1   **Title**

2   Division of Labor: A Democratic Approach to Understanding Manual Asymmetries in

3   Non-Human Primates

4

5   **Authors**

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13

14   **Abstract**

15   A consequence of the 'gold rush' like hunch for human-like handedness in non-

16   human primates has been that researchers have been continually analyzing

17   observations at the level of the population, ignoring the analysis at the level of an

18   individual and, consequently, have potentially missed revelations on the forms and

19   functions of manual asymmetries. Recently, consecutive studies on manual

20   asymmetries in bonnet macaques, *Macaca radiata* [Mangalam et al., 2014a;

21   Mangalam et al., 2014b] revealed both the functional and the adaptive significance

22   of manual asymmetries respectively, and pointed towards the division of labor as

23   being the general principle underlying the observed hand-usage patterns. We

24   review the studies on manual asymmetries in capuchin monkeys, *Cebus* spp. and

25   argue that the observed hand-usage patterns might reflect specialization of the two

26   hands for accomplishing tasks that require different dexterity types (i.e.,

27   maneuvering in three dimensional space or physical strength). To this end, we do a

28   step-by-step analysis of the various tasks used in the studies on manual

29   asymmetries in capuchin monkeys, wherein we: (a) analyze the different manual

30   tasks that have been used to study manual asymmetries in non-human primates on

31   the basis of the attributes such as the number of hands required to solve a given

32   task (i.e., unimanual, pseudo unimanual, or bimanual) and the spatiotemporal

33   progression of manual actions (i.e., sequential or concurrent). (b) Determine the

34   forms and functions of manual asymmetries that these tasks can potentially elicit

35   within the broader scope of the behavioral repertoire of an individual, a population,

36   or a species. (c) Qualify the scope of the inter-individual, -population, or -species

37   comparisons. We then describe the division of labor as a general principle

38   underlying manual asymmetries in non-human primates, and propose experimental

39   designs that would elaborate the forms and functions of manual asymmetries in

40   non-human primates, and the associated adaptive value.

43

44   **Introduction**

45   Approximately 90% humans preferentially use the right hand to perform complex

46   manual actions [Raymond and Pontier, 2004]. In order to understand the adaptive

47   value of this population-level right-handedness, which is peculiar to humans, it is

48   important to understand the evolutionary origin of manual asymmetries, in humans

49   as well as in their phylogenetic relatives, the non-human primates. Manual

50   asymmetries of some kind or the other are almost ubiquitous among the non-

51   human primates. However, for a long time the population-level lateral bias in hand

52   usage in non-human primates remained equivocal; considering that the exogenous

53   factors, such as the initial position of a stimulus with respect to a subject, body

54   posture of the subject, etc. might influence hand usage, researchers considered

55   manual asymmetries in non-human primates to be analogous and not homologous

56   to manual asymmetries in humans. Regardless of such an ambiguity, hand

57   preference in non-human primates has been hypothesized to have evolved owing to

58   functional and morphological adaptations to feeding in arboreal contexts [Bradshaw

59   and Rogers, 1993; Papademetriou et al., 2005; Ward and Hopkins, 1993].

60

61   As opposed to the prevailing ideas on population-level right-hand preference in

62   humans, MacNeilage et al. [1987] argued that human-like population-level lateral

63   bias in hand usage is evident in non-human primates, and proposed the postural

64   origins theory. According to the postural origins theory, among non-human

65   primates initially the left hand became specialized for visually guided movements,

66   and the right hand became specialized for postural support. Subsequently, in non-

67   human primate species that adopted a relatively more terrestrial lifestyle, the right

68   hand became more specialized for physical manipulation than for postural support,

69   owing to the decreasing demands on the right hand to support vertical posture.

70   However, the postural origins theory fails to describe why initially the left-hand

71   (and not the right hand) became specialized for visually guided reaching, and more

72   importantly, how a population-level right-handedness evolved during the transition

73   from monkeys to apes to humans [McGrew and Marchant, 1997]. Overall, the

74   postural origins theory incorporates the physical constraints on hand usage imposed

75   by the body posture, but does not explain the variations in hand-usage patterns,

76   corresponding to the novelty and the spatiotemporal scale of the manual actions.

77

78   In the earlier studies on manual asymmetries in non-human primates, terms such

79   as 'task complexity' and 'task demands' were used without ever being

80   comprehensively defined. For example, complexity of a reaching-for-food task was

81   measured in terms of the number of steps preceding the terminal act of reaching

82   for food, with almost no reference to the precision of movement in any of the

83   manual actions. This made it difficult to draw any conclusions with regard to the

84   forms and functions of manual asymmetries in non-human primates. Subsequently,

85   based on the perspective put forward by MacNeilage et al. [1987], while

86   simultaneously acknowledging the possibility that hand-usage patterns might vary

87   with novelty and the spatiotemporal scale of the manual actions, as indicated by

88   the previous studies on hand-usage patterns in non-human primates, Fagot and

89   Vauclair [1991] put forward the task complexity theory. The task complexity theory

90   proposes: (a) low-level tasks (i.e., tasks involving cognitively less demanding

91   actions that are practiced frequently) elicit symmetrical hand-usage patterns at the

92   level of the population and manual preferences at the level of an individual, not

93   necessarily indicative of any kind of specialization. (b) High-level tasks (i.e., tasks

94   involving cognitively more demanding manual actions that are practiced rarely)

95   elicit asymmetrical hand-usage patterns at the level of the population, likely to be

96   indicative of some kind of cognitive specialization. They also argued that

97   inconsistencies in directional biases arise owing to the diversity in the tasks used to

98   elicit manual asymmetries and the cognitive processes involved in solving them.

