla gorilla Savage, 1847, Pongo pygmaeus Linnaeus, 1760 and Hylobates lar Linnaeus, 1771) to identify stress distribution patterns on the pollical proximal phalanx during simulated hammerstone use. We expected the stress to be better distributed in our species than in other hominids based on the idea that, unlike apes, the human hand is adapted to tool-related behaviors. Our results indicate that the human phalanx unevenly distributes stresses and is one of the most fragile of all, especially when a small hammerstone is simulated. Tool orientation relative to the phalanx did not have a substantial effect on average stress or distribution. We conclude that great apes can resist loads exerted during this activity more efficiently than humans and that there were probably other evolutionary factors acting on this bone in our species.
INTRODUCTION

There is a widespread idea that the derived manual anatomy of humans is a result of selective pressures related to manipulative behaviors (e.g. Hamrick et al. 1998; Young 2003; Key & Dunmore 2015; Skinner et al. 2015; Kivell et al. 2016) as, among primates, humans exert unique, more efficient precision and power grips (e.g. Niewoehner 2001; Shrewsbury et al. 2003; Tocheri et al. 2003; Rolian et al. 2011; Marzke 2013; Key & Dunmore 2015; Bardo et al. 2017). Unlike humans, locomotion constitutes the primarily selective pressure on the hand for most primates (e.g. Tuttle 1969; Jouffroy et al. 1991). This is not to say that non-humans primates are unable of performing tool-based activities, as they have been reported in other primates (Prutz & Bertolani 2007; Wynn et al. 2011; Gumert & Malaivijitnond 2013; Visalberghi et al. 2015), and some of their tools, including stone hammers, and the behaviors involved (e.g. direct hard hammer knapping) are very similar or indistinguishable from Oldowan culture (Wynn & McGrew 1989; Wynn et al. 2011). However, the manual pressures and high muscle activities experienced by the hand during travel (Susman & Stern 1979; Wunderlich & Jungers 2009; Matazzato 2013; Samuel et al. 2018) play a more important role.

The selective pressures related to stone tool use supposedly started early in the human lineage. The intrinsic muscles of the thumb show high level forces during hard hammer percussion manufacture of Oldowan tools (Hamrick et al. 1998; Marzke et al. 1998). The thumb also experiences significant pressures during stone tool production (Key & Dunmore 2015; Williams-Hatala et al. 2018). In addition, some derived morphology facilitating manipulation of stone tools, as the expanded apical tuft of the distal thumb phalanx, were already present in *Orrorin* (Gommery & Senut 2006), although numerous derived conditions evolved later in a mosaic fashion until the fully-derived hand of Neanderthals and modern humans (for a review, see Tocheri et al. 2008, and also Key & Dunmore 2018). Changes in hominins in the shortening of the fingers relative to thumb length, which ensures the human-like precision grip capability, occurred in *Australopithecus* (Alba et al. 2003; Green & Gordon 2008; Tocheri et al. 2008). Robust first metacarpals have been identified in early Homo/Paranthropus (Susman 1988), which helps to produce stronger, efficient grips and tolerate higher joint stresses (Rolian et al. 2011; Key & Dunmore 2015; Key & Lycett 2018).

Even though most of the paleoanthropological literature agrees that hands of humans and non-human primates are adapted to different functions (i.e., manipulation vs locomotion), recent studies have concluded that some derived traits leading towards *Homo* (e.g. finger proportions) are not the product of selective pressures acting directly on the hands but on other region of the skeleton (i.e., the foot) (Rolian et al. 2010) which are related to terrestriality (Heldstab et al. 2016; Bardo et al. 2017) and were subsequently exapted for tool manipulation. This can explain why skillful hands were present long before the first record of lithic industry (Alba et al. 2003; Almécity et al. 2010).

How humans acquired this unique configuration of musculoskeletal traits in the hand which facilitates tool related behaviors has profound implications in our understanding of human evolution overall, considering that stone technology is a key element defining culture in our species (e.g. Foley & Lahr 2003). However, testing biological causality is hard to address and we may never be absolutely certain on the evolutionary mechanisms having shaped the human hand. Consequently, we think that new insights are needed to better assess whether the evolution of the human hand is driven by tool-related behaviors.

Here we use finite element analysis (FEA) to evaluate if stress on the human pollical proximal phalanx (PP1) fits with the functional adaptation (to tool use) hypothesis for the evolution of our hand. This method makes it possible to control and repeat biomechanical scenarios under modifiable conditions (for a review, see Rayfield 2007) making it suitable for morpho-functional problems such as this. To our knowledge, no study has applied FEA to evaluate the effect of stone tool use on the hand.

The stress distribution in the PP1 was analyzed in six Hominoidea taxa (*Homo sapiens* Linnaeus, 1758, *Homo neanderthalensis* King, 1864, *Pan troglodytes* Blumenbach, 1779, *Gorilla gorilla* Savage, 1847, *Pongo pygmaeus* Linnaeus, 1760 and *Hylobates lar*).
Simulated tool use and hand performance

**MATERIAL AND METHODS**

**SAMPLE AND DIGITALIZATION**

A recent modern human, a Neanderthal from Krapina (Vi 202) and four extant non-human hominoids were analyzed: chimpanzee, gorilla, orangutan and gibbon. All specimens were adults with no evident pathologies (Table 1).

The PP1 from the human individual was obtained from a fresh cadaver and scanned with a micro-CT (Perkin Elmer, model Quantum Fx, Hopkinton MA, United States). The orangutan PP1 is from the Senckenberg Museum in Frankfurt, Germany (SMF 74303) and was scanned on a BIR ACTIS 225/330 micro-CT scanner at the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology (Leipzig, Germany). The remaining specimens were obtained from digital databases; the micro-CT of the Neanderthal PP1 from NESPOS (www.nespos.org/display/PublicNesposSpace/Human+Fossils), whereas the CT scans from the rest of the non-human sample were downloaded from the Digital Morphology Museum, Kyoto University, Japan (KUPRI; dmm.pri.kyoto-u.ac.jp/dmm/WebGallery/index.html). Even though KUPRI CT scans have a relative low resolution (Table 1) and do not allow to observe bone segments in high detail, they can still provide relevant morphological information, as it has been shown that even medium-resolution scans can accurately quantify shape (Slizewski et al. 2010; McCarty et al. 2015). In fact, it has been shown that this resolution is sufficiently accurate to even identify intra-specific differences of relatively small specimens (Marcy et al. 2018).

