

1 **Title**

2 Division of Labor: A Democratic Approach to Understanding Manual Asymmetries in
3 Non-Human Primates

4

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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.

41 **Keywords:** capuchin monkey; *Cebus* sp.; hand performance; hand preference;
42 laterality; manual asymmetry; manual specialization

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-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

280 **(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 than 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 hardly 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 tripod 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

563 **(iii) Division of Labor in Hand Usage Is Likely to Improve Hand**

564 **Performance in Terms of the Efficiency of the Power and Precision Grips**

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