The relationship between distal trunk morphology and object grasping in the African savannah elephant (*Loxodonta africana*)

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Background. During reach-to-grasp movements, the human hand is preshaped depending on the properties of the object. Preshaping may result from learning, morphology, or motor control variability and can confer a selective advantage on that individual or species. This preshaping ability is known in several mammals (i.e., primates, carnivores and rodents). However, apart from the tongue preshaping of lizards and chameleons, little is known about preshaping of other grasping appendages. In particular, the elephant trunk, a muscular hydrostat, has impressive grasping skills and thus is commonly called a hand. Data on elephant trunk grasping strategies are scarce, and nothing is known about whether elephants preshape their trunk tip according to the properties of their food.

Methods. To determine the influence of food sizes and shapes on the form of the trunk tip, we investigated the morphology of the distal part of the trunk during grasping movements. The influence of food item form on trunk tip shape was quantified in six female African savannah elephants (*Loxodonta africana*). Three food item types were presented to the elephants (elongated, flat, and cubic), as well as three different sizes of cubic items. A total of 107 ± 10 grips per individual were video recorded, and the related trunk tip shapes were recorded with a 2D geometric morphometric approach.

Results. Half of the individuals adjusted the shape of the distal part of their trunk according to the object type. Of the three elephants that did not preshape their trunk tip, one was blind and another was subadult.

Discussion and perspectives. We found that elephants preshaped their trunk tip, similar to the preshaping of other species' hands or paws during reach-to-grasp movements. This preshaping may be influenced by visual feedback and individual learning. To confirm these results, this study could be replicated with a larger sample of elephants.

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Abstract

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Discussion and perspectives. We found that elephants preshaped their trunk tip, similar to the preshaping of other species' hands or paws during reach-to-grasp movements. This preshaping may be influenced by visual feedback and individual learning. To confirm these results, this study could be replicated with a larger sample of elephants.

Introduction

Grasping is an essential motion that is widespread among many tetrapod species and plays a fundamental role in feeding, social interactions and locomotion (Pouydebat et al., in press; Sustaita et al., 2013). Various grasping techniques can be performed with mouths, hands, paws, feet, or trunks (Christel, 1993; Sustaita et al. 2013). For example, elephants often grasp each

62 other's trunks during greeting ceremonies, bonding ceremonies and social play (Poole & Granli,

63 2011).

64   Hand grasping, in particular, has been widely studied among primates, including humans,

65 because of their individual fingers and ability to perform complex grasping and manipulation

66 tasks (Napier, 1956; Christel, 1993; Jones-Engel & Bard, 1996; Pouydebat et al., 2011). In

67 primates, objects, including tools and food, are grasped according to their physical properties,

68 such as size, shape, consistency, and mobility, and depending on the action planned (Ansuini et

69 al., 2006, 2008; Chieffi & Gentilucci, 1993; Jeannerod, 1984; Pouydebat et al., 2009; Santello,

70 2002; Santello, Flanders & Soechting, 2002).

71   Many primates preshape their hands according to food properties during grasping,

72 including chimpanzees (Jones-Engel & Bard, 1996; Pouydebat et al., 2009), macaques

73 (MacFarlane & Graziano, 2009; Sartori et al., 2013) and strepsirrhines (Peckre et al., 2019;

74 Reghem et al., 2011; Toussaint et al., 2013, 2015). However, when reaching to grasp the same

75 object, i.e., when the hand moves towards the same object to be grasped, the general shape of

76 macaque and human hands differ (Roy et al., 2000). In species besides primates, such as rats

77 (Whishaw & Coles, 1996; Sacrey, Alaverdashvili & Whishaw, 2009) and frogs (Anzeraey et al.,

78 2017), food properties also affect grasping strategies.

79   More precisely, during reach-to-grasp movements, the human hand gradually adjusts

80 (Santello & Soechting, 1998; Mason, Gomez & Ebner, 2001) to accommodate the object contour

81 (Jeannerod, 1984; Pellegrino, Klatzky & McCloskey, 1989; Chieffi & Gentilucci, 1993; Supuk,

82 Kodek & Bajd, 2005). Similar behaviour has been observed for other primate species, such as

83 macaques (Roy et al., 2000; Sartori et al., 2013) and capuchins (Christel & Fragaszy, 2000). The

84 object affordances (i.e., the properties of an object; Sartori, Straulino & Castiello, 2011) evoke

85 its use and function during grasping.

86   Preshaping enables increased grasping success (Sartori, Straulino & Castiello, 2011) and

87 can thus serve as a selective advantage for species or individuals. Preshaping may result from

88 learning or variability in appendage morphology or motor control.

89   While hand preshaping during reach-to-grasp movements in primates is well established,

90 data on other species is scarce. Only rats (Whishaw, Dringenberg & Pellis, 1992; Sacrey,

91 Alaverdashvili & Whishaw, 2009) and pigeons (Bermejo & Zeigler, 1989) have been studied in

92 terms of their ability to preshape their paw or beak when grasping an item. Despite the enormous

93   variability in trunk utilisation for grasping objects in elephants (Lefeuvre et al., 2020; Poole &

94   Granli, 2011; Wu et al., 2018; Yasui & Idani, 2017), studies have not yet investigate the potential

95   for elephant trunk preshaping during reach-to-grasp movements.

96   Elephant trunks are especially interesting appendages due to this grasping variability.

97   Elephants use their trunks in many situations, such as grasping food, congeners or other items in

98   their environment (Lefeuvre et al., 2020; Lee & Moss, 2014; Poole & Granli, 2011; Riyas

99   Ahamed, 2015; Yasui & Idani, 2017). The trunk is a muscular hydrostat that does not have hard

100 skeletal elements, similar to cephalopod tentacles and the tongues of many vertebrates; thus, it

101 can bend in any direction, elongate, shorten and lift heavy masses (Kier & Smith, 1985; Wilson

102 et al., 1991). Grasping techniques, mainly including the morphological and kinematic aspects,

103 are well studied in muscular hydrostats (Grasso, 2008; Ritter & Nishikawa, 1995). Elephant

104 grasping has also received increasing attention, especially the techniques that involve the distal

105 part of the trunk (Dagenais et al., 2021; Schulz et al., 2021). Although the most commonly used

106 grasping technique in muscular hydrostats is coiling around the item, elephant trunk tips can also

107 engage in pinch grasping (Rasmussen & Munger, 1996; Wu et al., 2018) as can chameleon

108 tongues (Herrel et al., 2000). Indeed, African elephant can perform precise pinch grasping

109 movements. According to the IUCN, there are two distinct African elephant species: the African

110 savannah elephant (*Loxodonta africana*) and the African forest elephant (*Loxodonta cyclotis*)

111 (Hart et al., 2021). Unlike Asian elephants, which have only one finger at the top of their trunk

112 tip, African elephants can pinch items with high precision between two fingers (one at the

113 bottom and one at the top of the trunk tip; Hoffmann, Montag & Dominy, 2004). The grasping

114 capacities of the African elephant trunk tip are sometimes compared to those of appendages of

115 other species, such as the human hand (Onodera & Philip Hicks, 1999; Hoffmann, Montag &

116 Dominy, 2004). Despite these intriguing grasping capacities, no studies have examined the

117 potential for preshaping in muscular hydrostats to date; thus, none have investigated the potential

118 for preshaping of trunk tips.

119   In this study, we aimed to understand grasping behaviours in African savannah elephants.

120 As grasping capacities are impacted by individual variability in the shape of the appendage, we

121 first investigated whether there were interindividual differences in the trunk tip shape. Then, we

122 determined whether elephants preshape their trunk tips during reach-to-grasp movements toward

123 food items and whether this potential preshaping influences grasping success. Last, we examined

124   whether grasping success increased as the trials progressed and whether all elephants exhibited

125   similar trunk grasping shapes for a given item by the end of the trials.

126   We predicted that each elephant has a unique distal trunk shape and that preshaping of

127   the trunk tip would occur during reach-to-grasp movements toward food items. We also expected

128   that preshaping of the trunk tip would increase grasping success and that over time an elephant's

129   grasping movements would become more efficient. Finally, we predicted that all individuals

130   would gradually converge toward the same distal trunk shape when reaching to grasp the same

131   object. To test these hypotheses, we quantified and visualised (with geometric morphometric

132   tools) the morphology of the distal part of the trunk during reach-to-grasp movements toward

133   food items for six female African savannah elephants (*Loxodonta africana*; Blumenbach, 1797).

134

135

136   **Materials & Methods**

137

138   **Subjects and housing**

139   Data presented in this study were collected on six African savannah elephants (*Loxodonta*

140   *africana*) from the ZooParc of Beauval in Loir-et-Cher, France: Ashanti, Juba, Marjorie, M'Kali,

141   N'Dala and Tana (Fig. 1B). Five of these elephants were approximately 32 years old at the

142   beginning of the experiment; Ashanti was a 16-year-old subadult. Comparisons between the

143   adults and the subadult allowed us to examine the role of experience in trunk preshaping

144   behaviours. All elephants except Ashanti were wild-born. They lived in two groups, each of

145   which had a specific dominance hierarchy. One of the females, N'Dala, had been blind for a year

146   by the time the study commenced. Thus, comparisons between sighted and blind elephants

147   allowed us to assess the importance of visual input for grasping behaviours. The elephant

148   characteristics can be found in Table 1.