In order to make models from different resolution scans comparable, trabecular bone was enclosed using the “Convex Hull” tool in Meshlab v.2016.12 (Cignoni et al. 2008) and the same mechanical properties were defined for all the specimens. Elements were then converted to CAD models. During this last step, irregularities in the surface caused by segmentation were repaired using refinement and smoothing tools (Launeschläger 2016) in Geomagic Studio® (3D Systems, v. 12, Rock Hill, SC, United States).

All scans were segmented using Seg3D software (CIBC, v. 2.4.0, 2017). The medullary cavity, trabeculae and compact bone were segmented on the specimens by applying a combination of case-specific thresholding values and manual painting techniques. Models of left PP1’s (Table 1) were reflected to enable meaningful comparisons.

To avoid possible problems when aligning different individuals (due to inter-specific morphological differences), we selected one individual as a reference (i.e., the chimpanzee representative) to perform a best-fit alignment to align all the models according to a common reference plane. This procedure was carried out in Geomagic Studio® (3D Systems, v. 12, Rock Hill, SC, United States) prior to FEA to align all the models, so that loads could be applied in the same axis and allow an easier interpretation of the results.

**MODEL PROPERTIES**

Structural static analysis was performed to evaluate the biomechanical behavior of the PP1s using the Finite Element Package ANSYS 17.1 in a Dell Precision™ Workstation T5500 with 48 GB and 5.33 GHz. Elastic, linear and homogeneous material properties were assumed for the cortical bone using the values of E (Young’s modulus) 18.6 GPa and v (Poisson’s ratio) 0.3, while for trabecular bone values of E 0.75 GPa and v 0.3 were assumed (Butz et al. 2012).

In this study, the focus in the comparison of the models is primarily on the von Mises stress distribution. Bone can be modeled as a brittle (Doblaré et al. 2004) or ductile (Dumont et al. 2009) material. According to Doblaré et al. (2004), the von Mises criterion is the most commonly applied and useful criterion for predicting the yield and fracture location in bone when ductile and isotropic material properties are assumed in cortical bone. The PP1 models were meshed using an adaptive hexahedral mesh and ANSYS® (Marcé-Nogué 2009) material. According to Doblaré et al. (2004), or ductile (Dumont et al. 2009) material. According to Doblaré et al. (2004), the von Mises criterion is the most commonly applied and useful criterion for predicting the yield and fracture location in bone when ductile and isotropic material properties are assumed in cortical bone. The PP1 models were meshed using an adaptive hexahedral mesh and ANSYS® (Marcé-Nogué 2009).

**Table 1. — Sample. Abbreviations: a, age of individuals, if known; unk, unknown. b, M: male; F: female. c, R: right; L: left.**

| Species                  | Common name      | Age | Sex | Side | Digital database/ n° | CT/microCT resolution (mm) |
|--------------------------|------------------|-----|-----|------|----------------------|---------------------------|
| Homo sapiens             | Modern human     | 59  | M   | R    | None                 | 0.08                      |
| Homo neanderthalensis    | Neanderthal      | unk | unk | R    | NESPOS/ Krapina 202  | 0.03                      |
| Pan troglodytes           | Chimpanzee       | 29  | M   | L    | KUPRI/345            | 0.219                     |
| Gorilla gorilla          | Gorilla          | 38  | M   | R    | KUPRI/1353           | 0.500                     |
| Pongo pygmaeus           | Orangutan        | 32  | F   | R    | None                 | 0.03                      |
| Hylobates lar             | Gibbon           | 33  | M   | R    | KUPRI/465            | 0.250                     |

**Table 2. — Percentage of main locomotor behavior of the non-human sample, according to Hunt (2004).**

| Taxon      | Climb | Braquiate | Clamber | Walk |
|------------|-------|-----------|---------|------|
| Chimpanzee | 6.5   | 0.8       | 0.0     | 89.9 |
| Gorilla    | 19.7  | 3.6       | 0.0     | 64.4 |
| Orangutan  | 31.3  | 15.5      | 40.7    | 12.0 |
| Gibbon     | 34.2  | 51.2      | 0.0     | 0.0  |
FIG. 1. — Biomechanical model of hammerstone use: B, corresponds to a zoom in palmar view of the area of interest during A, the grip of a human individual (based on Marzke et al. 1998). B, shows the angles of the muscular forces acting on the PP1. HRF is in 90° relative to the horizontal line for scenarios 1 and 2 and in 45° for scenarios 2 and 4. This force was applied on the entire palmar surface of the PP1 except in the joint areas and is represented with a hatched rectangle. Angles of the muscle forces are shown relative to the horizontal line. Abbreviations: FAP, Adductor Pollicis Force; FAPB, Abductor Pollicis Brevis Force; FFPB, Flexor Pollicis Brevis Force; EPB, direction force was applied in 16.7° and is not showed here as it attached on the dorsal surface of the PP1. Grey rectangles represent the origin areas of the muscles.

TABLE 3. — Mesh characteristics for each one of the specimens. Abbreviations: a, volume of the cortical bone; b, volume of trabecular bone; c, number of elements used to create the mesh for each FE model.

| Specimen        | Volume CB (mm³)a | Volume TB (mm³)b | N elements c |
|-----------------|------------------|------------------|--------------|
| Modern human    | 1012.8           | 651.1            | 225729       |
| Neanderthal     | 733.3            | 662.6            | 240469       |
| Chimpanzee      | 1046.1           | 178.6            | 160103       |
| Gorilla         | 1642.9           | 577.9            | 225710       |
| Orangutan       | 610.1            | 542.8            | 199857       |
| Gibbon          | 250.7            | 65.9             | 311431       |

et al. 2015). The model meshes ranged between 200,000 and 320,000 elements depending on the particular specimen and loading scenario (Table 3).

