Insights into the musculature of the bonobo hand

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Abstract

The human hand is well known for its unique dexterity, largely facilitated by a highly mobile, long and powerful thumb that enables both tool manufacturing and use, a key component of human evolution. The bonobo (*Pan paniscus*), the closest extant relative to modern humans together with the chimpanzee (*Pan troglodytes*), also possesses good manipulative capabilities but with lower dexterity than modern humans. Despite the close phylogenetic relationship between bonobos and humans, detailed quantitative data of the bonobo forelimb musculature remains largely lacking. To understand how morphology may influence dexterity, we investigated the functional anatomy of the bonobo hand using a unique sample of eight bonobo cadavers, along with one chimpanzee and one human (*Homo sapiens*) cadaver. We performed detailed dissections of unembalmed specimens to collect quantitative datasets of the extrinsic and intrinsic hand musculature, in addition to qualitative descriptions of the forelimb muscle configurations, allowing estimation of force-generating capacities for each functional group. Furthermore, we used medical imaging to quantify the articular surface of the trapeziometacarpal joint to estimate the intra-articular pressure.

Our results show that the force-generating capacity for most functional groups of the extrinsic and intrinsic hand muscles in bonobos is largely similar to that of humans, with differences in relative importance of the extensors and rotators. The bonobo thumb musculature has a lower force-generating capacity than observed in the human specimen, while the estimated maximal intra-articular pressure is higher in bonobos. Most importantly, bonobos show a higher degree of functional coupling between the muscles of the thumb, index and lateral fingers than observed in humans. It is conceivable that differentiation and individualisation of the hand muscles rather than relative muscle development explain the higher dexterity of humans compared to bonobos.

Keywords: primate anatomy, thumb, *Pan paniscus,* muscles

Introduction

The thumb plays a key role in the functioning of the primate hand, known for its unprecedented dexterity. The modern human (*Homo sapiens*) hand is the prime example of such dexterity with a thumb fully devoted to manipulation. Despite the fact that non-human primates use their hand in locomotion and manipulation, many non-human primates also show advanced manipulative abilities, used in grooming and for processing food (e.g. capuchins (Spinozzi et al. 2004), orangutans, chimpanzees, and bonobos (Colell et al. 1995; Furuichi & Thompson 2008)) or for making and using tools (e.g. capuchins (Fragaszy et al. 2004; Visalberghi et al. 2009), gorilla (Breuer et al. 2005), macaques (Gumert et al. 2011), chimpanzees and bonobos (Boesch et al. 2009; Jordan 1982; Takeshita & Walraven 1996; Toth et al. 1993)). As the primate hand displays large varieties of phenotypes where form and function of the thumb are closely correlated, understanding these phenotypes in closely-related primate species may facilitate the interpretation of function in an evolutionary context. Despite the high importance of the thumb in human evolution, being key to the unique human dexterity, a complete understanding of the adaptive signals and form-function relationship in the primate thumb is lacking.

Within the extant primates, the bonobo (*Pan paniscus*) is one of the modern human's closest relatives, sharing approximately 98.7 percent of their genetic blueprint with modern humans (Prüfer et al. 2012). The common *Homo-Pan* ancestor lived 7 to 13 million years ago (Young et al. 2015), while the split in the genus *Pan* has to be situated between 2 and 1 million years (Myr) ago (Kuhlwilm et al. 2016; Prado-Martinez 2013). Both bonobos and chimpanzees possess a very diverse locomotor repertoire, but the thumb is predominantly used during arboreal locomotion (e.g. vertical climbing and quadrumanous scrambling) as their thumb is relatively short compared to the other fingers so that it is not involved during knuckle-walking. During manipulation and locomotion, they are capable of using both fine precision grips, in-hand manipulation, and forceful power grips, similar to humans (Christel et al. 1998; Feix et al. 2015; Bardo et al. 2016; Crast et al. 2009). Additionally, they are capable of thumb opposition which seems to be facilitated by the saddle-shaped surfaces of the trapeziometacarpal (TMC) joint, as seen in modern humans (Marzke 1997). Bonobos and chimpanzees favour precision grips in picking up small objects in which the thumb tip makes contact with the radial aspect of the index finger, from the distal to the proximal phalanx (Butterworth & Itakura 1998; Christel et al. 1998). However, for grasping small objects, they do not always use their thumb whereas modern humans always use their thumb in precision gripping (Pouydebat et al. 2009). For grasping large objects, bonobos and chimpanzees mostly use a power grip (Pouydebat et al. 2009), but it does not provide the same accurate control as the power grip in modern humans (Marzke et al. 1992). In addition, both bonobos and chimpanzees are capable of using tools; a feature that has been observed both in captivity (Takeshita & Walraven 1996; Jordan 1982; Toth et al. 1993) and in their natural environment (Ingmanson 1998; Neufuss et al. 2017).