99   Overall, these two types of tasks, low-level and high-level, elicit two different types

100   of lateralization, hand preference and manual specialization.

101

102   Since the conception of the postural origins theory and the task complexity theory,

103   there have been a plethora of studies on manual asymmetries in non-human

104   primates with titles like "Laterality of hand functions in…," "Hand preferences in

105   different tasks in…," "Consistency of hand preference across low-level and high-level

106   tasks in…," "Hand preferences in unimanual and coordinated-bimanual tasks by…,"

107   "Posture and reaching in…," etc. These studies generally have not independently

108   considered the constraints consider by the task complexity theory and the postural

109   origins theory. The task complexity theory incorporates the physical constraints

110   imposed by tasks, whereas the postural origins theory incorporates the physical

111   constraints imposed by body postures. These different types of physical constraints,

112   however, may not necessarily elicit mutually consistent hand preferences. They

113   have focused essentially on hand preference (i.e., the relative incidence of the use

114   of either hand for responding) as the primary measure to assess manual

115   asymmetries, with almost no reference to the forms and functions. Moreover, they

116   have continually ignored several individual-specific traits, such as the feeding

117   ecology and niche structure, and task-specific characteristics, such as the

118   spatiotemporal requirements of the task, which might together influence hand-

119   usage patterns. In such a situation, conclusions drawn from studies incorporating

120   variable methodologies and task requirements, and not incorporating the

121   differences between individuals, populations, or species, are likely to be misleading.

122

123   During the course our study titled "Flexibility in food extraction techniques in urban

124   free-ranging bonnet macaques, *Macaca radiata* [Mangalam and Singh, 2013]," we

125   observed a peculiarity in the hand-usage patterns of the study individuals. The

126   hand used for the terminal act of reaching remained almost consistent irrespective

127   of the number of steps involved in the food extraction process. This, rather counter-

128   intuitive observation provoked us to carry out a systematic study on manual

129   asymmetries in bonnet macaques. Two consecutive studies [Mangalam et al. ,

130   2014a; Mangalam et al. , 2014b] revealed both the functional and the adaptive

131   significance of manual asymmetries respectively, and pointed towards the division

132   of labor as being the principle underlying the observed hand-usage patterns. In

133   contrast to the conventional ideas on manual asymmetries in non-human primates,

134   these observations demonstrated the specialization of the two hands for tasks

135   requiring maneuvering in three-dimensional space or those requiring physical

136   strength, as inferred by their consistent usage across a variety of spontaneous and

137   experimental tasks. Also, our task apparatus revealed some peculiarities in the

138   forms of manual asymmetries, which galvanized us to analyze the tasks used to

139   elicit manual asymmetries in the other studies. We thus decided to summarize our

140 analysis of these tasks and put forward our ideas on the division of labor in hand

141 usage in the present review article.

142

143 On the basis of our studies on manual asymmetries in bonnet macaques [Mangalam

144 et al. , 2014a; Mangalam et al. , 2014b], our review of studies on manual

145 asymmetries in capuchin monkeys, *Cebus* sp., and our analysis of the various tasks

146 used in these studies, we found that: (a) A consequence of the 'gold rush' like

147 hunch for human-like handedness in non-human primates has been that

148 researchers have been continually analyzing observations at the level of the

149 population, ignoring the analysis at the level of an individual and, consequently,

150 have potentially missed revelations on the forms and functions of manual

151 asymmetries. (b) These studies lack an a priori description of a cognitively

152 demanding and/or less-demanding manual action and the requirements of the task

153 in terms of the form (e.g., power or precision grip; see Napier [1956]) or function

154 (e.g., maneuvering in three-dimensional space and providing physical strength)

155 and, therefore, remain largely contextual. (c) In multi-step tasks, even when

156 requiring less precision, step(s) preceding the terminal act might not be a part of

157 the behavioral repertoire of an individual, a population, or a species, in which case,

158 inter-individual, -population, or -species comparisons of hand-usage patterns are

159 likely to be erroneous. Thus, in the present review, we emphasize the need to

160 explicitly study manual asymmetries in non-human primates with respect to the

161 forms and functions, and the associated adaptive value, propose the appropriate

162 experimental designs, and qualify the scope of inter-individual, -population, or –

163 species comparisons.

164

165   We review the studies on manual asymmetries in capuchin monkeys, *Cebus* spp.

166   and argue that the observed hand-usage patterns might reflect specialization of the

167   two hands for accomplishing tasks that require different dexterity types. To this

168   end, we do a step-by-step analysis of the various tasks used in the studies on

169   manual asymmetries in capuchin monkeys, wherein we: (a) analyze the different

170   manual tasks that have been used to study manual asymmetries in non-human

171   primates on the basis of the attributes such as the number of hands required to

172   solve a given task (i.e., unimanual, pseudo unimanual, or bimanual) and the

173   spatiotemporal progression of manual actions (i.e., sequential or concurrent). (b)

174   Determine the forms and functions of manual asymmetries that these tasks can

175   potentially elicit within the broader scope of the behavioral repertoire of an

176   individual, a population, or a species. (c) Qualify the scope of the inter-individual, -

177   population, or -species comparisons. We then describe the division of labor as a

178   general principle underlying manual asymmetries in non-human primates, and in

179   order to substantiate this possibility, propose experimental designs that would

180   elaborate the forms and functions of manual asymmetries in non-human primates,

181   and the associated adaptive value.