LOADING SCENARIOS AND BOUNDARY CONDITIONS
The hands were modeled using a free-body diagram approach in a precision three-jaw chuck grip (Fig. 1), following Marzke et al. (1998), since we obtained the applied muscle recruitment data from their study.

Forty-eight loading cases were generated. These included two hammerstone orientations relative to the PP1 and two muscle activity patterns associated with differences in hammerstone mass for the six individuals under study (Figs 1; 2). We also generated two different scaling scenarios for muscular data considering that for only two species (Homo sapiens and Pan troglodytes) there is enough muscular information to perform the simulations.

In the first scaling scenario, we scaled the forces of the Neanderthal, chimpanzee, gorilla, orangutan and gibbon using the extant human data as a reference, whereas in the second one, we used the chimpanzee muscular data as a reference to scale the forces of all the other representatives. In each of these two settings, the loads of the remaining specimens were scaled relative to the individuals of reference to yield identical force, i.e., the volume ratios (supplementary data Appendix 1). This way differences in stress distribution can be interpreted entirely as result of shape differences (Dumont et al. 2009). These values of muscular contraction pressure were calculated according to the method developed by Marcé-Noguè et al. (2013) and rearranged for 3D models by Fortuny et al. (2015).

Equation for this is $F_A = \frac{1}{4} V_A^2 F_B$, where $F_A$ is the scaled force, $F_B$ the reference force, and $V_A$ and $V_B$ the respective volumes for CB.

For the human, muscle forces were calculated by means of the physiological cross-sectional area (PCSA) collected from the forearm of a fresh cadaver of a 59-year-old man. All muscles attached at the PP1 were dissected: abductor pollicis brevis (APB), extensor pollicis brevis (EPB), flexor pollicis brevis (FPB), and adductor pollicis (AP) (cf. Sacks & Roy 1982). The PCSA obtained from the human cadaver were the following: FPB (0.6612 cm²), ADP (1.429 cm²), EPB (0.2121 cm²), and APB (0.2587 cm²). The insertion areas of the muscles involved were defined in the model to apply the forces of muscular contraction. The angles of the muscle tendons were estimated in situ. For the remaining specimens, tendon angles were assumed to be the same as for the human (Appendix 1), as areas of the bone in which muscles attached are similar between them (Diogo et al. 2011, 2012a, 2013a, b). PCSAs for chimpanzees were obtained from
Simulated tool use and hand performance

Hammer size

Models

Sc 1

Sc 2

Sc 3

Sc 4

FIG. 2.—Free-body diagram of the phalanx in the different scenarios. This figure depicts the boundary conditions, areas of insertion of muscles, and direction of forces. For all loading configurations, joint reaction forces resulted from the rigid boundary constraints that were fixed at the distal joint in X, Y and Z-axes (light blue area), and at the proximal joint in the X-axis (dark blue area). The hammer reaction force (HRF) was applied to the entire palmar surface of the bone. 3.29 N for the HRF was simulated for Sc 1 and 3, and 7.65 N for Sc 2 and 4. Phalanges are shown in palmar (right) and radial (left) views.

Marzke et al. (1999) for the APB, FPB and AD muscles, and from Kikuchi (2010) for EPB. The PCSA for the chimpanzee was: FPB (1.40 cm²), ADP (2.50 cm²), EPB (1.44 cm²), and APB (1.80 cm²) (Marzke et al. 1999; Kikuchi 2010).

The PCSA for FPB, APB, and EPB muscles was then adjusted to the levels of muscle activity described in the electromyography (EMG) study of Marzke et al. (1998). These data correspond to the active (i.e., dominant) hand and were recorded at the strike, so all scenarios were simulated at that specific moment. Following Maier & Hepp-Reymond (1995), we assumed that the activity for the APB, not monitored in Marzke et al. (1998), was similar to EPB.

Muscle activity was considered during the use of two hammerstone sizes (400 g and 780 g, respectively, which are equivalent to 3.92 N and 7.65 N and represent the HRF). Although it would be interesting to include the loads from the core, they can significantly vary in size, as well as during the reduction sequence. More importantly, the reaction force corresponding to the core would need to be considerably higher than the hammerstone reaction force to alter the stress distribution on the PP1, which is the focus of the present study.

We simulated two tool orientations relative to the PP1: one with the long axis of the bone parallel to horizontal line (Sc 1 and 2), and the other at 45° (Sc 3 and 4), as shown in Figures 1 and 2.

The hands were modeled using a free-body diagram approach. A biomechanical model (Fig. 1b) was constructed based on data about hand posture, muscles active during hammerstone use, the reaction forces from the hammerstone (HRF), and the joint reaction forces from metacarpal and distal phalanx (JRFmc and JRFd, respectively). Details of all loads involved are in Appendix 1.

Boundary conditions were defined to represent the fixed displacements that the models of PP1 experience during the loading scenarios. Once the models were solved, the joint reaction forces from the metacarpal (JRFmc) and from the distal phalanx (JRFd) were obtained. As boundary conditions have a great impact in the solution of the model, we intended to reproduce biological meaningful conditions for the PP1 to constrain the movements of the FEA models. The proximal part of the bone was fixed in the X dimension, and the distal part fixed in the X, Y and Z-axes (Fig. 2). All analyses were performed under these conditions (Appendix 1).

ANALYSIS OF VON MISES STRESS

We applied the recently-proposed quasi-ideal mesh (QIM) and its percentile values (M25, M50, M75, and M95) as a basis for our analysis (Marcé-Nogué et al. 2016). The use of a QIM mesh, corresponding to a mesh in which all the elements have practically the same size, facilitated between model comparisons, thus allowing the stress values obtained to be displayed as boxplots. Because the maximum value cannot be properly analyzed since it corresponds to artificially inflated values (Marcé-Nogué et al. 2015), here the M95 percentile is assumed as the peak value of stress following the concept introduced by Walmsley et al. (2013).
Fig. 3. — Von Mises stress maps for all analyzed species under different loading scenarios using the extant human as reference to scale the simulated muscular forces in all other specimens. Species are ordered from higher to lower peak stresses values. Phalanges are shown at the same length. MPa bar is set at 12 MPa.
FIG. 4. — Von Mises stress maps for all analyzed species under different loading scenarios using the chimpanzee as reference to scale the simulated muscular forces in all other specimens. Species are ordered from higher to lower peak stresses values. Images are not scaled. MPa is set at 25 MPa.
In addition, a quantitative single measurement of the relative strength of the structure under study was used to summarize the strength of the whole phalanx as the mesh-weighted arithmetic mean (MWAM) and the mesh-weighted median (MWM). These last values are also required to estimate the percentage error of the arithmetic mean (PEofAM) and the percentage error of the median (PEofM), which are statistics used to ensure that our models were reliable QIMs as described in Marcé-Nogué et al. (2016). This information can be found in supplementary data Appendices 2 and 3.