149   The elephants were housed together but were isolated during the experiment. They were

150   tested during their weekly training sessions. Every morning, one elephant was trained to

151   facilitate any future medical interventions; this corresponded to one training session per elephant

152   per week. The elephants were already experienced with grasping food items during these weekly

153   training sessions; thus, they were already experienced with the movements required for the

154 experiment. The running order of these training sessions changed each week. Thus, in total, we

155 conducted five to six experimentation sessions per elephant over six weeks in spring 2019.

156

157 **Ethical note**

158 As the data were collected by keepers during the weekly elephant training sessions, only

159 standard elephant-keeper interactions occurred, in accordance with zoo security regulations. All

160 procedures were conducted in accordance with the relevant CNRS guidelines and European

161 Union regulations (Directive 2010/63/EU).

162

163 **Object grasping**

164 The food items used in the experiments were found in the typical diet of captive Beauval

165 elephants and included carrots, apples and celery (Ullrey, Crissey & Hintz, 1997; Olson, 2004).

166 Three food item types were presented to the elephants: elongated objects with a constant

167 diameter (carrots), flat objects (apple slices, cut horizontally), and cubic objects of three sizes.

168 The objects consisted of diverse vegetables (according to availability), and the three cubic sizes

169 included small cubes (two centimetres per side), medium cubes (four centimetres per side) and

170 large cubes (eight centimetres per side). Food item dimensions are presented in Table 2. The

171 small cube size was determined by elephant participation: smaller cubes (i.e., one centimetre per

172 side) made the elephants impatient, and experiments with this size were inconclusive. The large

173 cube size was determined according to the maximum size of the largest vegetables (e.g.,

174 beetroots and celery). Three to six items of each type were provided during each session (Fig.

175 1A), depending on vegetable availability, except for the large cubes, which had low availability.

176

177 **Recordings of grasping movements**

178 To determine the influence of food item characteristics on the trunk tip form during grasping

179 behaviours, the items were laid out on a double transparent box. The bottom of the first box

180 contained the camera, set in polystyrene, and a second box, with a hole at its bottom for the lens

181 of the camera, was placed over the first box. The top of the second box was a transparent lid

182 (Fig. 1C) where the items were individually placed. This box-and-camera system was placed on

183 the ground in front of the animal by an animal keeper (Fig. 1D). Therefore, we were able to film

184   all grasping behaviours from below. An example film of a grasping behaviour can be found in

185   the Supplementary Material.

186   We recorded the reach-to-grasp movements of each individual with a digital video

187   camera (GoPro7). For each grasp, we took pictures of the distal part of the trunk. We captured

188   these images from the video frames when the elephant first touched the box and when the trunk

189   was flat against the box (Fig. 1E). Other grasping techniques, such as coiling, were removed

190   from the analysis. For each grasping attempt, we also noted when the trunk hit the box near the

191   food but missed the food item. As these grasping attempts require a readjustment of the trunk

192   towards the item, they are directly correlated with the time spent on a grasp. The elephants

193   almost never dropped food items but took longer to grasp them after missing. Therefore, we

194   termed these grasping attempts "failure before a grasp" to differentiate them.

195

196   **Geometric morphometrics and statistical analysis**

197   To describe the shape of the tip of the trunk, we used a 2D geometric morphometric (GM)

198   approach (Rohlf & Marcus, 1993; Adams, Rohlf & Slice, 2004; Gunz & Mitteroecker, 2013).

199   For each image of the trunk tip, the trunk tip was outlined with tpsDIG2 software, version 2.32

200   (Rohlf, 2016). To obtain these outlines, we placed an anatomical landmark on the top of each

201   trunk tip and placed 100 sliding semilandmarks on the curves (Gunz & Mitteroecker, 2013) to

202   outline the distal part of the trunk (Fig. 1F). These semilandmarks defined the borders of the

203   trunk tip. Every characteristic (the subject, food item, and number of failures) that might

204   influence the trunk tip contour was annotated. The film in the Supplementary Material shows a

205   part of this methodology (video recording of the grasp as well as the landmark and

206   semilandmarks on the trunk tip).

207   We performed a Generalised Procrustes Analysis (GPA) (Rohlf & Slice, 1990), using the

208   "gpagen" function of the package "geomorph" version 3.2.1 (Adams, Collyer &

209   Kaliontzopoulou, 2018) in R version 3.6.1 (R Core Team, 2018). This GPA aligned the different

210   distal trunk shapes with a Procrustes superposition to remove the effects of translation, rotation,

211   and scaling. We visualised the GPA using the "plotTangentSpace" function and retained 90% of

212   shape variability after reducing the dimensionality of the variables with a principal components

213   analysis (PCA) (Baylac & Friess, 2005). The PCA components were used as shape parameters in

214   the following analyses. To detect significant differences in the shape of the trunk according to

215 the object properties, individual, or number of grasping failures, we performed a MANOVA

216 using the "manova" function in R. A MANOVA was also used to detect significant differences

217 in trunk tip shape according to the object properties for each individual.

218  To optimise and visualise individual differences in trunk tip shapes, canonical variable

219 analysis (CVA) was performed using the "CVA" function in the package "Morpho" version 2.8

220 (Schlager, 2017). This CVA was applied to only five of the six elephants because one elephant,

221 N'Dala, had a deformed trunk tip caused by a previous injury. Her trunk tip thus differed from

222 those of the other five. To explore intact trunk tip shapes and obtain the most representative

223 variability between individuals, N'Dala was excluded from this analysis. All other analyses

224 included all six elephants.

225  A CVA was also performed for each individual to calculate the Mahalanobis distances

226 between food items. These Mahalanobis distance plots revealed the similarity between trunk

227 shapes for grasping different items. The Mahalanobis distances were calculated with the "hclust"

228 function in R, plotted in an "unrooted" form and then paired with deformation vector fields and

229 deformation isolines of the trunk tip shapes for each object. These thin plate spline (TPS)

230 deformations showed the difference in shape between the mean trunk tip shape for each

231 individual and the mean trunk tip form per object for each individual. To obtain these TPS

232 deformations, every dot of the mean distal form outline was slid to the position of the mean distal

233 form per object. A deformation grid was thus obtained, and the intensity and direction of the

234 deformations were indicated by smooth deformation isolines and deformation vector fields. The

235 deformation isolines indicated the location of the strongest differences in trunk tip form, and the

236 deformation vector fields showed the direction of these differences. These TPS visualisations

237 were performed with the functions "tps_arr" and "tps_iso" in the "Momocs" package (version

238 1.3.2) in R (Klingenberg, 2013).

239  The mean number of grasping failures per individual and per object for all trials were

240 also calculated. Linear regressions were performed to determine the change in the number of

241 failures over time for each individual and each object. These number of failure tendencies are

242 show along all the grasping attempts (all objects included). Finally, a GPA of the trunk tip shapes

243 of all individuals for each object was performed and paired with trajectory plots. These plots

244 were obtained in the Proscrustes space by joining for each individual the dots corresponding to

245 the outlines of the first and last grasping movement. We could therefore examine the trajectories

246 of the distal trunk shapes during grasping to see if different individuals's trunk tips converged on
247 similar shapes for the same object.

248

249

Results

251 We obtained a total of 639 grasps from 03:03 hours of video from all studied elephants. Of these
252 grasps, trunk tip contouring could be obtained from 491. In the remaining 148 grasps, the trunk
253 either did not lay flat on the box lid or the object or side of the box obscured a part of the trunk
254 tip. The distribution of the 491 grasps among each elephant and food item can be found in Table
255 3. The number of grasps were not equivalent for each individual and item type. These differences
256 can be explained by the 148 grasps that were removed and by variation in the availability of
257 vegetables in each session. Similarly, the low number of large-cube grasps is explained by the
258 low availability of vegetables to create this item. Moreover, in the 491 grasps included in the
259 final analysis, M'Kali only interacted once with a large cube; the other interactions between
260 M'Kali and the large cubes occurred in the 148 grasps that were removed.

261   Table 4 shows the results of the MANOVA on the trunk tip shape just before a grasp (the
262 preshape) and the individual, object and number of failures variables. The trunk tip shape varied
263 according to these variables. First, the distal trunk shape varied significantly by individual and by
264 object ($p < 0.05$). The significant association between the distal trunk shape and the individual
265 elephants supports the hypothesis of unique distal trunk shape. The significant association
266 between the distal trunk shape and the type of object supports the hypothesis of trunk tip
267 preshaping during a reach-to-grasp movement toward a food item. Thus, the trunk tip shape
268 corresponded to the individual and the type of object. Moreover, the trunk tip shapes for each
269 object were also dependent on the individual elephant. However, there was not a significant
270 association ($p > 0.05$) between the distal trunk shape and the number of failures. Therefore, in this
271 experiment, we were not able to establish a link between distal trunk shape and the number of
272 failures before a successful grasp.

