

1 **Title**

2 Division of Labor in Hand Usage Is Associated with Higher Hand Performance in  
3 Free-Ranging Bonnet Macaques, *Macaca radiata*

4

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15

16 **Abstract**

17 A practical approach to understanding lateral asymmetries in body, brain, and  
18 cognition would be to examine the performance advantages/disadvantages  
19 associated with the corresponding functions and behavior. In the present study,  
20 we examined whether the division of labor in hand usage, marked by the  
21 preferential usage of the two hands across manual operations requiring  
22 maneuvering in three-dimensional space (e.g., reaching for food, grooming, and  
23 hitting an opponent) and those requiring physical strength (e.g., climbing), is  
24 associated with higher hand performance in free-ranging bonnet macaques,  
25 *Macaca radiata*. We determined the extent to which the macaques exhibit  
26 laterality in hand usage in an experimental unimanual and a bimanual food-

27 reaching task, and the extent to which manual laterality is associated with hand  
28 performance in an experimental hand-performance-differentiation task. We  
29 observed negative relationships between (a) the latency in food extraction by  
30 the preferred hand in the hand-performance-differentiation task (wherein, lower  
31 latency implies higher performance), the preferred hand determined using the  
32 bimanual food-reaching task, and the normalized difference between the  
33 performance of the two hands, and (b) the normalized difference between the  
34 performance of the two hands and the absolute difference between the laterality  
35 in hand usage in the unimanual and the bimanual food-reaching tasks (wherein,  
36 lesser difference implies higher manual specialization). Collectively, these  
37 observations demonstrate that the division of labor between the two hands is  
38 associated with higher hand performance.

39

## 40 **Introduction**

41 Lateral asymmetries in body, brain, and cognition are almost ubiquitous among  
42 biological organisms [1-3]. An adaptationist would advocate that these  
43 asymmetries were evolutionarily selected because no bilateral organism can  
44 maneuver in three-dimensional space unless one side becomes dominant and  
45 always takes the lead [4]. Which side would become dominant, however, is  
46 beyond the scope of this hypothesis as there is no advantage or disadvantage  
47 evidently associated with either the left or the right side (see Glezer [5], an  
48 open-peer commentary on MacNeilage et al. [6]). Among all, manual  
49 asymmetries are a central theme of investigation because they are likely to have  
50 shaped primate evolution [7]. Manual asymmetries can manifest into (a) hand  
51 preference, that is, one hand majorly used while solving a unimanual task  
52 (which requires only one hand) or the hand used to execute the most complex

53 action while solving a bimanual task (which requires both hands); (b) hand  
54 performance, that is, one hand used to execute actions more efficiently.  
55 Fagot and Vauclair [8] reviewed studies on individual- and population-level  
56 manual asymmetries among nonhuman primates and proposed the 'task  
57 complexity' theory which states that the extent of manual asymmetry increases  
58 with the complexity of the task (here, the complexity is defined by the  
59 spatiotemporal progression of the movements, i.e., coarse versus fine).  
60 Observations on several nonhuman primate species are consistent with the task  
61 complexity theory. For example, the relatively more complex bimanual food-  
62 reaching tasks have been found to elicit greater manual asymmetries than the  
63 unimanual versions of the same tasks in capuchin monkeys, *Sapajus* spp. [9,10]  
64 and *Cebus capucinus* [11], and chimpanzees, *Pan troglodytes* [12].  
65  
66 Besides exhibiting hand preference and hand performance, several nonhuman  
67 primates have been found to exhibit manual specialization, that is, they  
68 preferentially use either the left or the right hand while solving some specific  
69 types of tasks. For example, while feeding arboreally, captive sifakas,  
70 *Propithecus* spp. preferentially used one hand to maintain postural support and  
71 the other hand to pluck leaves [13]. While extracting peanut butter from a PVC  
72 tube, wild Sichuan snub-nosed monkeys, *Rhinopithecus roxellana* [14], captive  
73 tufted capuchin monkeys [15], olive baboons, *Papio anubis* [16], and  
74 chimpanzees [17] preferentially used one hand to hold the tube and the other  
75 hand to extract the peanut butter. While foraging for food scattered on the  
76 ground, captive gorillas, *Gorilla gorilla* [18] and chimpanzees [19] preferentially  
77 used one hand to take the food items towards the mouth, and the other hand to  
78 hold the remaining ones. While extracting peanuts from a lidded box captive

79 tufted capuchin monkeys consistently used one hand to open the lid of the box  
80 and the other hand to reach for them [20]. While allogrooming, wild Sichuan  
81 snub-nosed monkeys [21] and both captive and wild chimpanzees [22]  
82 preferentially used one hand to hold the skin, and the other hand to remove dirt  
83 and ectoparasites. Mangalam et al. [23] argued that these observations might  
84 reflect specialization of the two hands for manual actions requiring different  
85 dexterity types (i.e., simple/complex hand movements in three-dimensional  
86 space, grasping, supporting the body, etc.), and along similar lines described  
87 division of labor in hand usage in free-ranging bonnet macaques, *Macaca*  
88 *radiata*. The macaques preferentially used the 'preferred' hand for manual  
89 actions requiring maneuvering in three-dimensional space (reaching for food,  
90 grooming, and hitting an opponent), and the 'nonpreferred' hand for those  
91 requiring physical strength (climbing). In a hand-performance-differentiation  
92 task that ergonomically forced the usage of one particular hand, the macaques  
93 extracted food faster with the maneuvering hand compared to the supporting  
94 hand, demonstrating the higher maneuvering dexterity of the maneuvering  
95 hand. However, whether such division of labor in hand usage improves hand  
96 performance in terms of the time and/or energy required to solve a given task  
97 remains unexplored.