RESULTS

The distribution of von Mises stress for each phalanx and scenario is shown in Figures 3 and 4. The specimen with the highest peak stress level was the gibbon, followed by the extant human, the Neanderthal, the orangutan, the gorilla and the chimpanzee representatives. This order was the same for all analyzed loading and scaling scenarios, except for the chimpanzee and gorilla, with the former having higher peak stresses than the gorilla in the first and second loading scenario (Homo-scaled), but lower in the remaining ones (Fig. 5).

Maximum von Mises stress values in the gibbon, extant human, Neanderthal and gorilla models were located in the center of the palmar surface of the phalanx body, decreasing towards the dorsal surface and the distal and proximal portions (Figs 3; 4). In these specimens, the lowest stress values were found in the joint areas and dorsal part, where the bone was not significantly affected by stress. Stress for the orangutan, chimpanzee and gorilla specimens were lower and more evenly distributed over the bone and, similarly to the humans and gibbon, did not affect the joint areas. In most cases, median stress values (MWM) for the extant human and Neanderthal representatives (Fig. 5) were lower and more focused than measured in chimpanzee, gorilla and orangutan (Figs 3; 4).

Peak and mean stress levels were considerably higher when the smaller hammerstone was simulated in all species (Fig. 5), while the effect of hammerstone orientation was less important. Overall, the effect of the hammerstone size was even greater than that related to the morphological differences between species (Fig. 5). Of all the scenarios, that showing the highest mean and peak values for all species was the one with the smaller hammerstone and the second bone orientation (Sc 3).

DISCUSSION

The objective of this study was to assess stress distribution in the pollical proximal phalanx (PP1) of the active hand during the simulated use of hammerstones in different Hominoidea species. In the analyses, we varied the size of the hammerstone, the orientation of the tool relative to the hand, and the muscular properties to see their effects in stress distribution over the bone. We expected human PP1 to behave more efficiently in every scenario, as we assumed its greater adaptation to tool-related behaviors. However, we found that, in all cases, the human phalanx behaved as one among the most fragile bones, second only to the gibbon (Figs 3; 5). Stress distribution in the human PP1 was uneven and its concentration at the center of the shaft indicates that it is less resistant to loads during forceful precision grip and is more prone to structural failure. These results indicate that non-human hominids (i.e., gorilla, chimpanzee and orangutan) can better withstand loads exerted during this activity as compared to humans, although other key anatomical characteristics, for instance finger proportions, facilitate this activity in the later (Napier 1960; Rolian et al. 2011).

Our results suggest that stresses in the PP1 during tool-related behaviors were not the main driving force explaining the morphology of this bone, otherwise a different stress distribution would have very likely been observed in the human PP1. It is possible that the selective pressures acting on the thumb during stone tool production were not as consistently high to affect the morphology of this bone. Although other studies have found that the biomechanical stresses experienced by the thumb are high during this activity (Hamrick et al. 1998; Marzke et al. 1998; Key & Dunmore 2015; Williams-Hatala et al. 2018), there is a noticeably high variability between individuals in the observed kinematics (Rein et al. 2014), muscle activity (Marzke et al. 1998), and manual pressures (Williams et al. 2012; Williams-Hatala et al. 2018). These results raise the possibility that there were other stronger selective pressures acting on the PP1 that may not be related to stone-tool use. The argument that the evolution of the human hand was driven by selective pressures other than manipulative capabilities has been introduced in some previous studies (Alba et al. 2003; Almécija et al. 2010; Rolian et al. 2010; Heldstab et al. 2016). Specifically, the concept that the evolution of thumbs is linked to the evolution of toes (Rolian 2009; Rolian et al. 2010), thus to locomotor functions, which imply higher biomechanical demands than manipulation. Accordingly, locomotor functions would represent the primarily selective pressures shaping feet and hands in primates, including humans.

Even though the mean (MWM) and median (MWAM) stress values of humans were found relatively similar to those of non-human hominoids (i.e., gorilla, chimpanzee and orangutan) (Fig. 5), the poor stress distribution observed on the human representative resulted in a more fragile PP1. The variation in the distribution of stress among the specimens is probably related to differences in the morphology of the PP1 (Figs 3; 4). Future analyses deepen the relation between PP1 morphology and stress distribution under stone tool use conditions might shed some light into this link. Previous studies provide some guidance to this problem, as anatomical variations in hand morphology and structure within and among primates has been described, notably with respect to cortices thickness (Susman 1979; Tsegai et al. 2017), trabecular bone organisation (Lazenby et al. 2011; Chirichir et al. 2015; Matarazzo 2015; Skinner et al. 2015; Stephens et al. 2016), external dimensions and proportions (Napier 1962; Susman 1979; Key & Lycett 2018), and joint surface shape (Tocheri et al. 2003, 2005; Marchi et al. 2017).
Simulated tool use and hand performance

FIG. 5. — Box-plots of von Mises stress (MPa) distribution for all species under different scenarios, until Q95 (Sc 1 in grey, Sc 2 in yellow, Sc 3 in green and Sc 4 in red). The first row shows stress distribution of the models using the extant human as a reference to scale muscular forces in all other specimens, whereas the second one shows the results when the chimpanzee is used as a reference. Species are ordered from higher to lower peak stresses.
Does the force scaling of the non-human sample affect these results? While comprehensive knowledge is available about human muscles (e.g. Tuttle 1969; Marzke et al. 1998; Diogo et al. 2012b) and, to a lesser extent, in chimpanzees (Marzke et al. 1999; Kikuchi 2010), there are no analogous studies about the levels of muscular forces and activation patterns during the use of hammerstones for the other primate taxa considered here. To solve this problem, following Marcé-Nogué et al. (2013) and Fortuny et al. (2015), we scaled the muscular forces in the non-human hominins using the human and chimpanzee data as a reference, which allowed us to compare the behaviors of the PP1 from species that differ in size and morphology. In spite of this assumption, what makes the human (and gibbon) PP1 fragile is the stress distribution along the bone, which in this comparative analysis is not affected by the level of activation of the muscles. This becomes apparent when results from the two muscle scaling scenarios (human and chimpanzee) are compared: while stress values increase when using the chimpanzee muscles as reference, the stress distribution was very similar to the human scaling reference (Figs 3; 5).