273

274 **Individual differences**

275 As seen in Table 4, trunk tip shapes differed according to the individuals. Interindividual
276 variability in the distal trunk shape during food item grasping is shown in Figure 2. This CVA of

277   the elephant trunk tip shape during food item grasping included only five of the six elephants
278   because one elephant, N'Dala, had a deformed trunk tip; therefore, she was not included in this
279   analysis. Each point in Figure 2 represents a grasp, each colour represents an individual, and the
280   shape at the end of each axis represents the shape of the maximum (red) and minimum (blue)
281   trunk tip.
282   In Figure 2, all distal trunk shapes are distinctly grouped by individual. Although Juba's
283   (light blue) and Marjorie's points (orange), are grouped together, their distal trunk shapes were
284   still very different from each other. There were pronounced individual differences in the distal
285   trunk shape between elephants.
286
287   **Trunk shapes and object characteristics**
288   Table 4 shows that the trunk tip shape varied according to the type of object grasped and the
289   individual elephant. Some of the studied elephants preshaped their trunk tip according to the
290   object properties. The results of the MANOVA on the trunk tip shape just before a grasp,
291   performed per individual and according to the type of object, are shown in Table 5. The trunk tip
292   shape significantly differed according to the type of object for M'Kali, Juba and Marjorie; thus,
293   there was a significant effect of object properties on trunk tip preshaping. The three other
294   elephants, N'Dala (the blind elephant), Ashanti (the subadult) and Tana, did not preshape their
295   trunk tip according to the food item properties. Thus, only half of the sampled individuals had
296   specific tip trunk shapes associated with object properties.
297   Specifically, Figures 3 to 5 display the trunk tip shapes of M'Kali (Fig. 3), Juba (Fig. 4)
298   and Marjorie (Fig. 5) and their variance according to the object properties. As M'Kali only
299   interacted with the large cube once in the analysed grasps, her trunk tip shape associated with the
300   large cube is not included in the figure. These three Mahalanobis distance plots paired with thin
301   plate spline deformation visualisations represent the three individuals who preshape their trunks
302   according to the object properties. The TPS deformations are the differences between the mean
303   distal trunk shape for each object and the general mean shape, for each individual. The isoline
304   visualisations show the location of these deformations: the red parts indicate areas with the
305   greatest deformation, and the blue parts indicate areas with the lowest deformation. The
306   deformation vector field visualisations show the directions of these deformations.

307   In Figure 3, it can be seen that M'Kali preshaped her trunk tip differently according to the type

308   of food item she reached to grasp. As the Mahalanobis distances show, her trunk tip shape was

309   similar when grasping apple slices and small cubes but different when grasping carrots or

310   medium cubes. For the apple slices and small cubes, the deformations (indicated in red) were

311   mostly on the sides of the trunk tip, and the vectors on these sides point toward the centre of the

312   trunk tip. Thus, when grasping apple slices and small cubes, M'Kali's trunk tip was more

313   elongated than usual. More specifically, when grasping apple slices, her trunk tip was more

314   ovular, and the top of the trunk tip was thicker; the shape of her trunk tip was similar when

315   grasping small cubes but narrower in area. When grasping carrots, her trunk tip was more

316   circular than usual, with a sharp top to the trunk tip, as indicated by the vector directions and

317   isoline colours. Finally, when grasping medium cubes, M'Kali's trunk tip shape isoline

318   visualisation was mainly blue. This trunk tip shape was similar to the usual shape, with only

319   three small areas of difference, creating a slightly more rounded shape.

320   Figure 4 shows how the distal part of Juba's trunk was preshaped according to the type of

321   food item grasped. Her trunk tip shape was similar when grasping small cubes and medium

322   cubes but different when grasping carrots and apple slices. Moreover, as the Mahalanobis

323   distances show, her trunk tip shape completely differed from the others shapes when grasping

324   large cubes. As the deformation vector field and isoline visualizations for the periphery of the

325   distal trunk shape show, her distal trunk shape became more circular than usual and the top of the

326   trunk tip became thinner. When grasping other food items, the top of the trunk tip was thicker.

327   Still according to the vector field and the isoline colours, when grasping small and medium

328   cubes, Juba's trunk tip shape was slightly more circular than usual, especially on the left side for

329   small cubes and the right side for medium cubes. When grasping carrots, her trunk tip shape was

330   close to usual but thicker on the top right side of the trunk tip. Finally, when grasping apple

331   slices, the general shape of the trunk tip was more ovular than usual.

332   Figure 5 displays how Marjorie's trunk tip preshape differed according to the type of

333   food item. Similar to M'Kali, her trunk tip shape was similar when grasping apple slices and

334   small cubes but different when grasping carrots, medium cubes and large cubes. From the vector

335   field and isoline colours of each object's distal trunk shape, we can see that when grasping apple

336   slices and small cubes, Marjorie's distal trunk shape was more ovular than usual, with

337   differences on the left and bottom right of the trunk tip. Moreover, the top of the trunk tip was

338 thicker than usual, especially on the left side. When grasping the three other types of food

339 (carrots, medium cubes and large cubes), the top of Marjorie's trunk tip was thinner. The distal

340 trunk shape was also more rounded than usual, especially on the right side when grasping

341 medium cubes, on the bottom right side when grasping large cubes, and on the left side when

342 grasping carrots.

343   Thus, M'Kali and Marjorie had more circular and thin-topped trunk tips when grasping

344 carrots and medium cubes, while the top of the trunk tip was thicker for Juba. When grasping

345 apple slices, the three elephants had more ovular and thick-topped trunk tips. For M'Kali and

346 Marjorie, the trunk tip shape when grasping small cubes was similar to that when grasping apple

347 slices, but for Juba, the trunk tip shape was more circular. Finally, Marjorie and Juba had the

348 same distal trunk shape when grasping large cubes: circular with a thin top.

349   The trunk tip shapes differed according to the type of object and individual, but the three

350 elephants had many similarities in distal trunk shape for grasping the same object. M'Kali and

351 Marjorie had the same trunk tip shapes when grasping the same objects. Juba tended to have the

352 same shape as well with some food items, but her distal trunk shape also differed for other items,

353 such as small cubes. Taken together, these results indicate that there are both similarities and

354 individual differences in trunk tip preshapes in the three elephants.

355   The distal part of the trunk was also preshaped in a way that matched the type of food

356 item in these three elephants. A rounder trunk tip allowed it to better conform to the contours of

357 food items such as carrots and medium and large cubes, with the sides of the trunk tip matching

358 the edges of the items. Small cubes and flat apple slices, which were more difficult to grasp,

359 required a more ovular distal trunk shape to apply maximal surface area to the item. The more

360 difficult the object was to grasp, the more ovular the trunk tip shape was. Conversely, if the

361 object offered more grip, as is the case for carrots, the distal trunk shape was closer to the shape

362 of the object.

363

364 **Grasping success**

365 Table 4 shows that trunk tip shape did not differ according to the number of failures before a

366 successful grasp, namely, when the trunk hit the box but missed the food. There was no link

367 between the distal trunk preshape and the number of failures for these individuals. Regardless of

368 the number of failures before a successful grasp, the trunk tip was preshaped just before a grasp.

369 Moreover, Table 6 represents the mean number of failures per individual and per object
370 for all the grasping attempts. Focusing on the individuals, the elephants that failed the most
371 before a successful grasp were M'Kali and N'Dala, while Ashanti and Juba had the fewest
372 failures. The three elephants that had the best grasping success (Ashanti, Juba and Tana) were
373 not necessarily the same elephants that preshaped their trunk tip according to the object
374 properties (M'Kali, Juba and Marjorie). Additionally, for these individuals, a distal trunk
375 preshape in accordance with the object properties was not linked with the success of a grasping
376 attempt.

377 The objects section of Table 6 displays the success of grasping attempts in general,
378 including the mean number of failures per object for all grasping attempts. Failure was less likely
379 when the elephants attempted to grasp large cubes and carrots and more likely when they
380 attempted to grasp apple slices and small cubes. Overall, grasps were more efficient for large and
381 thick food items.

382 However, over time (and with an increasing number of trials), the number of grasping
383 failures consistently increased or decreased depending on the individual and objects concerned.
384 Figure 6 shows the change in the number of failures on different grasping attempts for each
385 individual and object pair. M'Kali and Ashanti had fewer failures with all food items as the trials
386 progressed, notably improving their success of grasping small cubes (M'Kali) and carrots
387 (Ashanti). At the beginning of the experiment, M'Kali had the most failures in grasping the small
388 cubes of all elephants studied, but her number of failures quickly decreased as the trials
389 progressed. Tana, Juba, Marjorie and N'Dala had fewer failures for most food items as the trials
390 progressed, except for grasping carrots (Tana), apple slices and large cubes (Juba), apple slices
391 and carrots (Marjorie), and apple slices and medium cubes (N'Dala). In particular, Juba had
392 more failures in grasping the large cubes and fewer failures in grasping carrots as the trials
393 progressed. Marjorie had the largest decrease in failures when grasping medium cubes, while
394 N'Dala had the largest increase in failures when grasping medium cubes and the largest decrease
395 in failures when grasping small cubes.