182

183   **Manual Asymmetry Paradigms**

184   Manual asymmetries did not first evolve in primates, but hemispheric specialization

185   preceded manual symmetries instead, or in other words, evolved as a by-product of

186   a more fundamental cerebral asymmetry affecting sensorimotor functioning

187   [Witelson, 1988]. Accordingly, tasks that are likely to challenge the differential

188   abilities of the two hemispheres are more likely to elicit manual asymmetries: hand

189   preference, that is, the preferential usage of one hand to perform a unimanual task

190   or to execute the most complex action while performing a bimanual task, or hand

191   performance, that is, differential performance of the two hands in solving the same

192   task [Fagot and Vauclair, 1991]. In the manual preference paradigm, repetitive

193   presentations of a given task produce individual scores of right- and left-hand uses.

194   These scores are then used to derive the strength and the bias of manual

195   lateralization. The strength is obtained in several statistical ways, all of which

196   basically calculate some index of the deviation from a random 50% hand usage

197   regardless of the hand preferred, wherein the bias refers to the direction of manual

198   preference (left or right). In the manual performance paradigm, on the basis of the

199   differential reaction time or accuracy of the two hands in solving the same task

200   individuals are classified as right- or left-handers when one hand performs better

201   on average than the other. Studies on manual asymmetries in non-human primates

202   make use of an array of spontaneous and experimental tasks to describe the two

203   kinds of manual asymmetries, which we attempt analyzing below.

204

205   **(i) Quadrupedal (Pseudo) Unimanual Reaching-For-Food Tasks**

206   Typically, quadrupedal (pseudo) unimanual reaching-for-food tasks involve reaching

207   for food placed on the ground, on a platform, tray or in a vessel accessible directly

208   [Fragaszy and Mitchell, 1990; Garber et al., 2008; Lilak and Phillips, 2008; Meunier

209   and Vauclair, 2007; Parr et al., 1996; Spinozzi et al., 1998; Westergaard et al.,

210   1997; Westergaard et al., 1998a; Westergaard and Suomi, 1993a], or through a

211   hole [Spinozzi et al., 2004; Westergaard et al. , 1998a], using one hand (here, we

212   use the word 'pseudo' before unimanual because the whole process of obtaining

213   food does involve both hands as there just cannot be any unimanual reaching-for-

214   food task for any quadrupedal individual).

215

216   An appropriate assessment of hand preference with regard to unimanual reaching-

217   for-food tasks has several underlying assumptions: (a) a subject is equally likely to

218   use any of its two hands, which is practically possible only when the subject is

219   acquiring either sitting or bipedal posture such that there are no ergonomic

220   constraints on the usage of any of the two hands. (b) Food is located exactly on the

221   sagittal plane of the body of the subject so that its spatial arrangement does not

222   influence hand preference (though this assumption is almost always met as there is

223   an equal probability of food being located towards the right and left of the sagittal

224   plane).

225

226   Whereas quadrupedal (pseudo) unimanual reaching-for-food tasks are assumed to

227   involve only one hand, they implicitly involve the other hand which is required to

228   passively maintain tripedal posture. This hand faces an increase in physical load

229   when the other hand is set free for prehension. Thus, one hand is used to maintain

230   tripedal posture and the other hand is used to maneuver in three-dimensional

231   space or to make precision grips, following the principle of division of labor. Also,

232   under experimental conditions, ergonomic constraints imposed by the possible

233   asymmetries in the body posture of an individual, together with or independent of

234   the preferential use of one hand for maintaining tripedal posture, is likely to

235   influence hand preference in quadrupedal (pseudo) unimanual reaching-for-food

236   tasks. However, studies on hand preference in capuchins have drawn conclusions

237   with regard to the effect of the complexity of the tasks on hand preference without

238   ever deploying a purely unimanual task independent of these influences.

239

240   **(ii) Bipedal (Pseudo) Unimanual Reaching-For-Food Task**

241   Typically, bipedal (pseudo) unimanual reaching-for-food tasks involve obtaining a

242   single piece of food placed on a high-rise platform, tray or in a vessel accessible

243   directly [Spinozzi et al. , 1998; Westergaard et al. , 1997; Westergaard et al. ,

244   1998a] or through a hole [Parr et al. , 1996; Westergaard et al. , 1998a], using one

245   hand (as in the case of the quadrupedal (pseudo) unimanual reaching-for-food

246   tasks, we use the word 'pseudo' before unimanual).