A validation of FEA results against experimental data to see how precisely and accurately they reflect reality was not performed. Assumptions in our study for the non-human sample are related to muscle properties (tendon angles and forces), muscle activation patterns, and muscle function. Although detailed scenarios for each non-human representative would be ideal in such kind of analyses, these simplifications were necessary to evaluate the performance of each specimen which are difficult to access, such as muscle activation patterns during hammer use. Therefore, simulations were used to extract general patterns between species and should be interpreted in a comparative framework. This comparative approach has been successfully applied in several other studies using FEA (e.g. Serrano-Fochs et al. 2015; Püschel & Sellers 2016; Marcé-Nogué et al. 2017).

CONCLUSIONS

Non-human hominoids (i.e., gorilla, chimpanzee and orangutan) can better withstand loads exerted during simulations of hard hammer percussion than humans. Among extant Hominoidea, the human PP1s were relatively fragile at the moment of strike. Our results suggest that in humans the forces exerted during forceful precision gripping did not act as a strong selective pressure affecting the morphology of the first pollical phalanx.

Acknowledgements

We want to thank the University of Barcelona’s body donation service, especially Cristina Manzanares, Juan Antonio Camara, José Luis Ramón Cayuela, and Gemma Ramón Cayuela for their assistance. We are grateful to Dr. Tracy Kivell who gave us the micro-CT data of the orangutan phalanx and to the Senckenberg Museum in Frankfurt, where this specimen is housed. We are also grateful to Clément Zanollí for the translation into French. We acknowledge NESPOS, and KUPRI for the CT scans of the non-human primates used in this study and the original providers of the material: Tennoji Zoo, Fukuoka City Zoo and the Fukuchiyama City Zoo. This work was supported by the General Directorate of Research of the Spanish Ministry of Science and Technology (MCIINN-FEDER: grant number PGC2018-093925-B-C32); the Government of Catalonia (AGAUR: grant number 2017SGR 1040); the URV Project 2016 PFR-URV-B2-17; the Becas Chile Program of the Chilean National Commission for Scientific and Technological Research (CONICYT); the DFG, German Research Foundation (grant number KA 1525/9-2); and the Government of Catalonia’s CERCa program. T.A.P was funded by the Leverhulme Trust Early Career Fellowship (grant number ECF-2018-264).

REFERENCES

Alba D. M., Moya-Sola S. & Köhler M. 2003. — Morphological affinities of the Australopithecus afarensis hand on the basis of manual proportions and relative thumb length. *Journal of Human Evolution* 44: 225-254. https://doi.org/10.1016/S0047-2484(02)00207-5

Almeida S., Moya-Sola S. & Alba D. M. 2010. — Early Origin for Human-Like Precision Grasping: A Comparative study of Pollical distal Phalanges in Fossil Hominins. *Plus One 5*: 1-10. https://doi.org/10.1371/journal.pone.0011727

Bardo A., Cornette R., Borel À. & Pouydebat E. 2017. — Manual function and performance in humans, gorillas, and orangutans during the same tool use task. *American Journal of Physical Anthropology* 164: 1-16. https://doi.org/10.1002/ajpa.23323

Butz K. D., Merrell G. & Nauman E. A. 2012. — A Three-Dimensional Finite Element Analysis of Finger Joint Stresses in the MCP Joint While Performing Common Tasks. *HAND 7*: 341-345. https://doi.org/10.1016/j.s11552-012-9430-4

Chirichir H., Kivell T. L., Ruff C. B., Hublin J. J., Carlson K. J., Zippel B. & Richmond B. G. 2015. — Recent origin of low trabecular bone density in modern humans. *Proceedings of the National Academy of Sciences* 112: 366-371. https://doi.org/10.1073/pnas.1411696112

Cignoni P., Callieri M., Corsini M., Dellepiane M., Ganovelli F. & Ranzuglia G. 2008. — MeshLab: An open-source mesh processing tool. *Eurographics Italian chapter conference vol.* 2008, 129-136. http://doi.org/10.2312/LocalChapterEvents/ItaChap/ItalianChapConf2008/129-136

Diogo R., Potau J. M., Pastor J. F., de Paz F. J., Ferrero E. M., Belo G., Barbosa M. & Wood B. A. 2011. — Photographic and descriptive musculoskeletal atlas of Gorilla: With notes on the attachments, variations, innervation, synonymy and weight of the muscles. *Science Publishers, Enfield: 84*.

Diogo R., Potau J. M., Pastor J. F., de Paz F. J., Ferrero E. M., Belo G., Barbosa M., Azziz M. A., Burrows A. M., Arias-Martorell J. & Wood B. A. 2012a. — Photographic and descriptive musculoskeletal atlas of Gibbons and Siamangs (Hylobates): With notes on the attachments, variations, innervation, synonymy and weight of the muscles. *CRC Press, St. Heller: 168*.

Diogo R., Potau J. M., Pastor J. F., de Paz F. J., Ferrero E. M., Belo G., Barbosa M., Azziz M. A., Burrows A. M., Arias-Martorell J. & Wood B. A. 2013a. — Photographic and Descriptive Musculoskeletal Atlas of Chimpanzees: With notes on the attachments, variations, innervation, synonymy and weight of the muscles. *CRC Press, Boca Raton: 157*.
Simulated tool use and hand performance

DIOGO R., POTAU J. M., PASTOR J. F., DE PAZ F. J., FERRERO E. M., BELLÓ G., BARBOSA M., AZIZ M. A., ARIAS-MARTORELL J. & WOOD B. A. 2013b. — Photographic and Descriptive Musculoskeletal Atlas of Orangutans: With notes on the attachments, variations, innervation, synonymy and weight of the muscles. CRC Press, Boca Raton: 148.