While the anatomy of the chimpanzee hand has been studied in detail, based on dissections of approximately 50 arm specimens (e.g. (Tuttle 1969; Thorpe et al. 1999; Almécija et al. 2015; Lesnik et al. 2015; Myatt et al. 2012; Carlson & Lowe 2006; Oishi et al. 2009; Marzke 1997)), information about

3

75 the bonobo hand musculature is limited (Miller 1952; Diogo et al. 2017a; Diogo et al. 2017b). Most
76 previous studies focus only on hand proportions and external morphology of the hand and finger bones
77 (Inouye 1992; Alba et al. 2003; Tocheri et al. 2008; Almécija et al. 2015), while detailed quantitative
78 data on the surrounding soft-tissue are largely missing in the literature.
79
80 In this study, we describe and quantify the extrinsic and intrinsic hand musculature of bonobos. We
81 hypothesize that the bonobo hand, and specifically the thumb, musculature is relatively well developed,
82 in terms of volume and force-generating capacity, possibly comparable to humans. Furthermore we
83 expect morphological deviations from the human configuration that account for differences in the
84 manipulative capabilities of the hand. Here we investigate if such deviations are present, and if they
85 concern (a) quantitative differences in muscle volume and force-generating capacity, and/or (b)
86 qualitative differences, such as muscle paths and other changes in muscle configuration, that have
87 functional implications.

Materials and methods

Specimen selection

The hand and/or forearm of nine (sub)adult bonobos were obtained from different European zoos. All animals died of natural causes and were sampled opportunistically. The sample details are provided in **Table 1**. All specimens were stored at -18°C shortly after death and kept frozen until they were CT-scanned and dissected. Medical imaging (CT scanning) was obtained for all nine specimens while muscle data was obtained for eight of the nine animals; specimen Pp4 (Lomela; MIG12-29745517) was fixed in formaldehyde prior to freezing and it was impossible to dissect this specimen due to tissue dryness. in total, ten samples were dissected (forearm and hand (8/10) or only hand (2/10)) of which two samples of two specimens were dissected as part of the Bonobo Morphology Initiative which took place at the University of Antwerp in January 2016. As specimen Pp2 had been disarticulated at the elbow joint, not all of the extrinsic muscles could be quantified. The specimen has been included in the qualitative study for the muscles present, but it has been excluded from the quantitative analysis as total muscle mass could not be determined.

Some cadaver hands showed musculoskeletal injuries (4/10), which is also indicated in **Table 1**. In two specimens, several distal phalanges were missing, either entirely (Pp7R: DP3) or partially (Pp7R: DP2 and 4; Pp8R: DP2 and 4). Soft-tissue at level of the fingers had already healed pre-mortem, but the extent of the scar tissue indicates repeated damage to the digits. In two other specimens, there was evidence of a dislocation at the metacarpophalangeal joint (Pp2L: MCP1) or trapeziometacarpal joint (Pp1R: TMC).

For comparison, anatomical data from a fresh-frozen chimpanzee (*Pan troglodytes*; Pt1) and a human cadaver (*Homo sapiens*, Hs1) are included. The chimpanzee specimen was obtained from Burger's Zoo, Arnhem (The Netherlands) and the human specimen was obtained via the Human Body Donation Program of the university. Both specimens were also dissected and CT-scanned.

CT scanning and image segmentation

Prior to dissection, the entire hand of each specimen (either the left or the right hand) was CT-scanned at the local hospital (AZ Groeninge, Kortrijk, Belgium) using a 64 slice Discovery HD 750 CT scanner (GE Healthcare, Little Chalfont, UK; Display Field of View [DFOV]: 250 mm, slice thickness: 0.625 mm, voxel size: 0.150 mm^3, 100 kV, 180 mA, 512x512).

The CT images were segmented manually using Mimics software (Mimics for Research 18.0, Materialise, Leuven) and 3D surface models of the trapezium and first metacarpal (MC1) were reconstructed to be able to measure the articular area of the trapeziometacarpal (TMC) joint. The articular area of the trapezium and MC1 was determined by manually delineating the border of the

125   articular facet on each 3D bone model using 3-matic software (Materialise, Leuven). Articular area of

126   the trapezium and MC1 were obtained from five bonobo specimens (Pp5, Pp6, Pp7, Pp8 and Pp9), from

127   the chimpanzee (Pt1) and human (Hs1) and were used to estimate TMC joint pressure (see below).

128

129   *Dissection procedure*

130   The specimens were stored in freezers (-18°C) and were thawed at room temperature 24h-48h prior to

131   the dissections. All muscles were isolated one by one and their origin and insertion were determined,

132   using the same protocol as in previous anatomical studies (Vereecke et al. 2005; Channon et al. 2009).

133   A complete dissection of the left and/or right forearm and hand was performed for five bonobo

134   specimens (Pp5-9), but only one side per animal was included in the quantitative analysis. In addition,

135   the left or right hand of three bonobo specimens (Pp1-3) were also carefully dissected. As such, the

136   extrinsic hand musculature in five specimens and the intrinsic hand musculature in eight specimens

137   could be quantified. Incidences for presence/absence of muscles could be obtained for all dissected arms

138   (10 arms/hands from 8 bonobos).

139   For each muscle, the following parameters were measured: (1) muscle volume (V); (2) fascicle length

140   (FL), which is the approximate length of the muscle fibers; and (3) pennation angle (PA), the average

141   angle of the muscle fibers relative to the force-generating axis. Length measurements were taken to the

142   nearest 0.1 mm with a digital calliper (Mitutoyo, UK, accurate to 0.01 mm) and muscle volume was

143   determined to the nearest 0.1 ml by submersion in physiological saline solution (0.9% NaCl). Muscles

144   were cut lengthwise along the tendon to determine muscle fascicle length and pennation angle. Digital

145   photographs were taken of the muscles and pennation angle and fascicle length were measured using

146   Fiji software (Schindelin et al. 2012). The data provided for fascicle length and pennation angle are

147   average values of at least three independent measurements taken on different places along the muscle

148   belly.