247

248   Bipedal (pseudo) unimanual reaching-for-food tasks can only be solved using both

249   hands and in no less than two or three steps: (P1) two-step process: step 1:

250   setting one hand, hand-1 (i.e., either left or right hand), free from maintaining

251   quadrupedal posture and using it to hold a high-rise structure (this action is

252   physically demanding as the body is lifted/pulled upwards) while maintaining

253   tripedal posture using the other hand, hand-2; step 2: setting the other hand,

254   hand-2, free from tripedal posture and using it to reach for food while maintaining

255   bipedal posture using the other hand, hand-1. (P2) Three-step process: step 1:

256   setting one hand, hand-1, free from maintaining quadrupedal posture and using it

257   to hold a high-rise structure (as mentioned above, this action is physically

258   demanding as the body is lifted/pulled upwards) while maintaining tripedal posture

259   using the other hand, hand-2; step 2: setting the other hand, hand-1, free from

260   tripedal posture and using it to hold the high-rise structure; step 3: using one hand,

261   (P1a) hand-1 (in which case the sequence is functionally similar to the previous

262   one) or (P2b) hand-2, to reach for food.

263

264   These sequences of manual actions involve both hands, following the principle of

265   division of labor, that is, one hand is used to perform the actions demanding

266   relatively more physical strength (e.g., lifting/pulling the body) and the other hand

267   is used to perform the actions demanding more sophistication (e.g., making

268   precision grips or maneuvering in three-dimensional space). However, studies on

269   hand preference in capuchins have almost never reported the stepwise usage of

270   the two hands for solving bipedal (pseudo) unimanual reaching-for-for-food tasks

271   as described above, restricting their data collection and analysis only to manual

272   actions that are directly associated with prehension. Comparative assessment of

273   hand preference in the quadrupedal and bipedal (pseudo) unimanual reaching-for-

274   food tasks, as reported by Spinozzi et al. [1998] and Westergaard et al. [1997,

275   1998], demonstrates that capuchins consistently use one hand for prehension in

276   both types of tasks, which is possible only while following either the two-step

277   process (i.e., P1) or the second of the three-step processes (i.e., P2b) for solving

278   bipedal (pseudo) unimanual reaching-for-food tasks.

279

(iii) Quadrupedal/Bipedal Coordinated Bimanual Task

281 Typically, solving a coordinated bimanual task involves obtaining food from ∼ 10 to

282 15 cm long and ∼ 3 to 5 cm wide transparent/opaque tube [Lilak and Phillips,

283 2008; Meunier and Vauclair, 2007; Spinozzi et al. , 1998; Spinozzi et al., 2007;

284 Westergaard and Suomi, 1998]. An individual that is assuming a quadrupedal

285 position can solve the task in two or three steps: (P1) step 1: picking up the tube

286 with one hand, hand-1, while maintaining tripedal posture with the other hand,

287 hand-2; step 2: attaining bipedal posture by freeing hand-2 and extracting the food

288 from the tube with the same hand. (P2) step 1: picking up the tube with one hand,

289 hand-1, while maintaining tripedal posture with the other hand, hand-2; step 2:

290 attaining bipedal posture by freeing hand-2, and shifting the tube from hand-1 to

291 hand-2; step 3: extracting the food with hand-1. Thus, it needs to be determined

292 whether an individual continued holding the tube with the same hand or shifted it to

293 the other hand. In case of the shift the observed hand-usage pattern can be

294 explained using the principle of the division of labor (as described by Mangalam et

295 al. [2014a]); and in the other case as well as when an individual is assuming a

296 bipedal posture while picking up the tube, sequential planning of motor actions.

297 However, studies do not analyze manual asymmetries in solving coordinated

298 bimanual tube task from this perspective and, therefore, present only a partial

299 picture.

300

301 **(iv) Sequential Unimanual/Bimanual versus Concurrent Bimanual Tasks**

302 Typically, solving a box task involves obtaining a single piece of food placed on a

303 tray inside a clear plexiglass box. The box can be opened by lifting its lid that is

304 hinged to one of its walls. There are two different versions of the box task. In one

305 version, the lid may remain open once it is lifted beyond a point [Lilak and Phillips,

306 2008; Spinozzi and Truppa, 2002], in which case the task can be solved in either 2

307 steps: lifting the lid and reaching for food, in a sequential unimanual/bimanual

308 manner (L-L/R-R, L-R/R-L, B-L/B-R); or 3 steps: lifting the lid, holding the lid up,

309 and reaching for food, in a concurrent bimanual manner (L-RL/R-LR, L-LR/R-RL, B-

310 LR/B-RL). In another version, the box includes a stop screw on the back of the lid

311 which causes the lid to fall shut if it is not held open [Lilak and Phillips, 2008;

312 Spinozzi and Truppa, 2002], in which case the task can be solved only in 3 steps:

313 lifting the lid, holding the lid up, and reaching for food, in a concurrent bimanual

314 manner (L-RL/R-LR, L-LR/R-RL, B-LR/B-RL; in the latter two cases, the sequence is

315 functionally similar to the previous one).

316

317 Spinozzi and Truppa [2002] did an assessment of hand preference in 23 tufted

318 capuchins using the box tasks. While solving the sequential unimanual/bimanual

319 box task, the capuchins indiscriminately (in 48.8% and 36.9% trials) used the

320 strategies involving no differentiation (L-L/R-R, i.e., lifting the lid and reaching for

321 food with the same hand), and differentiation of roles for the two hands (L-R/R-L,

322 i.e., lifting the lid with one hand and reaching for food with the other hand); and

323   while solving the concurrent bimanual version of the task, the capuchins

324   predominantly (in 73.4% trials) used the strategy involving complete differentiation

325   of roles for the two hands (L-LR/R-RL, i.e., lifting the lid and holding it up with the

326   same hand, while simultaneously reaching for food with the other hand) more often

327   than the other two possible strategies (L-RL/R-LR and B-LR/B-RL). In a nutshell,

328   the capuchins did not show any difference in the direction and strength of hand

329   preference for prehension between the sequential unimanual/bimanual and

330   concurrent bimanual versions of the box task, demonstrating the similarity between

331   them.