98

99 In the present study, we examined whether the division of labor in hand usage,  
100 as described by Mangalam et al. [23], is associated with higher hand  
101 performance in free-ranging bonnet macaques, *Macaca radiata*. To this end, we  
102 determined the extent to which the macaques exhibit laterality in hand usage in  
103 two experimental unimanual and a bimanual food-reaching task, and the extent  
104 to which manual laterality is associated with hand performance in an

105 experimental hand-performance-differentiation task. If the division of labor  
106 between the two hands is associated with higher hand performance, we would  
107 expect negative correlations between (a) the latency in food extraction by the  
108 preferred hand in the hand-performance-differentiation task and the normalized  
109 difference between the performance of the two hands, which would imply that  
110 the macaques that show a greater difference in the performance of the two  
111 hands perform better than those that exhibit a smaller difference; and (b) the  
112 normalized difference between the performance of the two hands and the  
113 absolute difference between the laterality in hand usage in the unimanual and  
114 the bimanual food-reaching tasks, which would imply that the macaques that  
115 exhibit a higher manual specialization show a greater difference in the  
116 performance of the two hands.

117

## 118 **Methods**

### 119 Subjects and Study Site

120 The subjects were 16 free-ranging bonnet macaques: 2 adult males – AM1 and  
121 AM2, 1 subadult male – SM1, 4 juvenile males – JM1, JM2, JM3, and JM4, 8  
122 adult females – AF1, AF2, AF3, AF4, AF5, AF6, AF7, and AF8, and 1 juvenile  
123 female – JF1 (see Table 1), inhabiting the Chamundi Hill range in Mysore, India  
124 (GPS coordinates: 2°14'41"N 76°40'55"E) (Mangalam et al. [23] referred to AF5  
125 as JF1, AF6 as JF2, AF7 as JF3, AF8 as JF4, and JF1 as JF5).

126

### 127 Ethics Statement

128 We adhered to the American Society of Primatologists (ASP) "Principles for the  
129 Ethical Treatment of Nonhuman Primates" and conducted the present study as a  
130 part of an ongoing research project that was approved by the Institutional

131 Animal Ethics Committee (IAEC) at the University of Mysore (because we  
132 conducted our research on individuals which (a) did not belong to an endangered  
133 or a protected species, and (b) inhabited an unprotected land with an  
134 unrestricted public access, our research work did not require permission from  
135 any other authority).

136

#### 137 Experimental Procedure

138 We presented the macaques with 3 sets of 7 consecutive trials, that is, 21 trials,  
139 of experimental unimanual and bimanual food-reaching tasks. Solving the  
140 unimanual task required obtaining a grape from an unlidded wire mesh box  
141 (dimensions: 7.5 cm X 7.5 cm X 17.5 cm; these dimensions allowed the usage  
142 of only one particular hand at a time) fixed on a wooden platform (dimensions:  
143 90 cm X 60 cm) with one hand (Fig. 1A; Movie S1), whereas solving the  
144 bimanual task required opening and supporting the lid of a lidded wire mesh box  
145 with one hand and obtaining a grape with the other hand (Fig. 1B; Movie S2).  
146 We placed the task apparatus on the ground within ca. 1 m from the focal  
147 macaque when no conspecific was present within ca. 3 m from it and observed  
148 the corresponding hand usage.

149

150 **Figure 1. Apparatuses for the unimanual food-reaching task (a), the**  
151 **bimanual food-reaching task (b), and the hand-performance-**  
152 **differentiation task (c).** Reproduced, with permission from Wiley Periodicals,  
153 Inc., from Mangalam et al. [23] © 2013 Wiley Periodicals, Inc.

154

155 We then presented the macaques with a single trial of an experimental hand-  
156 performance-differentiation task that forced the usage of either the left or the

157 right hand. Solving this task required obtaining grapes from the wire mesh  
158 boxes attached towards the bottom on the either lateral extremities of a wooden  
159 platform (dimensions: 90 cm X 60 cm); this setup ergonomically forced the  
160 macaques to use either the left or the right hand (Fig. 1C; Movie S3). We put 7  
161 grapes in one of the boxes, placed the task apparatus on the ground when no  
162 conspecific was present within ca. 3 m from the focal macaque, and video  
163 recorded the corresponding extraction behavior. We then repeated the same  
164 procedure, but this time by putting the grapes in the other box. The macaques  
165 mostly took 4 to 7 bouts to take all 7 grapes out of the box. We analyzed the  
166 obtained videos frame-by-frame to determine the average latency in food  
167 extraction for all the bouts (each bout measured from when the hand entered  
168 the box to when it exited) to the nearest 0.04 s.