149

150   *Data analysis*

151   Muscles were categorized into functional groups to facilitate comparison (**Table 2**). Physiological cross-

152   sectional area (PCSA) of a muscle was calculated using equation 1.

153     $PCSA = \frac{muscle\ volume \times \cos(pennation\ angle)}{muscle\ fascicle\ length}$ [1]

154   However, we chose to omit pennation angle from the PCSA equation as (1) we observed that pennation

155   angle is difficult to measure accurately during dissections, (2) the *in vitro* measurements are not fully

156   representative of the pennation angles *in vivo* given that pennation angles changes during muscle

157   contraction, and (3) the pennation angle of most muscles ranges between 0 and 30 degrees, the cosine

158   of which ranges between 1 and 0.87, having only a minor influence on PCSA calculation. Therefore,

159   equation 2 was used in our final analysis.

160 $$PCSA = \frac{muscle\ volume}{muscle\ fascicle\ length}$$ [2]

161 To obtain an estimate of the force generating capacity of a muscle (Fmax), PCSA was multiplied by 0.3

162 MPa, i.e. the maximal isometric stress of vertebrate muscle (Wells 1965; Medler 2002). The force

163 generating capacity was calculated for the extrinsic thumb muscles and thenar muscles (for a definition

164 see **Table 2**). To obtain an estimate of the maximal compressive force occurring in the bonobo TMC

165 joint compared to the chimpanzee and human TMC joint, we calculated the total force-generating

166 capacity of the muscles that cross the TMC joint (sum of PCSA values multiplied by 30 N/m^2). By

167 dividing the total force-generating capacity by articular area of the trapezium (i.e. surface of the distal

168 facet), we estimate the pressure occurring at the joint. These values were acquired for each specimen

169 individually (n=5; only for the specimens for which both extrinsic and intrinsic hand muscles could be

170 quantified). Average and standard deviation were calculated for the bonobo (based on the five pressure

171 estimates) to allow comparison with the chimpanzee and human data.

172 **Results**

173

174 *Observations on bonobo hand musculature*

175 <u>Extrinsic hand musculature</u>

176 The origin, insertion and function of all extrinsic hand muscles are listed in the Supplementary material

177 (Error! Reference source not found.. Differences regarding the origin and insertion between the

178 specimens (n=8) are indicated in the table, but the most conspicuous differences are discussed below.

179

180 The *m. flexor carpi radialis* (FCR) originates from the medial epicondyle of the humerus (8/8). The

181 FCR inserts either on the base of MC1 (3/8) or MC2 (5/8), and in case of the latter it may also extend

182 towards MC3 with an additional tendon (1/8) or tendon slip (1/8) from MC2.

183

184 The *m. palmaris longus* (PL) originates from the medial epicondyle of the humerus, it inserts radially

185 on the radial palmar aponeurosis and connects to the fascia of the *m. abductor pollicis brevis* (APB)

186 (8/8). Occasional fusion with the FCR (3/8) is observed.

187

188 The *m. flexor digitorum superficialis* (FDS), in bonobos, usually consists of three muscle bellies, one

189 for digit 2 (FDS II: 7/8), one for digits 3 and 4 (FDS III-IV: 8/8) and one for digit 5 (FDS V: 6/8).

190 However, occasionally FDS II (1/8) and FDS V (2/8) might also be fused with the FDS III-IV belly. In

191 most specimens, the FDS II shows a distinctive double muscle-tendon unit (MTU) configuration (5/8)

192 (**Fig. 1**). FDS II originates from the medial epicondyle of the humerus (8/8) and from the proximal ulna

193 (1/8) and inserts on the intermediate phalanx of digit 2 (8/8) with an occasional cross-over tendon to the

194 FDS III tendon (3/8). FDS III-IV originates from both the medial epicondyle (8/8) and proximal radius

195 (7/8). In one specimen, FDS III-IV originates from the ulna instead of the radius. Its individual tendons

196 insert on the intermediate phalanges of the digits 3 and 4 (8/8). FDS V originates from the medial

197 epicondyle of the humerus (8/8) or from the radius (1/8) and inserts on the intermediate phalanx of digit

198 5 (7/8). In one specimen, FDS V inserts on the distal phalanx.

199

200 The *m. flexor digitorum profundus* (FDP) is separated into two muscle bellies. One head (FDP I-II)

201 originates from the shaft of the radius – between the *m. supinator* (SUP) and *m. pronator quadratus*

202 (PQ) – and inserts onto the distal phalanx of digit 1 and 2 (**Fig. 2**). The other head (FDP III-IV-V)

203 originates from the interosseous membrane and the shaft of the ulna and inserts on the distal phalanx of

204 digit 3, 4 and 5. In one specimen, FDP I and V are absent, subsequently the *m. lumbricalis* to the fifth

205 digit (LUMB IV) is absent as well. Additionally, there is an extra tendon from FDP III-IV to the base

206 of the lumbrical inserting on digit 2 (LUMB I).

207 The *m. flexor pollicis longus* (FPL) is not present as a separate muscle in bonobos. Instead, a tendon,

208 here described as the FDP I tendon, splits from the FDP II tendon and inserts onto the distal phalanx of

209 the thumb (7/8) (**Fig. 2**).