DIOGO R., RICHMOND B. G. & WOOD B. 2012b. — Evolution and homologies of primate and modern human hand and forearm muscles, with notes on thumb movements and tool use. Journal of Human Evolution 63: 64-78. https://doi.org/10.1016/j.jhevol.2012.04.001

DOBLARÉ M., GARCIA J. M. & GÓMEZ M. J. J. 2008. — Metacarpal proportions in Australopithecus africanus. Journal of Human Evolution 54: 705-719. https://doi.org/10.1016/j.jhevol.2007.10.007

GOMMERY D. & SENUT B. 2013. — Long-tailed macaques select mass of stone tools according to food type. Philosophical Transactions of the Royal Society, B 368: 20120413. https://doi.org/10.1098/rstb.2012.0413

HAMBRICK M. W., CHURCHILL S. E., SCHMITT D. & HYLANER W. L. 1998. — EMG of the human flexor pollicis longus muscle: Implications for the evolution of hominin tool use. Journal of Human Evolution 34: 123-136. https://doi.org/10.1006/jhev.1997.0177

HELDSTAB S. A., KOSONEN Z. K., KOSONEN J. J., DE ESTEBAN-TRIVIGNO S. & GIL L. 2013. — Manipulation complexity in Apes, humans and South African early hominins. Comptes Rendus Paleo 16 (5-6): 645-654. https://doi.org/10.1016/j.crpv.2016.09.002

MCURRY M. R., EVANS A. R. & MCHENRY C. R. 2015. — Low resolution scans can provide a sufficiently accurate, cost-and time-effective alternative to high resolution scans for 3D shape analyses. Peerj 6: e5032. https://doi.org/10.7717/peerj.5032

MARZKE M. W. 2013. — Tool making, hand morphology and fossil hominins. Philosophical Transactions of the Royal Society, B 368: 20120414. https://doi.org/10.1098/rstb.2012.0414

MARZKE M. W., MARZKE R. F., LINSDEID R. L., SMUTZ P., STEINBERG B., REECE S. & AN K. N. 1999. — Chimpanzee thumb muscle cross sections, moment arms and potential torques, and comparisons with humans. American Journal of Physical Anthropology 110: 163-178.

MARZKE M. W., TOOTH N., SCHICK K. & REECE S. 1998. — EMG study of hand muscle recruitment during hard hammer percussion manufacture of Oldowan tools. American Journal of Physical Anthropology 105: 315-332.

MATARAZZO S. 2013. — Manual pressure distribution patterns of knuckle-walking apes. American Journal of Physical Anthropology 152: 44-50. https://doi.org/10.1002/ajpa.22325

MATARAZZO S. A. 2015. — Trabecular Architecture of the Manual Elements Reﬂects Locomotor Patterns in Primates. Plos One 10: e0120436. https://doi.org/10.1371/journal.pone.0120436

MCCURRY M. R., EVANS A. R. & MCHENRY C. R. 2015. — The sensitivity of biological ﬁnite element models to the resolution of surface geometry: a case study of crocodilian crania. Peerj 3: e988. https://doi.org/10.7717/peerj.988
Serrano-Fochs S., de Esteban-Trivigno S., Marcé-Nogué J., Pruetz J. D. & Bertolani P. Niewoehner W. A. Napier J. R. — New postcranial remains from Swartkrans and their bearing on the functional morphology and behavior of Paranthropus robustus in Grine F. E. (ed.), The evolutionary history of the “robust” australopithecines. Aldeine de Gryuter, New York: 149-172.

Napier J. R. & Stem J. T. 1979. — Telemetered electromyography of flexor digitorum profundus and flexor digitorum superficialis in Pan troglodytes and implications for interpretation of the O. H. 7 hand. American Journal of Physical Anthropology 50: 565-574. https://doi.org/10.1002/ajpa.1330500408

Tocheri M. W., Marzke M. W., Liu D., Bae M., Jones G. P., Williams R. C. & Razdanz A. 2003. — Functional capabilities of modern and fossil hominid hands: Three-dimensional analysis of trapezia. American Journal of Physical Anthropology 122: 101-112. https://doi.org/10.1002/ajpa.10235

Tocheri M. W., Orr C. M., Jacobsky M. C. & Marzke M. W. 2008. — The evolutionary history of the hominin hand since the last common ancestor of Pan and Homo. Journal of Anatomy 212: 544-562. https://doi.org/10.1111/j.1469-7580.2008.00865.x

Tocheri M. W., Razdanz A., Williams R. C. & Marzke M. W. 2005. — A 3D quantitative comparison of trapezium and trapezoid relative articular and nonarticular surface areas in modern humans and great apes. Journal of Human Evolution 49: 570-586. https://doi.org/10.1016/j.jhevol.2005.06.005

Tsegai Z. J., Stephens N. B., Treece G. M., Skinner M. M., Kivell T. L. & Gee A. H. 2017. — Cortical bone mapping: an application to hand and foot bones in hominoids. Comptes Rendus Palevol 16: 690-701. https://doi.org/10.1016/j.crpv.2016.11.001

Tuttle R. H. 1969. — Quantitative and functional studies on the hands of the Anthropoidea. Journal of Morphology 128: 309-363. https://doi.org/10.1002/jmor.1051280304

Visalberghi E., Sirianni G., Fragsasy D. & Boesch C. 2015. — Percussive tool use by Tai Western chimpanzees and Fazenda Boa Vista bearded capuchin monkeys: A comparison. Philosophical Transactions of the Royal Society, B 370: 20140351. https://doi.org/10.1098/rstb.2014.0351

Walsmley C. W., Smiths P. D., Quayle M. R., McCurry M. R., Richards H. S., Oldfield C. C., Whoé S., Clausen P. D. & McHenry C. R. 2013. — Why the Long Face? The Mechanics of Mandibular Synymphsis Proportions in Crocodiles. Plos One 8: e53873. https://doi.org/10.1371%2Fjournal.pone.0053873