396 All the studied elephants improved in grasping efficiency over time, with all or the
397 majority of the food items. However, each elephant improved on different objects.

398 Finally, we investigated whether the trunk tip shapes of all the individuals converged
399 when grasping the same object by examining the trajectories of distal trunk shapes over time.

400 Figure 7 displays these trajectories for all studied elephants when grasping medium cubes. The

401 trajectories when grasping the other types of food items are provided in the Supplementary

402 Material. In Figure 7, each individual's distal trunk shape when grasping medium cubes changed

403 over time. However, no individual's preshapes clearly trended in the same direction. Thus, their

404 trajectories when grasping medium cubes did not converge. The results were similar for the

405 trajectories when grasping other food items. Taken together, these results did not indicate a

406 convergence of individual distal trunk shapes when elephants grasped the same type of object.

407

408

409 Discussion

410 We found that elephants preshaped their trunk tip in reach-to-grasp movements toward food

411 items according to the characteristics of the different food items. Preshaping varied between

412 individuals, which each had a unique distal trunk shape, but was not linked to grasping success.

413

414 Individual differences

415 As shown by our results, all the elephants in our study had a unique trunk tip shape. Similar

416 results are found in the human literature: individual and interpopulation variation in human hand

417 forms are well documented (Králík, Katina & Urbanová, 2014) and have a real impact on hand

418 utilisation and related abilities. For example, some sports modify and intensify these individual

419 differences in hand shape, which confers an advantage for certain hand shapes in these

420 disciplines (Barut, Demirel & Kıran, 2008; Fallahi & Jadidian, 2011). Thus, we assume the same

421 applies to elephants: different trunk tip shapes may lead to different reach and grasping skills in

422 individuals. These individual differences may influence (and predict) individual grasping

423 performances.

424

425 Trunk tip shapes and object characteristics

426 We highlighted a significant effect of food item properties on the trunk tip preshape of three out

427 of the six elephants. M'Kali, Juba and Marjorie adjusted the shape of their trunk tip according to

428 the object properties, consistent with findings of preshaping in the hands or paws of other species

429 (Chieffi & Gentilucci, 1993; Christel & Fragaszy, 2000; Roy et al., 2000; Sacrey, Alaverdashvili

430 & Whishaw, 2009; Sartori et al., 2013). These elephants also showed similar distal trunk

431   preshapes for almost all the types of food items in our experiment; the preshapes matched the

432   shape of the food and its difficulty to grasp. This adaptation of trunk tip shape may allow

433   individuals to grasp more efficiently. Comparable results are found in studies on hand or paw

434   preshaping according to object properties (Christel, 1993; Pouydebat et al., 2011). In animals

435   such as primates, preshaping sometimes provides more appropriate and optimal grasping

436   (Pellegrino, Klatzky & McCloskey, 1989; Christel, 1993; Supuk, Kodek & Bajd, 2005;

437   Pouydebat et al., 2009).

438   Interestingly, preshaping of the trunk tip according to the object properties does not occur

439   in all elephants, as half of our sample did not show any trunk tip shape adaptation. Although the

440   preshaping of hands or paws is found in many primates and rats (Napier, 1993; Sacrey &

441   Whishaw, 2012), it is not always widespread in all subjects. Preshaping can result from

442   individual differences in hand, paw or trunk tip morphology but may also be the result of

443   individual variability in motor control.

444   Interestingly, the group of elephants that did not preshape their trunk according to the

445   food item properties included the blind elephant. According to Jeannerod, preshaping is

446   controlled by visuomotor channels and, more precisely, by visual data of the object shape

447   (Jeannerod 1981, 1988). In 1994, Weir corroborated this idea. In humans, a grasping movement

448   without visual feedback will have an increased hand aperture (Uno et al., 1993; Winges, Weber

449   & Santello, 2003; Tipper, Paul & Hayes, 2006; Sacrey & Whishaw, 2012). Although Santello,

450   Flanders and Soechting (2002) showed that continuous visual feedback from the object or the

451   hand is not necessary for adequate preshaping, a degree of visual input remains essential. Some

452   primates and other animals cannot preshape their hands or paws because of vision impairments

453   (Uno et al., 1993; Winges, Weber & Santello, 2003; Tipper, Paul & Hayes, 2006). This may be

454   the case for the blind elephant, N'Dala, that did not exhibit trunk tip preshaping in accordance

455   with the properties of the object grasped. To verify this hypothesis, the experiment could be

456   redone with entirely blind grasping tests for all subjects. However, like the other elephants,

457   N'Dala still managed to grasp all the food items. These results confirms the idea that vision, one

458   of elephants' less-used senses (O'Connell-Rodwell, 2007; Moss & al., 2013; Plotnik et al.,

459   2013), is not necessary for grasping food items with the trunk.

460   The subadult elephant, Ashanti, also did not exhibit trunk tip preshaping according to the

461   properties of the food item. This may be due to her relatively young age and interactions with

462   other elephants; in some species young and subadult individuals do not exhibit preshaping or use

463   adult grasping strategies (Forssberg et al., 1991; Butterworth & Itakura, 1998; Pouydebat et al.,

464   2011; Le Brazidec et al., 2017). Thus, preshaping of the trunk tip according to the object

465   properties may result from learning.

466

467   **Grasping success**

468   We did not find a link between the trunk tip shape just before a grasp and the number of failures

469   before a successful grasp. Moreover, unlike what we hypothesised and what is found in other

470   species (Christel, 1993; Supuk, Kodek & Bajd, 2005), preshaping the trunk tip did not increase

471   grasping success. Therefore, trunk tip preshaping may not confer a selective advantage in terms

472   of reducing the number of failures before a successful grasp for these elephants.

473   Although grasping is logically more efficient with large and thick food items, all the

474   studied elephants improved in grasping efficiency over time, each with different objects. This

475   result suggests that each individual developed, over the trials, her own grasping strategies to

476   increase grasping success. This individuality of grasping success for individual–object pairs

477   might indicate taste preferences. Individuals may be motivated to improve grasping success for

478   foods that they prefer and may be less motivated when they find the food less appealing. These

479   differences in grasping success can also be explained by the constraints of the experiment: we

480   could not control the posture of the elephant in front of the box or the position of the head

481   relative to the bars. The elephants may have experienced different visual obstructions while

482   grasping the food items; however, N'Dala, the blind elephant, did not have significantly lower

483   grasping success than two of the elephants that preshaped their trunk tip according to the object

484   properties (Marjorie and Juba). Thus, vision may have little importance to grasping success of

485   specific objects by individuals. As olfaction is essential in elephant life (Polla, Grueter & Smith,

486   2018; Plotnik et al., 2013, 2019), we assume that elephant trunk grasping success depends more

487   on olfaction than on vision.

488   Finally, in contrast to our hypothesis, individuals' distal trunk shapes did not converge

489   when grasping the same object. Although the three individuals who preshaped their trunk tip

490   according to the object properties tended to have the same general shape when grasping the same

491   type of object (more ovular or more rounded), over time, they did not develop similar grasping

492 shapes. This was also true for the three other elephants. In the studied elephants, there was no

493 general convergence of trunk tip shape over time to optimise grasping success.

494

495

496 Conclusions

497 To conclude, our results indicate that three out of the six studied African savannah elephants

498 adjusted their distal trunk shape to that of the object. Preshaping varied depending on the

499 individual, each of whom had a unique distal trunk shape. This study is the first time that

500 preshaping has been demonstrated with a muscular hydrostat, in other words, with a grasping

501 appendage that has no joints. Grasping strategies can be similar even if the grasping appendage

502 operates in a completely different way. We found that the blind elephant could grasp but did not

503 optimally preshape its trunk. This finding reveals that elephant trunk grasping success may

504 depends more on olfaction than on vision, but preshaping during reach-to-grasp movements is

505 probably, as in other species, mostly controlled by visuomotor channels. Moreover, as the blind

506 elephant had a similar increase in success grasping objects as the other elephants, we assumed

507 that grasping success did not depend only on vision. Preshaping may also result from learning, as

508 one of the other elephants that did not exhibit optimal preshaping was a subadult. The third

509 elephant in this group, Tana, did not show an optimal preshaping. This may be due to her life

510 history, such as experience or learning during development. It would be interesting to investigate

511 further, perhaps by conducting a developmental preshaping study. However, preshaping of the

512 trunk tip did not increase grasping success and thus may not confer a selective advantage in these

513 elephants. We observed increases in grasping success that differed according to objects and

514 individuals, probably influenced by learning and food taste preferences.