210   The *m. abductor pollicis longus* (APL) consists of two proximally fused muscle bellies, each its own

211   insertion (8/8). Both originate from the interosseous membrane and the posterior side of the shaft of the

212   radius and ulna, and are sometimes proximally fused with the *m. supinator* (3/8). One tendon (APL I)

213   always inserts on the base of the MC1 (8/8), however, the second insertion (APL II) is variable. Most

214   frequently it inserts on the trapezium (7/8), occasionally with an additional insertion on the pre-pollex

215   (1/8), the dorsal ligament of the thumb (1/8) or the MC1 base (1/8) (**Fig. 3**). The APL II tendon can also

216   insert solely on the pre-pollex (1/8), a sesamoid bone present in 7/8 of the specimens, located at the base

217   of the thumb, generally articulating with the scaphoid and trapezium.

218

219   The *m. brachioradialis* (BR) invariably originates from the supracondylar ridge of the humerus and

220   inserts onto the styloid process of the radius. The tendon either inserts directly onto the styloid process

221   (5/8) or onto the shaft of the radius proximal to the styloid, continuing to the styloid process (2/8). In

222   one specimen, the tendon is split in two distally, with one slip inserting on the styloid process and the

223   other slip inserting adjacent to the groove of the APL.

224

225   The *m. extensor carpi radialis longus* (ECRL) and *m. extensor carpi radialis brevis* (ECRB) are clearly

226   separated in the bonobo specimens. The ECRL usually inserts onto the base of MC2 (5/8) but can in

227   addition insert onto MC1 as well (3/8). The ECRB inserts onto the dorsal side of the MC3 base (8/8)

228   and can also be connected to the *mm. intermetacarpales* (IM) I and II (3/8).

229

230   The *m. extensor digitorum* (ED) originates from the lateral epicondyle of the humerus and is fused

231   proximally with the *m. extensor carpi ulnaris* (ECU) (8/8). Its four differentiated muscle bellies are

232   fused proximally to a varying degree. In most cases, each individual tendon inserts on its respective

233   distal phalanx, after forming the extensor mechanism with the *m. lumbricalis* and *mm. interossei* (see

234   intrinsic musculature) (7/8). Additionally, some tendons may interconnect between the digits (5/8). The

235   ED IV and ED V muscle bellies may be completely fused, here a single tendon splits into two distally

236   to insert onto digit 4 and 5 (1/8). On occasion, the ED V and EDM tendons also be fused, together

237   inserting on the extensor mechanism of digit 5 (1/8) (**Fig. 4**).

238

239   The *m. extensor indicis* (EI) inserts distally to the *m. extensor pollicis longus* (EPL) on the ulnar shaft

240   and both muscles may be fused proximally (2/8). The EI has an underdeveloped tendon relative to other

241   forearm muscles and its insertion is variable. It may insert dorsally on the proximal phalanx of the index

242   finger (5/8) or dorsally on the MC2 base (1/8). On occasion, the EI tendon splits in two distally, with

243   one slip inserting on the MCP2 and the other on the MCP3 joint (1/8). Furthermore, the EI may have

244   two distinct tendons, one inserting on the proximal phalanx of digit 2, the other to that of digit 4 (1/8).

245   The *m. extensor pollicis brevis* (EPB) as found in humans is not present in bonobos (8/8).

246

247 The *m. extensor digiti minimi* (EDM) originates from the lateral epicondyle of the humerus accompanied
248 by the ECU (7/8) and is sometimes fused with the *m. extensor digitorum* (ED) proximally (2/8). The
249 EDM tendon inserts either on the extensor mechanism of digit 5 together with the tendon of ED V (3/8),
250 or on the proximal phalanx of digit 5 (4/8). In one specimen, in addition to its insertion onto digit 5, two
251 short tendons inserting on the extensor retinaculum were observed. The EDM may also be absent in its
252 entirety (1/8).
253
254 <u>Intrinsic hand musculature</u>
255 The origin, insertion and function of all intrinsic hand muscles are listed in the Supplementary material
256 (Error! Reference source not found.. Differences regarding the origin and insertion between the
257 specimens (n=10) are indicated in the table, but the most important differences are discussed below (see
258 also **Fig. 2**).
259
260 In the majority of our specimens, each *m. intermetacarpalis* (IM I-IV) is fused with the *m. flexor brevis*
261 *profundi* (FBP) of the respective digit (FBP III, V, VI and VIII) to form the *mm. interossei dorsales*
262 (IOD I-IV), common to the human configuration (7/10) (**Fig. 5**). A minority displayed the ancestral non-
263 human primate configuration of separated IM and FBP muscles (1/10) or an intermediate configuration
264 where only one or two IOD are present while the other muscles are separated (2/10). These bonobo
265 specimens thus show a continuum between the non-human primate configuration and the configuration
266 associated with modern humans. A detailed visualisation of individual specimen's hand muscle
267 configurations (i.e. IM and FPB, or IOD) is reported in the Supplementary material (**Fig. S1**).
268
269 The *m. abductor pollicis brevis* (APB) originates from the flexor retinaculum in all specimens. However,
270 additional origins from the shaft of MC3 (5/10) or pre-pollex (2/10) as well as fusions with the *m.*
271 *opponens pollicis* (OPP) (3/10) and/or *m. flexor pollicis brevis* (FPB) (2/10) are present among the
272 specimens. The APB inserts onto the radial sesamoid bone of the MCP1 joint but variations such as
273 insertion on MC1 base (1/10) may occur.
274
275 The *m. flexor pollicis brevis* (FPB) consists of a single MTU (10/10), in contrast to humans where a
276 deep (*FPB profundum*) and a superficial (*FPB superficiale*) head can be distinguished. Additionally, the
277 FPB may be fused proximally with the APB and OPP (2/10). The FPB originates from the flexor
278 retinaculum and inserts onto the APB tendon, which in turn inserts onto the radial sesamoid bone of the
279 MCP1 joint (10/10).
280
281 The *m. opponens pollicis* (OPP) originates from the flexor retinaculum similar to the origin of the APB
282 and FPB and inserts onto to the radial side of the MC1 shaft (10/10), occasionally continuing onto the
283 APB tendon (2/10) or onto the radial sesamoid of MC1 directly (1/10). Sometimes, it also can be fused
284 with either APB (1/10), or both APB and FPB (2/10).