Williams E. M., Gordon A. D. & Richmond B. G. 2012. — Hand pressure distribution during Oldowan stone tool production. Journal of Human Evolution 62: 520-532. https://doi.org/10.1016/j.jhevol.2012.02.005

Williams-Hatalla E. M., Hatalla K. G., Gordon M., Key A., Kasper M. & Kivell T. L. 2018. — The manual pressures of stone tool behaviors and their implications for the evolution of the human hand. Journal of Human Evolution 119: 14-26. https://doi.org/10.1016/j.jhevol.2018.02.008

Wunderlich R. E. & Jungers W. L. 2009. — Manual digital pressures during knuckle-walking in chimpanzees (Pan troglodytes). American Journal of Physical Anthropology 139: 394-403. https://doi.org/10.1002/ajpa.20994

Wynn T., Hernandez-Aguilar R. A., Marchant L. F. & McGrew W. C. 2011. — “An ap’s view of the Oldowan” revisited. Evolutionary Anthropology 20: 181-197. https://doi.org/10.1002/evan.20323

Wynn T. & McGrew W. C. 1989. — An ape’s view of the Oldowan. Man 24: 383-398. https://doi.org/10.2307/2802697

Young R. W. 2003. — Evolution of the human hand: The role of throwing and clubbing. Journal of Anatomy 202: 165-174. https://doi.org/10.1046/j.1469-7580.2003.00144.x

Submitted on 17 August 2019; accepted on 18 October 2019; published on 10 August 2020.
| Specimen      |  SC | HRF<sup>a</sup> | FPB HS / EPB PT<sup>b</sup> | AP HS / AP PT<sup>b</sup> | EPB HS / EPB PT<sup>b</sup> | ABP HS / ABP PT<sup>b</sup> | JRF<sub>c</sub><sup>e</sup> | JRF<sub>mc</sub><sup>e</sup> |
|---------------|----|---------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Modern Human  |    | 1  3.92      | 90              | 17.95/37.20     | 38.79/66.43     | 61.2            | 4.33/28.75      | 5.28/35.94      | 180             | 44.06/89.27     | 180             | 38.81/114.1     | 180             |
|               |    | 2  7.65      | 90              | 13.49/27.95     | 29.15/49.91     | 61.2            | 2.74/18.18      | 3.34/22.72      | 180             | 28.26/61.46     | 180             | 28.02/78.76     | 180             |
|               |    | 3  3.92      | 45              | 17.95/37.20     | 38.79/66.43     | 61.2            | 4.33/28.75      | 5.28/35.94      | 180             | 45.21/90.33     | 180             | 37.96/113.3     | 180             |
|               |    | 4  7.65      | 45              | 13.49/27.95     | 29.15/49.91     | 61.2            | 2.74/18.18      | 3.34/22.72      | 180             | 30.70/63.62     | 180             | 26.36/77.14     | 180             |
| Neanderthal   |    | 1  3.92      | 90              | 14.47/29.99     | 31.28/53.56     | 61.2            | 3.49/23.18      | 4.26/28.98      | 180             | 35.55/72.02     | 180             | 30.75/91.35     | 180             |
|               |    | 2  7.65      | 90              | 10.87/22.54     | 23.50/40.24     | 61.2            | 2.21/14.66      | 2.69/18.32      | 180             | 22.79/49.58     | 180             | 22.36/63.11     | 180             |
|               |    | 3  3.92      | 45              | 14.47/29.99     | 31.28/53.56     | 61.2            | 3.49/23.18      | 4.26/28.98      | 180             | 36.46/72.85     | 180             | 30.27/90.88     | 180             |
|               |    | 4  7.65      | 45              | 10.87/22.54     | 23.50/40.24     | 61.2            | 2.21/14.66      | 2.69/22.72      | 180             | 24.75/51.29     | 180             | 21.41/62.18     | 180             |
| Chimpanzee    |    | 1  3.92      | 90              | 18.34/38.01     | 39.64/67.88     | 61.2            | –              | –              | 180             | 43.78/82.63     | 180             | 35.51/90.61     | 180             |
|               |    | 2  7.65      | 90              | 13.78/28.56     | 29.78/51.00     | 61.2            | –              | –              | 180             | 28.05/57.36     | 180             | 26.15/64.17     | 180             |
|               |    | 3  3.92      | 45              | 18.34/38.01     | 39.64/67.88     | 61.2            | –              | –              | 180             | 45.11/83.92     | 180             | 35.78/90.89     | 180             |
| Gorilla       |    | 1  3.92      | 90              | 24.78/51.36     | 53.55/91.71     | 61.2            | 5.97/39.69      | 7.29/49.61      | 180             | 61.17/125.1     | 180             | 49.14/144.11    | 180             |
|               |    | 2  7.65      | 90              | 18.62/38.59     | 40.24/68.91     | 61.2            | 3.78/25.10      | 4.61/31.37      | 180             | 39.33/86.13     | 180             | 35.31/99.38     | 180             |
|               |    | 3  3.92      | 45              | 24.78/51.36     | 53.55/91.71     | 61.2            | 5.97/39.69      | 7.29/49.61      | 180             | 64.27/128.2     | 180             | 49.57/144.53    | 180             |
|               |    | 4  7.65      | 45              | 18.62/38.36     | 40.24/68.91     | 61.2            | 3.78/25.10      | 4.61/31.37      | 180             | 45.94/92.39     | 180             | 36.15/100.2     | 180             |
| Orangutan     |    | 1  3.92      | 90              | 19.74/40.91     | 42.66/73.06     | 61.2            | –              | –              | 180             | 47.62/89.76     | 180             | 47.85/117.2     | 180             |
|               |    | 2  7.65      | 90              | 14.83/30.74     | 32.06/54.90     | 61.2            | –              | –              | 180             | 30.56/62.34     | 180             | 34.51/62.77     | 180             |
|               |    | 3  3.92      | 45              | 19.74/40.91     | 42.66/73.06     | 61.2            | –              | –              | 180             | 49.01/91.09     | 180             | 50.55/119.84    | 180             |
| Gibbon        |    | 1  3.92      | 90              | 7.08/14.66      | 15.29/26.1      | 61.2            | –              | –              | 180             | 17.75/32.87     | 180             | 19.08/45.46     | 180             |
|               |    | 2  7.65      | 90              | 5.32/11.02      | 11.49/19.68     | 61.2            | –              | –              | 180             | 11.25/22.87     | 180             | 13.75/32.18     | 180             |
|               |    | 3  3.92      | 45              | 7.08/14.66      | 15.29/26.1      | 61.2            | –              | –              | 180             | 17.88/33.25     | 180             | 19.64/46.00     | 180             |
|               |    | 4  7.65      | 45              | 5.32/11.02      | 11.49/19.68     | 61.2            | –              | –              | 180             | 12.12/23.65     | 180             | 14.84/33.24     | 180             |
APPENDIX 2. — Number of elements (N elements), mesh-weighted arithmetic mean (MWAM), mesh-weighted median (MWM), quartiles values (Q25, 50, 75 and 95), percentage error of the arithmetic mean (PEofAM) and percentage error of the median (PEofM) for each species and loading scenario, under human-scaled conditions.