515 Finally, our study was based on a sample of six African savannah elephants. It would be

516 interesting to increase the sample size and to carry out a similar study in Asian elephants, which

517 have only one finger on their trunk, to understand preshaping strategies in elephants more

518 broadly.

519

520

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530

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818

Figure 1

The materials and methods used for the experiments.

(A) Example of food items used for the experiment. Here we presented to the elephant five type of item: carrots, flat apple slice, two centimeter side-length celery cube, four centimeter side-length sweet potato cube and eight centimeter side-length celery cube, with a repeatability of four for each. (B) Three of the six African savannah elephants (*Loxodonta africana*) of the ZooParc of Beauval. (C) The double box system used to film the experiment. It is a double transparent box inlay in one another, the first one contains the camera and polystyrene to maintain it, and the second one had a hole at its bottom for the lens of the camera. (D) The items were put down on the transparent top of the second box and carried in front of the animal. (E) Example of a screenshot of a four centimeter side-length food cube just before grasp, in order to take the print of the distal part of the trunk. (F) Example of a trunk tip contouring during a grasp. The red dot corresponds to the anatomical landmark at the top of the trunk tip, and the 100 orange dots correspond to the sliding semi-landmarks around the outlines of the distal part.

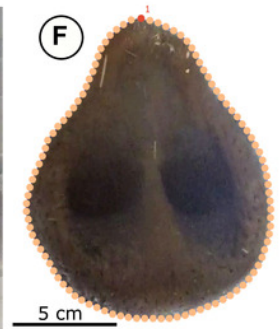
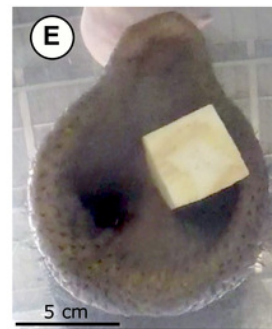
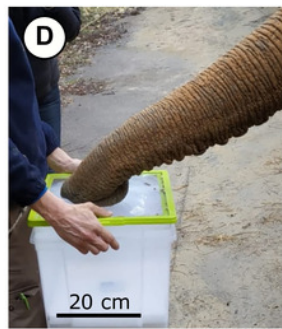
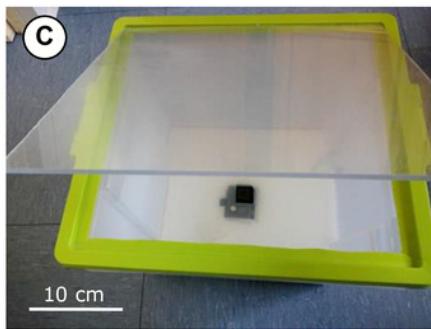
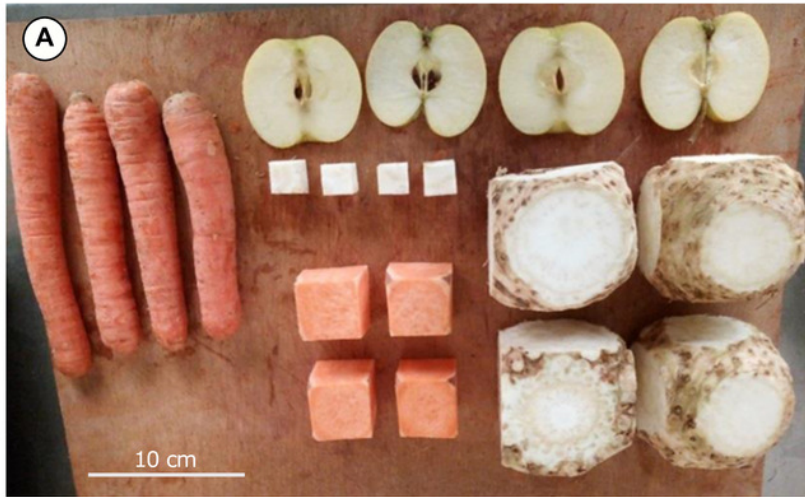



Figure 2

Canonical Variate Analysis visualisation of five elephant trunk tip shapes during food grasp.

Each point represents a grasp, each colour an individual, and each end of the axis the maximum (red) and minimum (blue) distal parts shapes.

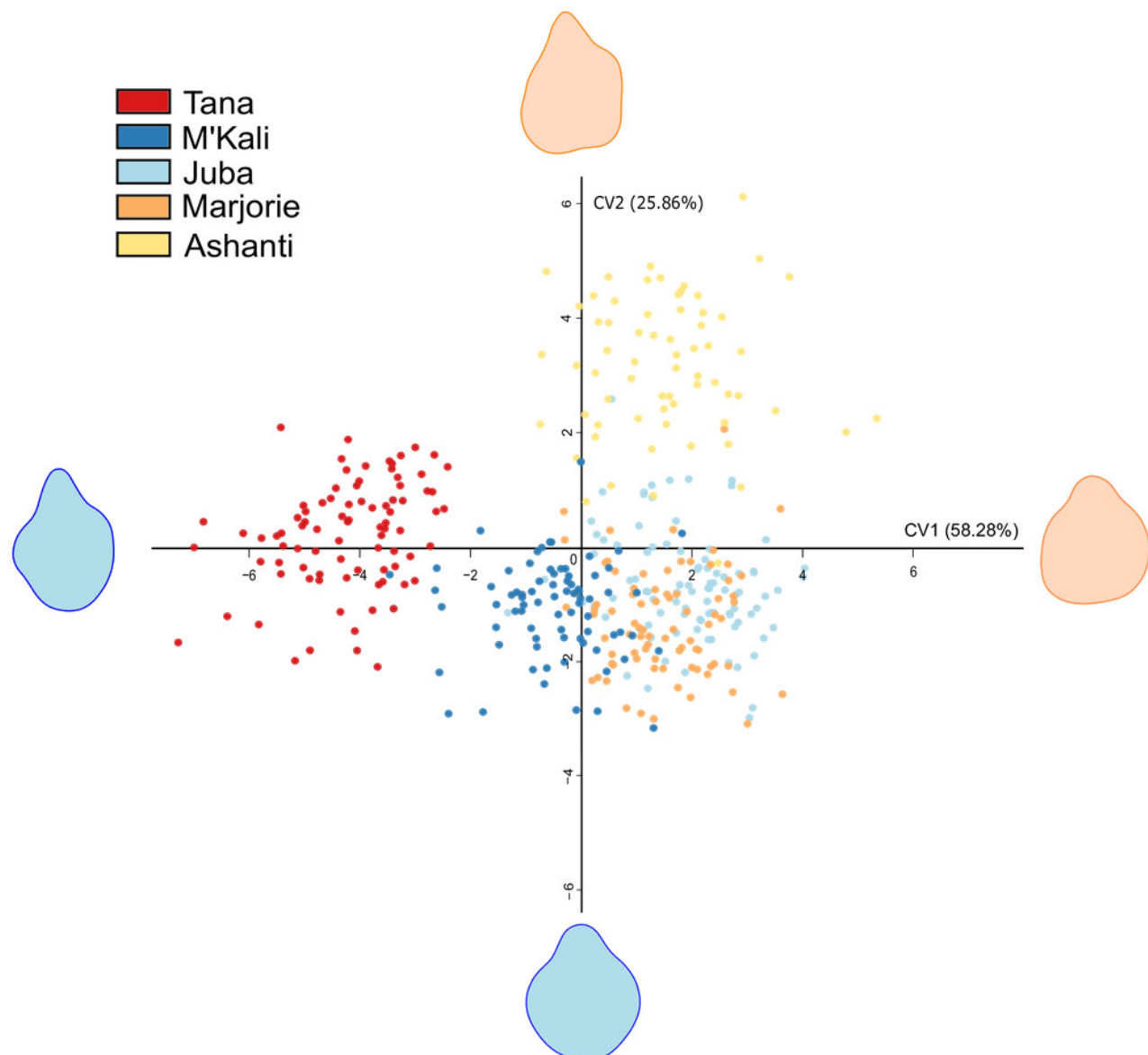



Figure 3

Mahalanobis distance plots paired with thin plate splines deformation visualisations (vectors field deformations and isolines deformations) of trunk tip according to the object grasp, for M'Kali.

These Mahalanobis distance plots show through discriminant space the similarity between the different distal shapes obtained per object. The Thin Plate Splines deformations specify where and how the differences in form are on the distal shapes. Red parts on the isolines deformations reveal where the distal shapes change the most, and the blues parts where it change the least. Arrows on the vectors field deformations show in which direction the deformations occur.