332

333   This example demonstrates that sequential unimanual/bimanual and concurrent

334   bimanual box tasks elicit similar direction and strength of hand preference. This

335   also holds true for several other tasks as described above. In fact, a general

336   principle involving partial/complete differentiation of roles for the two hands is likely

337   to underlie manual asymmetries and, therefore, sequential unimanual/bimanual

338   and concurrent bimanual tasks should not be treated differently.

339

340   **(v) Haptic Search Tasks**

341   Typically, solving a haptic search task involves obtaining food mixed with some

342   non-edible material [Parr et al. , 1996; Spinozzi and Cacchiarelli, 2000] or placed in

343   the crevices on the surface of variably shaped objects [Lacreuse, 1999; Lacreuse

344   and Fragaszy, 1996; Lacreuse and Fragaszy, 1997] from the inside of an opaque

345   box (~ 15 to 30 cm X 15 to 30 cm X 15 to 30 cm) through a small opening

346   (diameter < 5 cm; these dimensions allow inserting only one hand at a time).

347   Haptic discrimination has been found to be more difficult that visual discrimination

348   in non-human primates (see, for example, Wilson [1965] in rhesus macaques),

349   perhaps because haptic perception without visual guidance is uncommon in natural

350   settings. Thus, haptic judgments are likely to be novel and consequently,

351   cognitively more demanding as compared to visually guided judgments. Studies on

352   manual asymmetries therefore make use of haptic search tasks to differentially

353   challenge the perceptual motor abilities of the hands, which are likely to be affected

354   by functional differences between the left and right hemispheres. However, studies

355   do not compare hand-usage patterns between haptic and visually guided reaching

356   (though Spinozzi and Cacchiarelli [2000] and Lacreuse [1999] stand out as an

357   exception), rather just describe manual asymmetries in haptic search tasks; this

358   hardy reveals something substantial as studying haptic judgments in isolation from

359   visually guided judgments, fail to resolve manual asymmetries stemming from the

360   absence of the visual cues alone.

361

362   **(vi) Probing/Tool-Using Tasks**

363   Typically, solving a (pseudo) unimanual probing task involves manipulating a

364   wooden dowel inserted into a small hole in a clear Plexiglas box in order to displace

365   a food reward off a shelf where it could be retrieved manually [Garber et al. ,

366   2008], using a stick to obtain food material present inside a vessel with a narrow

367   opening while maintaining a tripedal posture [Anderson et al., 1996; Westergaard

368   et al. , 1998a; Westergaard et al., 1998b; Westergaard and Suomi, 1994a;

369   Westergaard and Suomi, 1994b] (another version may involve using a sponge

370   [Westergaard and Suomi, 1993a]) or a bipedal posture [Lilak and Phillips, 2008;

371   Westergaard, 1991; Westergaard et al. , 1998a]; another tool-using task is nut-

372   cracking that involves coordinated bimanual handling of stones to crack nuts

373   [Westergaard and Suomi, 1993b; Westergaard and Suomi, 1996]. It is important to

374   note here that the above probing/tool-using tasks are similar in terms of the

375   number of hands required to solve the task (i.e., unimanual, pseudo unimanual, or

376   bimanual) and the spatiotemporal progression of manual actions (i.e., sequential or

377   concurrent) except for the fact that they involve an extension of the body,

378   controlling which requires finer finger adjustments through response-produced

379   feedback. Thus, functionally similar to simple reaching-for-food tasks, probing/tool-

380   using tasks are likely to prove helpful only if the form of manual asymmetries (i.e.,

381   with respect to grip type) is considered.

382

383   **(vii) Spontaneous Tasks**

384   Hand-usage patterns in tasks such as grooming [Fragaszy and Mitchell, 1990],

385   maternal cradling and infant positioning [Hopkins, 2004; Panger and Wolfe, 2000;

386   Westergaard et al., 1999]are more likely to be influenced by the specialization of

387   the two hands for more common activities such as feeding than these tasks

388   themselves. For example, a female capuchin which has its left hand specialized for

389   fine finer adjustments or maneuvering in three dimensional space and its right hand

390   specialized for physical support is more likely to use its right hand for maternal

391   cradling and infant positioning just to keep its left hand free for the usual feeding

392   activities (as they require more sophisticated manual actions). However, studies

393   merely describe the hand used for these activities without considering the forms

394   and functions of the associated manual asymmetries.