285

The *m. adductor pollicis* (ADP) consists of an oblique and transverse head, which both insert onto the ulnar sesamoid bone of the MCP1 joint. The oblique head most commonly originates from the palmar base of MC3 (7/10) or from the base of MC2 + MC3 (3/10). The transverse head often originates from the palmar side of the entire MC3 (6/10), with additional attachments on the head of MC2 (1/10) or MC4 (1/10). However, several variations on the site of origin of the transverse head were observed, originating from the *contrahens raphe* of MC3 + MC4 (2/10) or with an origin from the entire MC4 (1/10). In two specimens, a *m. adductor pollicis accessorius* (APA) was observed, consisting of a small bundle of muscle fibers originating distally from the *contrahens raphe* near the head of MC2 and inserting on the ulnar side of the MC1.

The hypothenar muscles (*m. palmaris brevis* (PB), *m. abductor digiti minimi* (ADM), *m. flexor digiti minimi* (FDM), *m. opponens digiti minimi* (ODM)) have a rather constant configuration similar to that seen in humans. However, a strong fusion between ADM, FDM and ODM was observed in one specimen.

Quantification of bonobo hand muscles

A detailed documentation of the quantitative muscle parameters discussed below is provided in the Supplementary material (**Table S3**). Additionally, an overview of both muscle fascicle length and pennation angle of the bonobo hand muscles can be found in the Supplementary material (**Fig. S2 and S3**).

Functional muscle groups

The PCSA of the functional muscle groups as a percentage of total forelimb muscle PCSA is depicted in **Figure 6** for each of the dissected specimens (5 bonobos, 1 chimpanzee and 1 human). Bonobos have an average flexor/extensor ratio of 3:1 with the PCSA of the forearm flexors making up on average 39.3% (s.d.: 2.6%) of the total forearm muscle PCSA, while the extensors on average only make up 13.2% (s.d.: 2.3%). The chimpanzee has a flexor/extensor ratio of about 2.1:1 with the flexors' PCSA amounting to 35.2% and the extensors PCSA to 16.7% of the total forearm muscle PCSA. The human specimen has a flexor/extensor ratio of 1.3:1 with 35.4% of the forearm muscle PCSA comprising flexors and 27.0% extensors. The rotators take up a greater proportion of the total forearm muscle PCSA in bonobos and chimpanzee (20.6% and 25.6% respectively) compared to the human specimen (14.0%).

If we look at the intrinsic hand muscles as a percentage of total forearm muscle PCSA, we observe that these amount to, on average, 20.5% in bonobos, 16.1% in the chimpanzee and 14.8% in the human specimen (**Fig. 7C**). The configuration of the intrinsic hand muscles differs markedly between *Pan* and

Homo, with a dominant development (%PCSA) of the intermediate hand muscles in *Pan* (~60%) and a similar development of the thenar and intermediate hand muscles in *Homo* (~42%).

Thumb muscles

The muscles that move and stabilize the thumb are composed of the extrinsic thumb muscles (APL, EPB, EPL, FPL), the thenar muscles (OPP, APB, FPB, ADP), and the first dorsal interosseous muscle (IOD I). The proportion of the thumb muscle PCSA as a percentage of total forearm muscle PCSA amounts to, on average, 10.6% in bonobos and 9.3% and 17.5% in respectively the chimpanzee and human specimen (**Fig. 7A**). Furthermore, the percentage of thenar musculature in proportion to the intrinsic hand muscles amounts to 25.1% on average in bonobos, 19.3% in the chimpanzee, and 45.8% in the human. The APL, in bonobos, takes up 5% of the total forearm muscle PCSA, similar to that found in the chimpanzee (5.3%). The relative contribution of the APL is lower in the human specimen (3.8%), even when including the EPB (4%), but falls within the large range observed for the bonobo specimens. However, in *Pan*, the APL appears to be the most important muscle within the thumb musculature, accounting for on average 47% of thumb muscle PCSA in bonobos and 58% in the chimpanzee, while the contribution in *Homo* is much lower (21%) (**Fig. 7B**).

Finally, by dividing the maximal force-generating capacity of the muscles crossing the TMC joint by the trapezial articular area, an estimate of the maximal pressure at the TMC joint was obtained. The pressure estimate amounts on average to 3.0 MPa for the bonobos, 3.2 MPa for the chimpanzee and 2.6 MPa in the human (**Table 3**).

Discussion

This study identifies important features of the hand musculature in bonobos, in comparison to the chimpanzee and human configuration, based on the detailed dissection of a unique sample of bonobo specimens. The three major findings are (1) the high variability in bonobo hand musculature, (2) the well-developed thumb musculature, and (3) the presence of functional coupling between muscles.