Carrot
16 cm

Apple
7,5 cm

M'Kali

Medium cube
4 cm

Small cube
2 cm

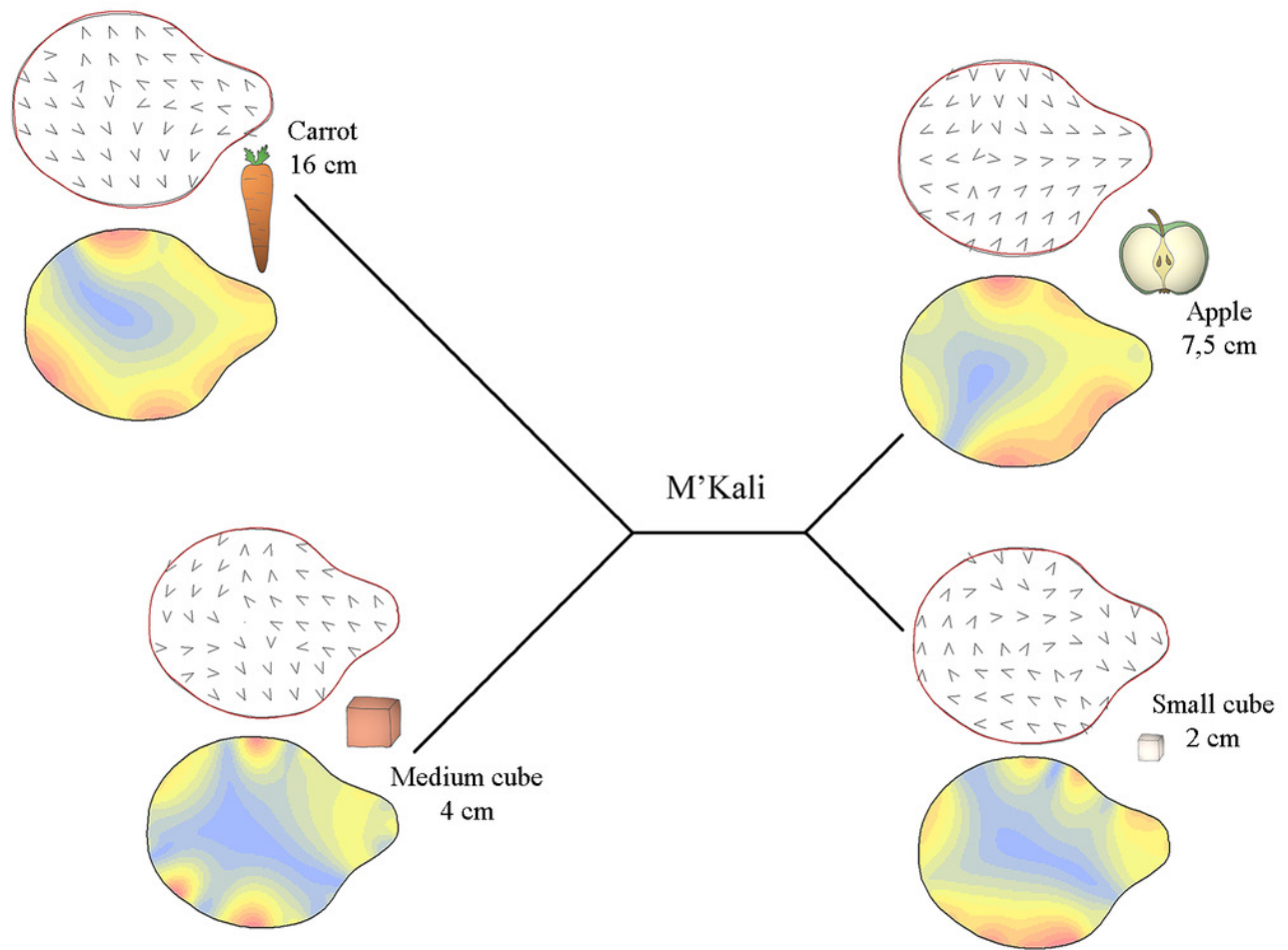



Figure 4

Mahalanobis distance plots paired with thin plate splines deformation visualisations (vectors field deformations and isolines deformations) of trunk tip according to the object grasp, for Juba.

These Mahalanobis distance plots show through discriminant space the similarity between the different distal shapes obtained per object. The Thin Plate Splines deformations specify where and how the differences in form are on the distal shapes. Red parts on the isolines deformations reveal where the distal shapes change the most, and the blues parts where it change the least. Arrows on the vectors field deformations show in which direction the deformations occur.

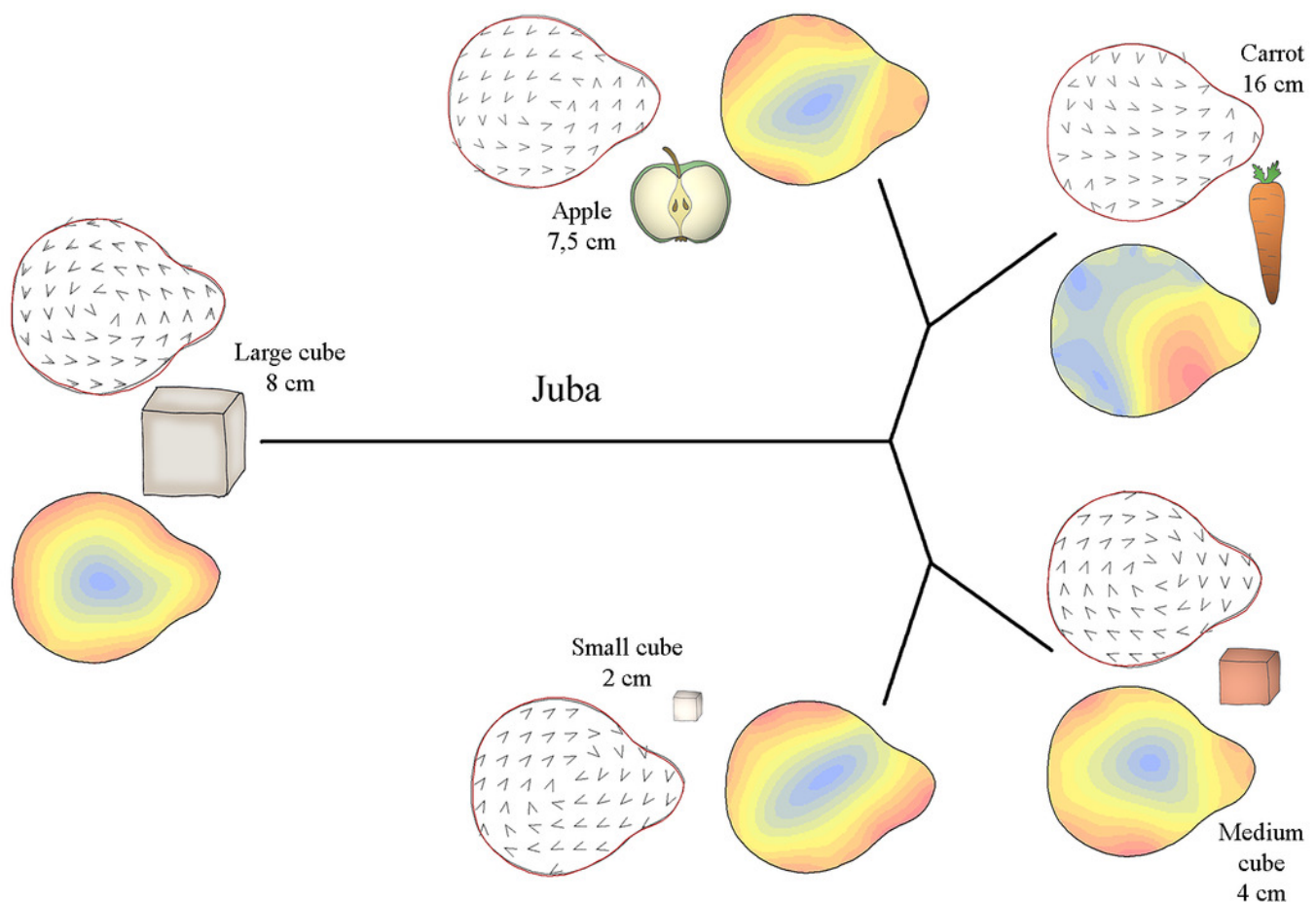



Figure 5

Mahalanobis distance plots paired with thin plate splines deformation visualisations (vectors field deformations and isolines deformations) of trunk tip according to the object grasp, for Marjorie.

These Mahalanobis distance plots show through discriminant space the similarity between the different distal shapes obtained per object. The Thin Plate Splines deformations specify where and how the differences in form are on the distal shapes. Red parts on the isolines deformations reveal where the distal shapes change the most, and the blues parts where it change the least. Arrows on the vectors field deformations show in which direction the deformations occur.