395

396   **Forms and Functions of Manual Asymmetries**

397   The corticomotoneuronal connections innervating the hands regulate the timing and

398   precision of the muscular forces required for fine finger adjustments through

399   response-produced feedback (see, for example, Porter [1985]). It follows from this

400   fact that actions with finer sequential finger movements are more likely to elicit

401   manual asymmetries than simpler actions, as Elliott and Chua [1996] proposed in

402   humans (also see Healey et al. [1986], Steenhuis [1996], and Steenhuis and

403   Bryden [1989]). There exists a possibility that lateral asymmetry in the number of

404   corticomotoneuronal connections innervating the hands govern the forms and

405   functions of manual asymmetries: the hand with lesser corticomotoneuronal

406   connections is specialized for manual operations that primarily involve physical

407   strength or those that require power grips, and the hand with greater

408   corticomotoneuronal connections is specialized for manual actions that involve

409   maneuvering in three-dimensional space or those that require precision grips (see

410   Mangalam et al. [2014b]). A step-by-step analysis of any of the above tasks

411   reveals sequential or concurrent fundamental manual actions. These fundamental

412   manual actions can then be classified in terms of the form into either the power or

413   precision grip, or in terms of the function into either 'maneuvering in three

414   dimensional space or providing physical strength.

415

416 **Inter-Individual, -Population, or -Species Comparisons**

417 Some intermediate step(s) involved in solving a multi-step task might not be a part

418 of the behavioral repertoire of an individual, a population, or a species.

419 Consequently, the perceived complexity of a task might vary across individuals,

420 populations, or species, making inter-individual, -population, or -species

421 comparisons of hand preferences across complex tasks erroneous. Diversity in

422 factors causing spatiotemporal inter-individual, -population, or -species variations

423 in manual actions may also influence hand-usage patterns at multiple levels of

424 organization. For example, Sfar et al. [2014] did a comparative assessment of hand

425 preference in red howlers, *Alouatta seniculus* and yellow-breasted capuchins,

426 *Sapajus xanthosternos*: the red howlers, which habitually use the mouth to obtain

427 food, selectively took part in the reaching-for-food tasks and also exhibited stronger

428 hand preferences than the yellow-breasted capuchins in the tasks that were

429 relatively simple to solve. However, differences in the strength of hand preference

430 diminished with the increasing complexity of the reaching-for-food tasks, that is,

431 the relatively more complex tasks were perceived as equally complex by both the

432 red howlers and the yellow-breasted capuchins. Both these observations

433 demonstrate that the feeding ecology and niche structure influence hand-usage

434 patterns, bringing about the differences in hand preference out of the contingent

435 nature of the complexity of a task. Thus, manual asymmetries in non-human

436 primates should be investigated not just in isolation, but within the broader scope

437 of the behavioral repertoire of an individual, a population, or a species.

438

439 **Division of Labor as a General Principle**

440 Our experience with studies on hand-usage patterns in bonnet macaques

441 [Mangalam et al. , 2014a; Mangalam et al. , 2014b; Sfar et al. , 2014], our review

442 of studies on hand-usage patterns in capuchins, and our analysis of various tasks

443 used in these studies, collectively suggest that 'division of labor' is a general

444 principle underlying manual asymmetries in non-human primates. In order to

445 substantiate this possibility, we propose that:

446

447 **(i) Division of Labor in Hand Usage Is Likely to Be Prominently Visible in**

448 **Transitions between Tasks with Variable Requirements**

449 Individuals may have to make transitions between tasks with variable requirements

450 and depending on these, vary hand usage. Suppose, for example, an individual that

451 preferentially uses the left hand to make power grips and the right hand to make

452 precision grips is solving a reaching-for-food task that involves obtaining food items

453 from a portable container (e.g., a water bottle); the individual holds the container

454 in the left hand and retrieves the food items with the right hand. A conspecific then

455 approaches this focal individual and so it moves with the bottle to some other

456 location, say to a nearby high-rise platform, or to a distant branch. There can be

457 two ways an individual can do that: (a) by holding the bottle in the left hand and

458 climbing with the right hand or (b) by shifting the bottle to the right hand, setting

459 the left hand free, and climbing with the left hand. If one hand is specialized for

460 manual operations that require power grips and the other hand is specialized for

461 manual operations that require precision grips, or alternatively for maneuvering in

462 three-dimensional space and providing physical strength, the second way seems

463 more plausible (see Mangalam et al. [2014b] for another such example). So, if the

464   transition involves tasks with variable requirements, division of labor becomes

465   evident. We propose an experimental design to observe the division of labor in

466   hand usage based on task demands. One should examine hand preference across

467   situations synonymous to that in the above example. Stringent changes in hand-

468   usage patterns while shifting contexts would demonstrate division of labor in hand

469   usage.

470

471   **(ii) Division of Labor in Hand Usage Is Likely to Be Visible and Understood**

472   **in Tasks with Differential Requirements**

473   Napier [1956] described prehensile functions of the human hand, such as grasping

474   and gripping: an object can be grasped/gripped by either holding it in a clamp

475   formed by partly flexed fingers and palm, while applying a counter pressure by the

476   thumb lying more or less in plane of the palm–the 'power' grip, or pinching it

477   between the flexor aspects of the fingers and the opposing thumb–the 'precision'

478   grip. Performing certain manual operations primarily requires power and precision

479   plays a secondary role, whereas performing certain other manual operations

480   primarily requires precision and power plays a secondary role. And this task-specific

481   requirement of power and precision grip is likely to influence hand-usage patterns

482   in a given manual operation. In New World monkey species, the typical hinge-

483   shaped joint of the thumb at the base of the palm allows abduction/adduction and

484   flexion/extension movements, but not rotational movement, the key factor in

485   opposability [Napier and Napier, 1967]. For a long time it was thus held, that no