High variability of bonobo hand musculature

Both the qualitative and quantitative analysis of the bonobo hand musculature indicate a high variation among individuals. From the qualitative analysis, we report incidences of all observed configurations for all dissected specimens, also including left and right hands from the same animal. We find a particularly high degree of variability for the configuration of the intermediate hand muscles as well as many, often small, variations on site of insertion of the extrinsic hand muscles, most notable the long flexors (FDS, FDP) and EI muscle. Similarly, the quantitative analysis, which only includes unilateral sampling and a lower sample size (n=5), yields marked intra-specific variations in muscle volume and PCSA. We focus on muscle PCSA as this is the most functionally relevant parameter, being strongly correlated with force-generating capacity of a muscle (Marzke & Marzke 2000; Vereecke et al. 2005). However, analyses on muscle mass show similar results. We speculate that this high inter-individual variation in the soft-tissue configuration of the bonobo hand might be an indication that this region is under only mild selective pressure, and/or that the functional implications of these variations are limited. In contrast, variability in the bonobo thenar and extrinsic thumb muscles is relatively low. Such consistency may suggest that this region is more strictly regulated by selective pressure.

Despite the variability observed in the bonobo hand muscles, we are able to identify some diverging general trends for the muscle configuration between *Pan* and *Homo*. For example, when we look at the relative proportion of the different functional muscle groups, we observe a similar organization in the bonobo and chimpanzee specimens which deviates from the human configuration. Most importantly, the proportion of wrist extensors is increased in *Homo* relative to *Pan*, a trait potentially linked to tool use due to the importance of wrist extension during tool-making (Williams et al. 2010), while *Pan* has a stronger development of the forearm rotators. The large amount of rotators has also been shown in previous anatomical studies on great apes (e.g. (Thorpe et al. 1999; Myatt et al. 2012)) and can be explained by the importance of pro-supination movements during arboreal locomotion of bonobos and chimpanzees. Wrist flexors show a similar relative development in *Pan* and *Homo*, in agreement with previous studies (Tuttle 1969; Thorpe et al. 1999). Other functional group ratios (e.g. wrist flexor to extensor ratio, thenar to intrinsic hand musculature) were found to be in agreement with Tuttle's results as well, despite the dissimilarity in methods used, *Gorilla gorilla* being included in *Pan*, and without inclusion of bonobos (Tuttle 1969). The large amount of (wrist and finger) flexors in *Pan* is most likely due to their involvement in arboreal locomotion. Consequently, the emphasis on flexors may restrict extension of the wrist, favouring knuckle-walking over palmigrade quadrupedalism during terrestrial

13

locomotion. Additionally, the recruitment of wrist flexors as shock absorbers during knuckle-walking (Simpson et al. 2018) may further reinforce the prominence of flexor muscles in the forearm of knuckle-walkers. Another example that may reflect differences in locomotion is found in the proportion of intrinsic hand muscle PCSA. Bonobos, on average, possess a somewhat larger proportion of intrinsic hand muscles compared to humans, although humans fall within the large range of bonobos (**Fig. 7C**). The difference between bonobos and humans is, however, most pronounced for the relative development of the intermediate hand muscles, which account for on average 13.6% of the total PCSA in bonobos and merely 6.4% in humans (**Fig. 7**). This too may be explained in the context of locomotion, either arboreal in the form of grasping which is of major importance for vertical climbing and clambering, or in the context of terrestrial knuckle walking, where the intermediates might play an important role (Susman & Stern 1980), although, these two are not mutually exclusive.

Differences in forelimb musculature between bonobo and chimpanzee are limited. This was already indicated in a recent publication by Diogo and colleagues that points to an evolutionary stasis in the *Pan* clade using soft-tissue characters to underline the low divergence between chimpanzees and bonobos (Diogo et al. 2017b). One of the three divergent characters in the forelimb musculature described is the different configuration of the intermediate hand muscles in chimpanzees and bonobos. Our dissections indicate that, contrary to the statements of Diogo et al. (2017b), bonobos can have distinct intermetacarpales common to the configuration found in chimpanzees. Rather than invariably presenting the human configuration with four dorsal interossei (fusion of FBP III, V, VI, VIII with the intermetacarpales I-IV) and three palmar interossei (FBP IV, VII, IX), bonobos display all kinds of variations, and these variations can also occur between the left and right hand of one individual. The high variability seen in the organization of the intermediate hand muscles of bonobos suggests that the functional implications are limited and that this trait cannot be used as divergent character of bonobos.

Bonobo thumb musculature

This study shows that bonobos possess a well-developed thumb musculature, on par with that of humans. While the relative PCSA of the thumb muscles in humans is higher, the estimate of intra-articular pressure to which the TMC is subjected is higher in bonobos (and chimpanzee). Moreover, this estimate is likely an underestimation of the actual maximal pressure in the bonobo as (i) the contribution of the FDP I is not accounted for in bonobos while FPL is included in the human pressure estimate, and (ii) in some bonobo specimens, the FCR and/or ECRL also cross the TMC joint and can therefore also generate compressive forces at this joint. Despite the strong thumb musculature of bonobos, they do have a lower dexterity compared to that of modern humans (Kivell 2015; Bardo et al. 2016; Neufuss et al. 2017). A simple correlation between the force-generating capacity of the thumb muscles and dexterity does not apply; in addition to size, muscle configuration (and motor control) plays an important role.