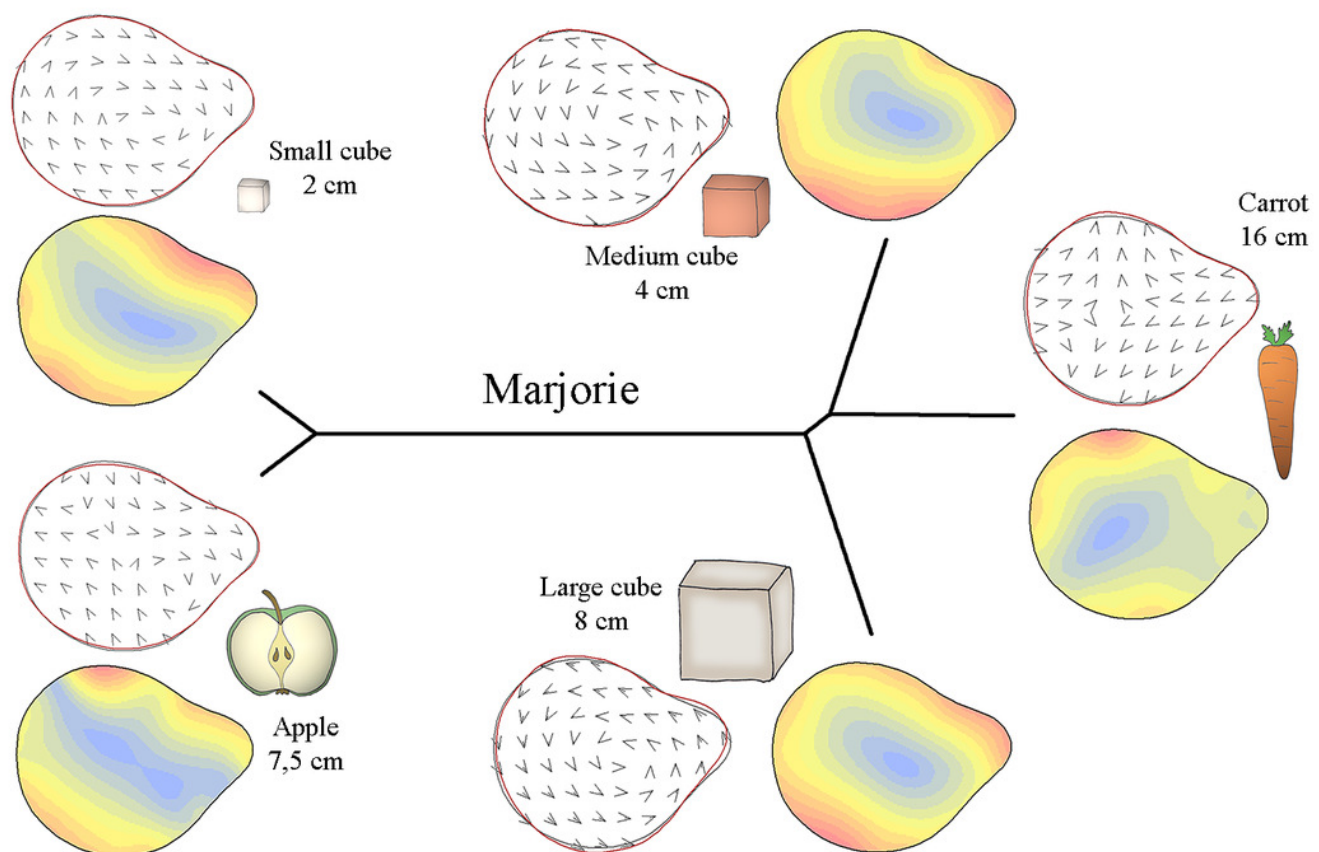



Figure 6

Number of failures along the grasping per individual and object.

The x-axes correspond to all the grasping perform over time by an individual, with all the objects. As we introduce the objects to the elephants one after the other each week, each object first grasp number then depends on when the elephant was first introduce to the object in its attempts. The y-axes represent the number of failure before a successful grasp, namely when the trunk hit the box but missed the food. The straight lines show these number of failure tendency along the attempts and per object, for each individual.

M'Kali

Ashanti

Object
- apple slice 7,5 cm
- carrot 16 cm
- small cube 2 cm
- medium cube 4 cm
- large cube 8 cm