486   New World monkey species could grasp objects with precision [Bishop, 1964;

487   Napier, 1993; Napier and Napier, 1967]. However, comparative behavioral studies

488   demonstrated that capuchins stand out from other platyrrhine species because of

489   their (a) high degree of manual dexterity [Fragaszy, 1986; Lacreuse and Fragaszy,

490   1996; Panger, 1988], (b) frequent use of precision grips that mainly involve lateral

491   aspects of digits for picking up small objects [Christel and Fragaszy, 2000; Costello

492   and Fragaszy, 1988; Spinozzi et al. , 2004], and (c) capacity to perform relatively

493   independent movements of the digits [Christel and Fragaszy, 2000; Costello and

494   Fragaszy, 1988].

495

496   Anatomical and physiological features of the neural substrate that control manual

497   actions might explain the high manual dexterity in capuchins. Capuchins can act out

498   highly fractionated movements of the fingers/digits owing to the large number and

499   extension of the corticomotoneuronal connections that innervate the hand

500   [Kuypers, 1981; Lemon, 1993; Muir and Lemon, 1983; Shinoda et al., 1981], as

501   observed in humans and chimpanzees [Bortoff and Strick, 1993]. Moreover, studies

502   reported that the individuals that preferentially used the right hand to reach for

503   food in a concurrent bimanual tube task, exhibited a greater leftward bias of the

504   anterior cerebellum [Phillips and Hopkins, 2007], and had a shallower central sulcus

505   [Phillips and Sherwood, 2005] as well as a smaller overall corpus callosum in the

506   contralateral hemisphere [Phillips et al., 2007], compared to those that

507   preferentially used the left hand or did not show hand preference; although there

508   was no difference in the size of the left-frontal petalia between the two [Phillips and

509   Sherwood, 2007].

510

511 A few studies investigated manual asymmetries with respect to the control and

512 movement of the fingers/digits in capuchins. Christel and Fragaszy [2000] reported

513 that the individuals did not exhibit considerable patterns in hand preference or hand

514 performance with respect to the power or precision grips used to grasp currants

515 and grapes lying on a tray. Spinozzi et al. [2004] reported that the individuals

516 preferentially used one hand to grasp a food item fixed on a tray, and did not show

517 any difference in performance with respect to the power or precision grips, but

518 extracted the food faster with the preferred hand than the non-preferred hand with

519 respect to the precision grips (and not with respect to the power grips). Spinozzi et

520 al. [2007] reported that the individuals preferentially used one hand to retrieve a

521 raisin from a transparent hollow tube fixed horizontally to the upper end of a

522 vertical metal bar, and extracted the food faster with the preferred hand than the

523 other hand. Whereas these findings indicate that precise control/movement of the

524 fingers/digits are more likely to elicit manual asymmetries than the imprecise ones,

525 there are problems with the experimental setups.

526

527 If, suppose, one hand is specialized for manual operations that primarily involve

528 physical strength and, therefore, require power grips, and the other hand is

529 specialized for those that involve maneuvering in three-dimensional space and,

530 therefore, require precision grips, a manual operation that primarily requires either

531 one or the other of the two forms and functions of the hand is likely to influence

532 hand-usage patterns with respect to a particular type of grip as well as grip-

533 formation patterns with respect to a particular hand. The three studies–Christel and

534 Fragaszy [2000], Spinozzi et al. [2004], and Spinozzi et al. [2007]–employ

535 reaching-for-food tasks that primarily involve maneuvering in three-dimensional

536 space and, therefore, require precision grip. This is likely to be the reason why

537 Christel and Fragaszy [2000] did not find manual asymmetries with respect to the

538 types of grips and Spinozzi et al. [2004] did not find a difference in performance

539 between the two hands with respect to the power grips, presenting a distorted and

540 partial picture of manual asymmetries.

541

542 We propose an experimental design to unambiguously determining the forms and

543 functions of manual asymmetries in non-human primates. One should examine

544 hand preference in a concurrent, bimanual reaching-for-food task. In one scenario,

545 the manual operations should require a power grip followed by a precision grip; in

546 another scenario, the manual operations should require a precision grip followed by

547 a power grip. Contrasting hand-usage patterns in these two scenarios would

548 indicate that the individuals preferentially used the two hands depending on the

549 requirements of the tasks, that is, one hand to perform the manual operations

550 involving maneuvering in three-dimensional space and the other hand to perform

551 those involving physical strength. One should then examine hand performance with

552 regard to the requirements of the tasks in a concurrent, bimanual hand-

553 performance-differentiation task. In one scenario, this task should ergonomically

554 force the usage of either the left or the right hand to perform a manual operation

555 requiring either a power grip or a precision grip; in another scenario, this task

556 should ergonomically force the usage of either the left or the right hand to perform

557 a manual operation requiring a precision grip and the other hand to perform the

558 one requiring a power grip. A more effective and/or efficient power grip in one

559   scenario and a precision grip in the other scenario would indicate that the

560   individuals used the two hands depending on the specializations, that is, difference

561   in the manual dexterity of the two hands.