One of the more explicit examples of differences in muscle configuration between humans, bonobos and chimpanzees can be found in the diverging morphology of the extrinsic thumb flexor. In

chimpanzees, this flexor is present in the form of a vestigial tendon coming from the FDP II tendon that inserts onto the distal phalanx of the thumb, as observed both in our chimpanzee specimen and as reported in the literature (see figure 19 in Tuttle (1969)), but it can also be absent (Susman 1998). In bonobos, however, we see that the tendon of the FDP to digit 1 is well developed, with similar dimensions as the tendons acting on other digits (**Fig. 2**) and as the human m. flexor pollicis longus (FPL). In humans, the FDP I has differentiated into a separate muscle, the FPL, and its presence has been linked to the unique dexterity of modern humans (Skinner et al. 2015; Wolfe et al. 2006; Marzke 1997). The muscle is important for precision control and manipulation, and appears to be particularly active during power squeeze grips, rather than during precision grips (Kivell 2015). Although gibbons also have a distinct FPL (Susman 1998), it has been posited that the presence of the FPL in modern humans fulfils the specific functional requirements of the thumb to be able to perform a variety of complex functions (Skinner et al. 2015; Tocheri et al. 2008). We believe that the configuration found in bonobos, with a stout tendon to the thumb and a shared muscle belly for FDP I and II, has important functional consequences regarding individual finger control and dexterity.

Functional coupling

Functional coupling between muscles results in a concerted action. The association between thumb and index finger flexion, enables bonobos to move digit 1 and 2 independently from digits 3, 4 and 5, which might contribute to differences in grasping capability, particularly in precision gripping in which the thumb and index finger play a very important role (Christel et al. 1998). A similar fusion was also observed between EPL and EI in two bonobo specimens, which points to a developmental relationship between these neighbouring muscles. A fusion between EPL and EI is also found in some New World monkeys, such as *Alouatta fusca* and *Saguinus geoffroyi*, forming a structure referred to as "*extensor pollicis et indicis longus*" (Aversi-Ferreira et al. 2010). Such configuration might lead to joined extension of thumb and index finger. On the one hand, such functional coupling may be crucial to executing certain coordinated hand movements, on the other hand, it also complicates individual digit mobility and thus dexterity. In modern humans, as well as in common chimpanzees and our other bonobo specimens, the EPL goes exclusively to digit I and is not fused to the EI, resulting in a functional dissociation between the extension of the thumb and the index finger. This individualization is found more often in the more dextrous primates, with humans as a prime example. With the distinct FPL, EPL and EI configuration, we see this in the human thumb especially. It is therefore very likely that the increased amount of functional coupling found in bonobos compared to humans, rather than a difference in muscle development, plays a major role in the difference in dexterity.

449 *Critical considerations*

450 Our findings are based on a detailed dissection of eight bonobo specimens which were obtained from

451 different European zoos. Although this is the largest series of bonobos that has been dissected so far, it

452 remains a relatively small and heterogeneous sample (age, sex, body size). It is not possible to evaluate

453 the effect of age and sex in the current dataset, but no apparent differences were observed for the subadult

454 specimen (female of 8 years, unfused growth plates) or between the male and female specimens. This is

455 to be expected for a species with a low sexual dimorphism (Zihlman & Bolter 2015; Coolidge & Shea

456 1982). To allow for comparison between specimens of different size (total forelimb muscle mass ranges

457 from 500g to 1100g), we used total forelimb PCSA as a normalizing factor. Additionally, as our

458 specimens originate from various zoos, the effect of captivity on muscle development should not go

459 unremarked. Furthermore, for interspecific comparison we have made use of only one chimpanzee, and

460 one human specimen. These were included as a representative for their species, an indication of how the

461 bonobo relates to its close relatives. Therefore, no significant conclusions on interspecific variations

462 between these species can be made. This has to be kept in mind while interpreting these data. Despite

463 these limitations, we were able to fully document the bonobo forelimb musculature, both qualitatively

464 and quantitatively, using a consistent protocol on a unique series of unembalmed bonobo cadavers. Not

465 only is this research important to generate a general view of the bonobo anatomy, but in combination

466 with in vivo research and behavioural studies, it can be translated to complete form-function

467 relationships of the thumb. This will provide important insights into the form-function relationship of

468 the thumb in modern humans and aid accurate interpretation of hominin fossil remains.

469

470 **Conclusions**

471 This study shows that the bonobo forelimb musculature displays a relatively high variability and

472 although the muscles of the hand and thumb are well developed, they show an increased amount of

473 functional coupling compared to humans. It is likely that the strong differentiation and individualisation

474 of the hand muscles in humans, rather than relative muscle development, explains the higher dexterity

475 compared to bonobos.

487

488 **Author contributions**

489 EEV conceived the study; EEV, TvL and MJMV further designed the study; JS provided the specimens

490 and assisted in data collection; TvL, MJMV, FDK, and EEV performed the dissections; TvL, MJMV

491 and EEV analysed the data and wrote the manuscript; all authors reviewed and approved the article. TvL

492 and MJMV are joint first author on this publication.