Tana

Juba

Marjorie

N'Dala

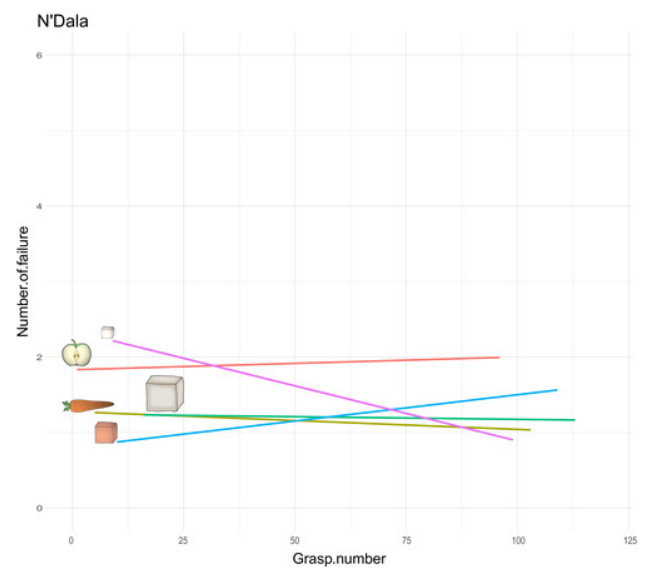
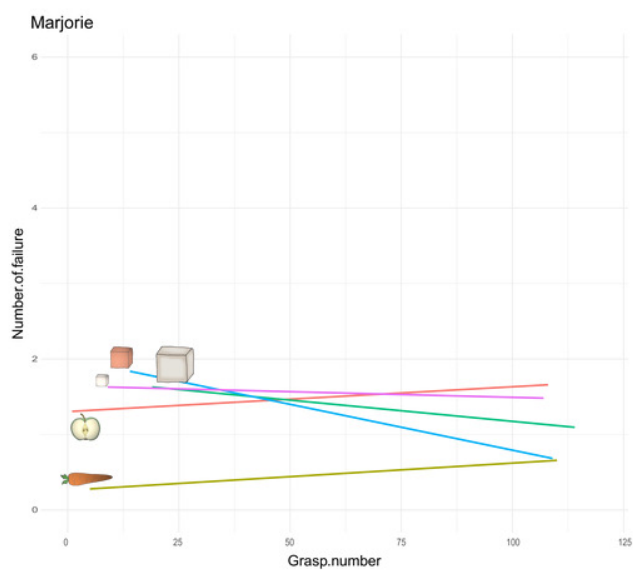
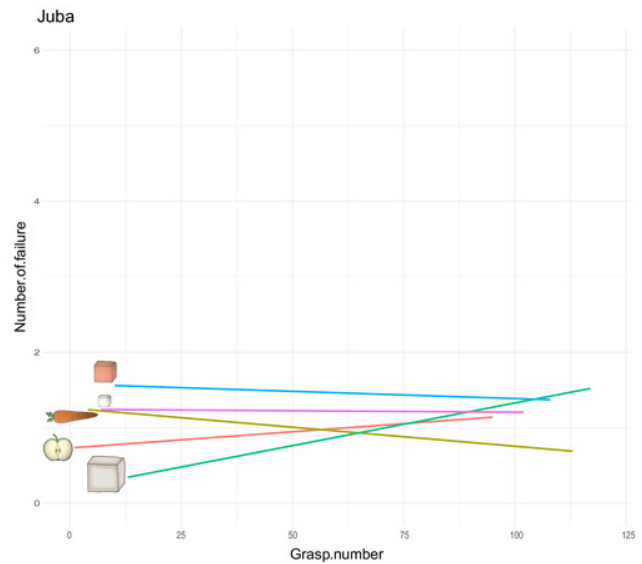
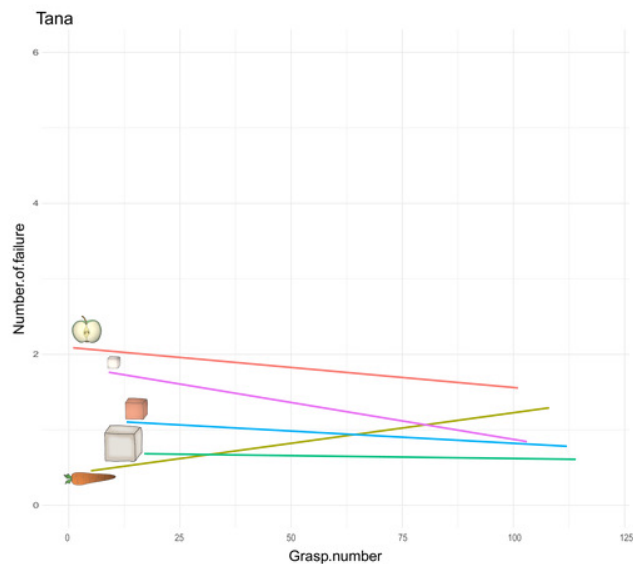
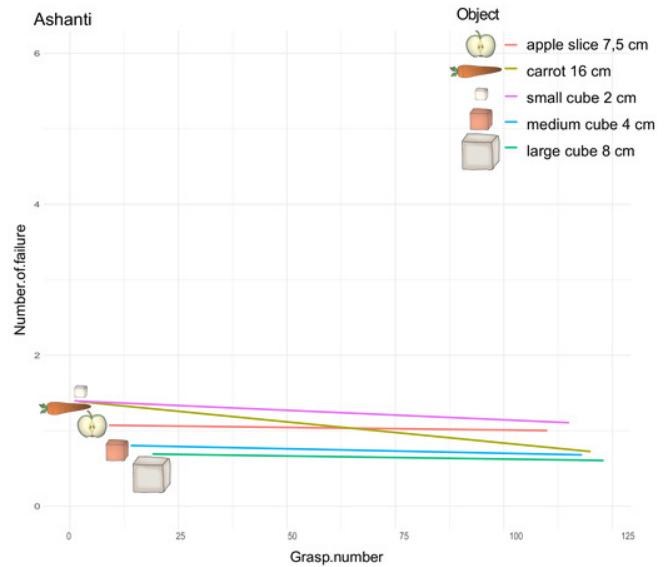
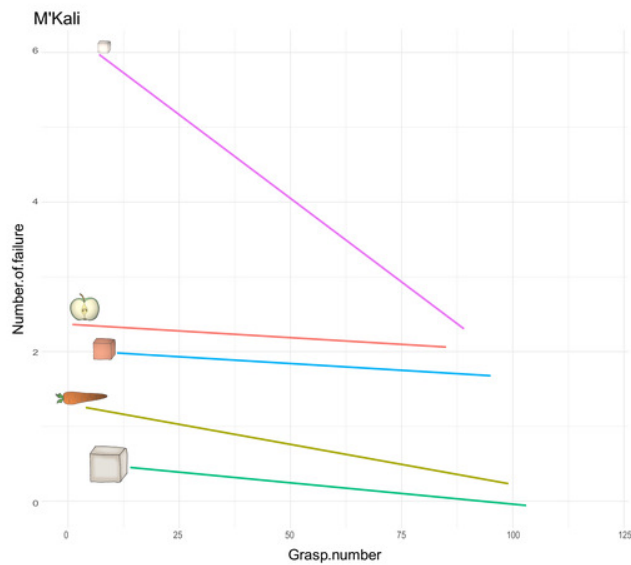
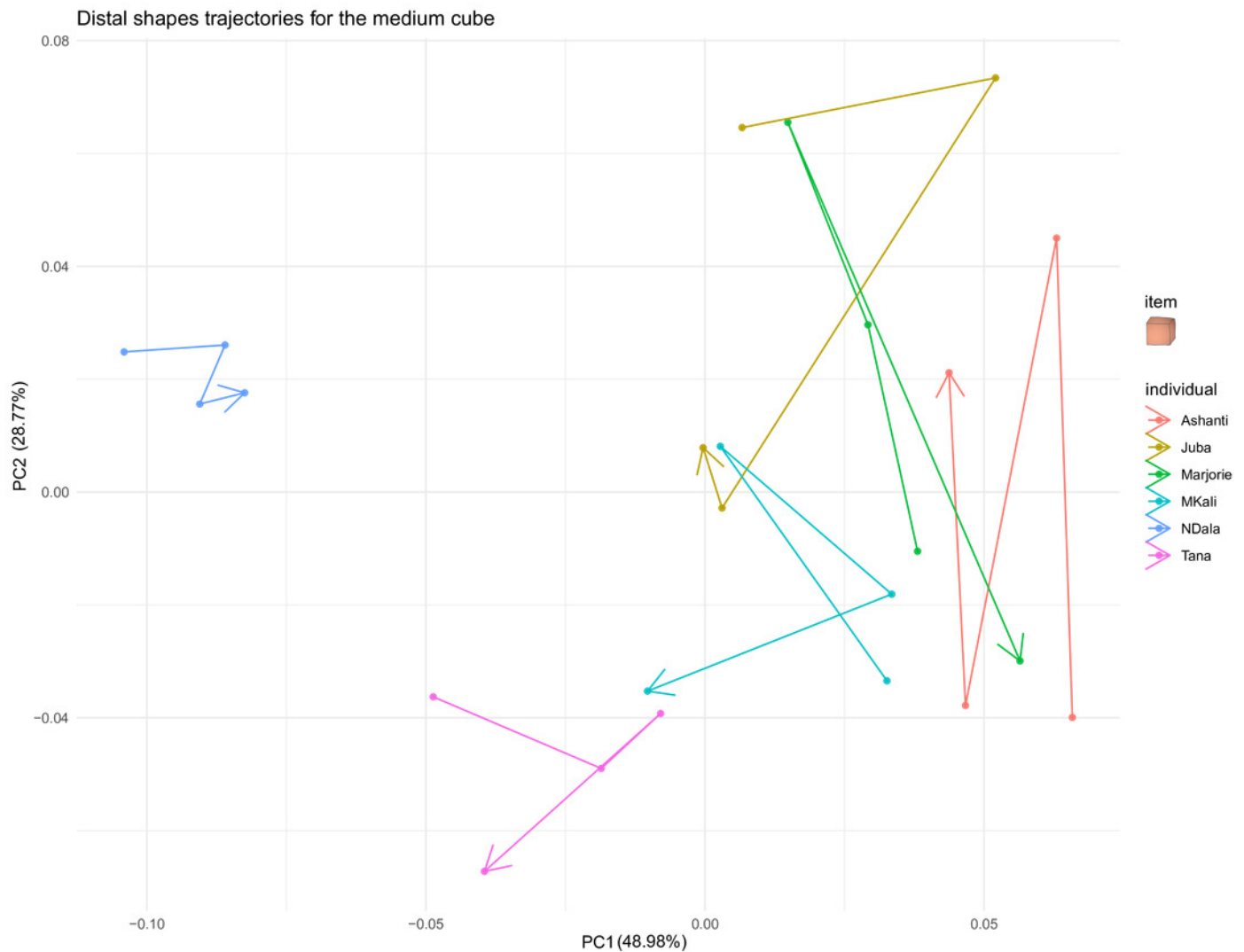



Figure 7

Distal shapes trajectories of all the individuals when grasping a medium cube.

Subjects characteristics.

These characteristics include the names of the elephants, their sex, age, hierarchical rank, origin and physical particularities.

Name	Sex	Age (year)	Hierarchical rank	Origins	Physical particularities
Ashanti	Female	16	Medium rank	Knowsley Safari Park (UK)	Smallest elephant
Juba	Female	32	High rank	Zimbabwe	-
Marjorie	Female	33	High rank	Zimbabwe	Largest elephant
M'Kali	Female	30	Low rank	Namibia	Tall
N'Dala	Female	30	Medium rank	Namibia	Blind, trunk tip deformity
Tana	Female	32	Medium rank	Zimbabwe	-

Dimensions of the food items grasped by the elephants.

Dimensions in millimetres.

Food item	Dimensions (mm)
Apple slice	75 (diameter)
Carrot	160 (length) * 25 (diameter)
Small cube	20*20*20
Medium cube	40*40*40
Large cube	80*80*80

Number of grasping attempts per individual and per food item.

All these grasping were included in the analyses.

Number of grasping attempts		Individual					
		Ashanti	*Juba*	*Marge*	*M'Kali*	*N'Dala*	*Tana*
Food item	*Apple slice*	13	20	21	18	27	26
	Carrot	14	23	15	18	18	17
	Small cube	19	25	23	20	20	20
	Medium cube	15	19	15	20	20	19
	Large cube	4	6	6	1	5	4
Total grasping attempts		65	93	80	77	90	86

Results of the variance analyses MANOVA performed on all the individuals trunk tip shapes just before a grasp and some variables.

All elephants trunk tip shapes according to	Pillai's Trace	F	df	P-value
Individuals	2.67	93.12	5	2.2e-16 ***
Objects	0.10	1.79	5	0.0051 **
Individuals * objects	0.35	1.23	20	0.0363 *
Number of failures	0.12	1.10	9	0.2873

Results of the variance analyses MANOVA performed per individuals on the trunk tip shapes just before a grasp according to objects.

Trunk tip shapes according to objects per individuals	Pillai's Trace	F	df	P-value
M'Kali	0.49	2.29	3	0.0028 **
Juba	0.50	1.76	4	0.0113 *
Marjorie	0.34	1.79	4	0.0311 *
N'Dala	0.48	1.22	4	0.1848
Ashanti	0.51	1.20	4	0.2289
Tana	0.28	0.85	4	0.6762

Mean of number of failures per individuals and per objects for all the grasping attempts.

The mean number of failure before a successful grasp, for each individual and for each object, on all grasping attempts, were calculated and are presented in this table.

Variables		Number of failures: mean
Individual	Ashanti	0.98
	Juba	1.10
	Tana	1.18
	Marjorie	1.27
	N'Dala	1.43
	M'Kali	1.91
Object	Large cube	0.82
	Carrot	0.89
	Medium cube	1.24
	Apple slice	1.54
	Small cube	1.79