| SPECIE SCENARIO | N of Elements | MWAM | MWM | Q25 | Q50 | Q75 | M95 | PEofAM | PEofM |
|-----------------|---------------|------|-----|-----|-----|-----|-----|--------|-------|
| Chimpanzee 1    | 160104        | 8.0122 | 7.6599 | 4.2909 | 7.8345 | 11.4830 | 14.6530 | 0.0387 | 2.2794 |
| Chimpanzee 2    | 160104        | 5.7312 | 5.4881 | 3.0880 | 5.6170 | 8.2101 | 10.4363 | 0.0341 | 2.3483 |
| Chimpanzee 3    | 160104        | 8.0071 | 7.7090 | 4.3233 | 7.8665 | 11.5780 | 14.7900 | 0.0317 | 2.3024 |
| Chimpanzee 4    | 160104        | 5.8607 | 5.5899 | 3.1557 | 5.7215 | 8.3844 | 10.7170 | 0.0419 | 2.3594 |
| Modern Human 1  | 225743        | 7.5983 | 5.4499 | 3.0316 | 5.5620 | 11.3770 | 19.8150 | 0.7364 | 2.1135 |
| Modern Human 2  | 225743        | 5.3623 | 3.8494 | 2.1389 | 3.9323 | 8.0325 | 13.9420 | 0.7334 | 2.1536 |
| Modern Human 3  | 225720        | 7.6821 | 5.4907 | 3.0617 | 5.6072 | 11.4980 | 20.0690 | 0.7328 | 2.1222 |
| Modern Human 4  | 225689        | 7.5029 | 5.3340 | 2.1951 | 4.0167 | 8.2813 | 14.4290 | 0.7156 | 2.1020 |
| Neanderthal 1   | 240649        | 7.5408 | 5.7398 | 3.1415 | 5.8463 | 10.7260 | 19.1300 | 1.6003 | 1.8559 |
| Neanderthal 2   | 240641        | 5.1022 | 4.0635 | 2.2448 | 4.1316 | 7.5691 | 13.4480 | 1.5817 | 1.9064 |
| Neanderthal 3   | 240649        | 7.6103 | 5.7887 | 3.1663 | 5.8917 | 10.8170 | 19.3540 | 1.6076 | 1.7799 |
| Neanderthal 4   | 240640        | 5.4615 | 4.1433 | 2.2936 | 4.2210 | 7.7516 | 13.9010 | 1.6017 | 1.8739 |
| Gorilla 1       | 327267        | 7.5484 | 6.5180 | 4.1315 | 6.6614 | 10.0078 | 15.9652 | 0.1499 | 2.2001 |
| Gorilla 2       | 327267        | 5.3112 | 4.5847 | 2.9071 | 4.6850 | 6.9811 | 11.1340 | 0.1473 | 2.1877 |
| Gorilla 3       | 327267        | 7.0302 | 5.9956 | 4.1616 | 6.7425 | 10.1980 | 16.2770 | 0.1521 | 2.1272 |
| Gorilla 4       | 327267        | 5.5459 | 4.7386 | 2.9746 | 4.8493 | 7.3571 | 11.7390 | 0.1536 | 2.3361 |
| Orangutan 1     | 199857        | 7.9291 | 6.5783 | 4.2297 | 6.7471 | 10.3643 | 18.0617 | 0.6350 | 2.5660 |
| Orangutan 2     | 199857        | 5.6296 | 4.6925 | 3.0326 | 4.8168 | 7.3231 | 12.7377 | 0.6308 | 2.6495 |
| Orangutan 3     | 199782        | 8.0069 | 6.6472 | 4.2716 | 6.8239 | 10.4630 | 19.2554 | 0.6575 | 2.6582 |
| Orangutan 4     | 199782        | 5.7984 | 4.8286 | 3.1119 | 4.9592 | 7.5206 | 13.1060 | 0.6481 | 2.7040 |
| Gibbon 1        | 311442        | 12.1044 | 10.4260 | 6.1984 | 10.5940 | 16.2630 | 26.8950 | 0.1734 | 1.6114 |
| Gibbon 2        | 311431        | 8.6667 | 7.4740 | 4.4483 | 7.5885 | 11.6390 | 19.2340 | 0.1762 | 1.5325 |
| Gibbon 3        | 311442        | 12.1825 | 10.4940 | 6.2322 | 10.6650 | 16.3650 | 27.0820 | 0.1744 | 1.6295 |
| Gibbon 4        | 311442        | 8.8241 | 7.6109 | 4.5179 | 7.7380 | 11.8330 | 19.6238 | 0.1753 | 1.6704 |

APPENDIX 3. — Mesh-weighted arithmetic mean (MWAM), mesh-weighted median (MWM), quartiles values (Q25, 50, 75 and 95), percentage error of the arithmetic mean (PEofAM) and percentage error of the median (PEofM) for each species and loading scenario, under chimpanzee-scaled conditions.