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618

619 **Supplementary material**

620 Table S1 – Extrinsic hand muscles: origin, insertion and function

621 Table S2 – Intrinsic hand muscles: origin, insertion and function

622 Table S3 – Anatomical dataset of all dissected specimens

623 Figure S1 – Configuration of intermediate hand muscles of each bonobo specimen

624 Figure S2 – Muscle fascicle lengths of the bonobo specimens (n=5)

625 Figure S3 – Muscle pennation angles of the bonobo specimens (n=5)

626 **Tables**

627 **Table 1. Specimen details**

Code	Subject identifier	Sex	Age	Injury	Sample	Origin
Pp1	Dzeeta* 11957872	F	adult 31yr	TMC	R hand	Royal Zoological Society Antwerp, Belgium
Pp2	Zorba* 8365526	M	adult 35yr	MCP1	L forearm and hand	Wilhelma Zoo, Stuttgart, Germany
Pp3	X	?	adult	-	L hand	Royal Zoological Society Antwerp, Belgium
Pp4	Lomela MIG12-29745517	F	adult 17yr	-	no dissection, only CT scanning	Royal Zoological Society Antwerp, Belgium
Pp5	Jasiri 15295295	F	sub-adult 8yr	-	L+R forearm and hand	Royal Zoological Society Antwerp, Belgium
Pp6	Kidogo MIG12-27564614	M	adult 25yr	-	L+R forearm and hand	Royal Zoological Society Antwerp, Belgium
Pp7	Ludwig MIG12-29882197	M	adult 32yr	DP2-3-4	R forearm and hand	Zoo Frankfurt, Germany
Pp8	Kirembo SB:177	M	adult 24yr	DP2 and 4	R forearm and hand	La Vallée des Singes, Le Gureau, France
Pp9	Hermien* 27641621	F	adult 39yr	-	L forearm and hand	Wilhelma Zoo, Stuttgart, Germany
Pt1	Marlene 208210000495828	F	adult 42yr	-	R forearm and hand	Burger's Zoo, Arnhem, The Netherlands
Hs1	692	M	adult 60yr	-	L forearm and hand	University of Leuven, Kortrijk, Belgium

628 *wild born, F: female, M: male, TMC: trapeziometacarpal joint, MCP: metacarpophalangeal joint, DP:
629 distal phalanx.

630   **Table 2. Functional muscle groups**

Muscle group	Muscle	Abbreviation	Crossing TMC joint*
Extrinsic hand muscles			
wrist flexors	m. flexor digitorum superficialis m. flexor digitorum profundus m. flexor carpi radialis m. flexor carpi ulnaris m. palmaris longus m. brachioradialis	FDS FDP FCR FCU PL BR	only FDP1 variable
wrist extensors	m. extensor digitorum m. extensor carpi radialis longus m. extensor carpi radialis brevis m. extensor digiti minimi m. extensor carpi ulnaris m. extensor indicis	ED ECRL ECRB EDM ECU EI	variable
arm rotators	m. pronator teres m. pronator quadratus m. supinator	PT PQ SUP	
thumb	m. abductor pollicis longus m. extensor pollicis longus	APL EPL	only APL I X
Intrinsic hand muscles			
thenar	m. flexor pollicis brevis m. abductor pollicis brevis m. adductor pollicis m. opponens pollicis	FPB APB ADP OPP	X X X X
intermediate	m. intermetacarpalis I, II, III, IV m. flexor brevis profundi III, IV, V, VI, VII, IIX, IX m. interosseous dorsalis I, II, III m. lumbricalis II, III, IV, V	IM FBP IOD LUMB	
hypothenar	m. palmaris brevis m. abductor digiti minimi m. flexor digiti minimi m. opponens digiti minimi	PB ADM FDM ODM	

631   *the PCSA of the muscles that are consistently crossing the TMC joint were included in the estimation
632   of TMC joint pressure.

633 **Table 3. Estimated trapeziometacarpal joint pressure**

TMC pressure	Pp5	Pp6	Pp7	Pp8	Pp9	Bonobo average	Chimp Pt1	Human Hs1
Surface area (mm^2)	100.7	106.4	145.0	130.0	138.1	**124.0**	**132.7**	**178.9**
PCSA (mm^2)	899.1	1827.2	1635.1	930.8	750.7	**1208.6**	**1401.8**	**1563.5**
Force (N)	269.7	548.2	490.5	279.3	225.2	**362.6**	**420.5**	**469.1**
Pressure (MPa)	2.7	5.2	3.4	2.2	1.6	**3.0**	**3.2**	**2.6**

634

635 **Figure legends**

636 Fig. 1 – Photo of the m. flexor digitorum superficialis to digit 2 (FDS II), showing serial MTU
637 organization.

638 Fig. 2 – Palmar view of the superficial flexor muscles of the fingers. The m. opponens pollicis (OPP)
639 and m. opponens digiti minimi (ODM) are not visible here. The m. flexor digitorum profundus has a
640 mutual tendon going to the distal phalanx of the thumb (*; FDP I) and a tendon to digit 2 (FDP II).

641 Fig. 3 – The insertion of m. abductor pollicis longus (APL). The tendon of APL I always inserts on the
642 base of the MC1. The tendon of APL II inserts on the trapezium.

643 Fig. 4 – Dorsal view of the extrinsic extensor muscles. The muscle bellies of the m. extensor digitorum
644 (ED) and m. extensor digiti minimi (EDM) are fused proximally. The tendon of ED V is fused with the
645 EDM tendon, together inserting on the extensor mechanism of digit 5.

646 Fig. 5 – Human versus hominoid primate configuration of the mm. intermetacarpales (IM), mm. flexores
647 breves profundi (FBP), mm. interossei dorsales (IOD) and mm. interossei palmares (IOP). In modern
648 humans, the IM and FBP are fused to form the IOD.

649 Fig. 6 – Functional muscle group PCSA as a percentage of total forelimb PCSA in bonobos (Pp),
650 chimpanzee (Pt) and human (Hs).

651 Fig. 7 – A comparison of the PCSA of the (A) thumb muscles, (B) APL, (C) intrinsic hand muscles, and
652 (D) intermediate hand muscles, as a percentage of total PCSA in bonobos (Pp), chimpanzee (Pt) and
653 human (Hs).