562

(iii) Division of Labor in Hand Usage Is Likely to Improve Hand Performance in Terms of the Efficiency of the Power and Precision Grips

Manual asymmetries might have ecological disadvantages as they can potentially make an individual vulnerable to attack/defend appropriately only when the prey/predator is present on a particular side. Also, as the stimuli are randomly located with respect to the sagittal plane of an individual, i.e., towards left or towards right, it might make it difficult to solve a particular task. However, manual asymmetries are likely to help increasing manual specialization, the benefits of which surpass the associated ecological disadvantages (reviewed by Vallortigara and Rogers [2005]). Trehub [1983] drew a distinction between mere hand preference and manual specialization by exemplifying human infants who exhibit manual specialization and not hand preference (this idea was carried forward by Fagot and Vauclair [1991] in non-human primates). According to Trehub [1983], hand preference refers to the consistent usage of one hand to solve familiar, relatively simple, and highly practiced tasks, and may not be necessarily accompanied by an improvement in hand performance; whereas manual specialization refers to the consistent usage of one hand to solve novel, relatively complex, and not-practiced tasks that require peculiar action patterns, and is necessarily accompanied by an improvement in hand performance. Trehub [1983] also described that individuals generally exhibit manual specialization only in the context of tasks that involve cognitively demanding manual actions (see, for example, Mangalam et al. [2014b] that showed manual specialization in bonnet macaques in tasks requiring peculiar action patterns viz., in terms of tasks that

586   require either higher maneuvering dexterity or higher physical strength). Thus,

587   there exists a marked difference between hand preference and manual

588   specialization in terms of the resulting difference in performance of the two hands,

589   evidently visible while considering the forms and functions of manual asymmetries,

590   as described in the previous section.

591

592   Only one study examined the relationship between strength of hand preference and

593   the corresponding hand performance in capuchins. Fragaszy and Mitchell [1990]

594   reported that the individuals exhibited a weak, but statistically non-significant,

595   positive relationship between strength of hand preference and the corresponding

596   hand performance in the (pseudo) unimanual and bimanual versions of the box

597   task. However, Fragaszy and Mitchell [1990] acknowledged that the strength of

598   hand preference could have affected the timing of the hand movements, thereby

599   affecting the relationship between strength of hand preference and the

600   corresponding hand performance. A similar study in another non-human primate

601   species–the bonnet macaque, Mangalam et al. [2014a], reported a negative

602   relationship between (a) hand performance of the preferred hand and the difference

603   in hand performance between the two hands in a hand-performance-differentiation

604   task, and (b) difference in hand performance between the two hands and the

605   difference in the strength of hand preference in another (pseudo) unimanual and

606   bimanual versions of the box task in bonnet macaques. These findings indicate that

607   a greater strength of hand preference is associated with a higher difference in the

608   performance of the two hands. However, research lacks sufficient evidence

609   supporting the hypothesis that hand preference, or better yet, division of labor in

610   hand usage improves hand performance in terms of the time and/or energy

611   required to perform a given task.

612

613   We propose an experimental design to determine the adaptive value of hand

614   preference. One should examine hand preference in a (pseudo) unimanual

615   reaching-for-food task (wherein, the manual operation should require either a

616   power grip or a precision grip) and a concurrent, bimanual reaching-for-food task

617   (wherein, the manual operations should require a power grip with one hand

618   followed by a precision grip with the other hand, or a precision grip with one hand

619   followed by a power grip with the other hand). One should then examine hand

620   performance in a hand-performance-differentiation task that should ergonomically

621   force the usage of either the left or the right hand to perform a manual operation

622   requiring either a power grip or a precision grip, thus allowing to measure hand

623   performance independent of ceiling effects as this task is unlikely to elicit, or better

624   yet, prime any motor actions associated with the opposite hand). A positive

625   relationship between (a) hand performance of the hand with higher performance in

626   the hand-performance-differentiation task and normalized difference in hand

627   performance for the two hands, and (b) difference in hand performance for the two

628   hands in the hand-performance-differentiation task and difference in strength of

629   hand preference in the (pseudo) unimanual and bimanual reaching-for-food tasks,

630   with respect to the power grips, the precision grips, or both, would indicate that the

631   division of labor in hand usage improves hand performance.

632

633 **Conclusions**

634 Studies have investigated the evolutionary origin of hand-preference in non-human

635 primates. A careful analysis points towards the division of labor as being a general

636 principle underlying manual asymmetries. This principle is based on the difference

637 in the intrinsic requirements of the tasks, which can be broadly divided into

638 maneuvering in three-dimensional space and providing physical support, acquiring

639 power and precision grips respectively. Our review of studies on hand-usage

640 patterns in non-human primates reveals conceptual and logistic problems with the

641 spontaneous and experimental tasks used to determine hand-usage patterns;

642 moreover, methodology differs and confounding variables are often not

643 appropriately addressed. We suggest that studies on manual asymmetries in non-

644 human primates should design experiments that do not undermine this possibility.

645 As far as the adaptive value of manual asymmetries are concerned, we suggest

646 that, to obtain more unambiguous answers, studies should be conducted with

647 experimental designs that allow comparing hand-usage patterns across species that

648 vary in their phylogenetic relatedness and/or ecology, over a range of spontaneous

649 activities and experimental tasks. It might be useful to study manual preferences

650 not just in isolation, but within the broader scope of the behavioral repertoire of the

651 species. Also, it might be advantageous to study the ontogeny of manual

652 preferences. Studies of these kinds may help to understand the forms and functions

653 of manual asymmetries, and the potential selection pressures under which manual

654 asymmetries are likely to appear and evolve.

655

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