169

170 For each macaque, we determined the handedness index (HI) values for taking  
171 the food out of the wire mesh box in the unimanual and the bimanual food-  
172 reaching tasks, using the formula:  $HI = (R - L)/(R + L)$  (where 'R' and 'L'  
173 represent the frequency of usage of the right and the left hand respectively).  
174 The obtained HI values could range from - 1 to + 1, with positive values  
175 indicating a bias towards the right-hand use and negative values indicating a  
176 bias towards the left-hand use, and the absolute HI values indicating the  
177 strength of the bias. We then determined the absolute difference between the  
178 laterality in hand usage in the unimanual and the bimanual food-reaching tasks  
179 (lesser difference = higher manual specialization), using the formula = abs.  
180 ( $HI_{Bimanual} - HI_{Unimanual}$ ). We determined the hand majorly used for taking the food  
181 out of the box in the bimanual food-reaching task, which we referred to as the  
182 'preferred hand,' and the opposite hand, which we referred to as the

183 'nonpreferred hand' (previously, in Mangalam et al. [23], we referred to these as  
184 the 'maneuvering' and the 'supporting' hand respectively). Moreover, we  
185 determined the laterality in hand performance (LHP) in the hand-performance-  
186 differentiation task, using the formula:  $LHP = (\text{latency in food extraction using}$   
187  $\text{the nonpreferred hand} - \text{latency in food extraction using the preferred hand}) /$   
188  $(\text{latency in food extraction using the nonpreferred hand} + \text{latency in food}$   
189  $\text{extraction using the preferred hand})$ . The obtained LHP values could range from  
190  $- 1$  to  $+ 1$ , indicating the normalized difference in the performance between the  
191 two hands.

192

### 193 **Results**

194 Table 1 reports the raw data on hand usage for the macaques (whereas all 16  
195 macaques responded to the unimanual and the bimanual food-reaching tasks,  
196 only 10 macaques responded to the hand-performance-differentiation task  
197 perhaps because of a lower motivation to solve a relatively more difficult and  
198 time-consuming activity). We found strong negative correlations between (a) the  
199 latency in food extraction by the preferred hand in the hand-performance-  
200 differentiation task and the laterality in hand performance (LHP) (Spearman's  
201 rank correlation:  $r_s = - 0.772$ ,  $n = 10$ ,  $p = 0.009$ ; Fig. 2A), and (b) the LHP in  
202 the hand-performance-differentiation task and the absolute difference between  
203 the laterality in hand usage in the unimanual and the bimanual food-reaching  
204 tasks (Spearman's rank correlation:  $r_s = - 0.752$ ,  $n = 10$ ,  $p = 0.012$ ; Fig. 2B).  
205 There was no difference between the two hands in the number of bouts for  
206 taking all 7 grapes out of the box in the hand-performance-differentiation task  
207 (Wilcoxon signed-rank test:  $Z = - 1.511$ ,  $p = 0.131$ ).



8 **Table 1.** Raw data on hand usage for the macaques in the unimanual and the bimanual food-reaching tasks (n = 16), and the hand-  
 9 performance-differentiation task (n = 10).

| Individual | Hand usage in the food-reaching tasks |    |         |              |    |         |          | Hand usage in the hand-performance-differentiation task |                            |         |                                      |
|------------|---------------------------------------|----|---------|--------------|----|---------|----------|---|----------------------------|---------|--------------------------------------|
|            | Tasks                                 |    |         |              |    |         | Outcomes |   | Latency in food extraction |         | Laterality in hand performance (LHP) |
|            | Unimanual (U)                         |    |         | Bimanual (B) |    |         | PH       | Abs. ( $HI_{\text{Bimanual}} - HI_{\text{Unimanual}}$ ) | PH (s)                     | NPH (s) |                                      |
|            | L                                     | R  | HI      | L            | R  | HI      |          |   |                            |         |                                      |
| AM1        | 19                                    | 2  | - 0.810 | 21           | 0  | - 1.000 | L        | 0.190   | -                          | -       | -                                    |
| AM2        | 0                                     | 21 | 1.000   | 0            | 21 | 1.000   | R        | 0.000   | -                          | -       | -                                    |
| SM1        | 0                                     | 21 | 1.000   | 0            | 21 | 1.000   | R        | 0.000   | -                          | -       | -                                    |
| JM1        | 0                                     | 21 | 1.000   | 1            | 20 | 0.905   | R        | 0.095   | 2.847                      | 3.040   | 0.033                                |
| JM2        | 5                                     | 16 | 0.524   | 21           | 0  | - 1.000 | L        | 1.523   | 3.696                      | 3.856   | 0.021                                |
| JM3        | 21                                    | 0  | - 1.000 | 21           | 0  | - 1.000 | L        | 0.000   | 1.887                      | 3.968   | 0.355                                |
| JM4        | 20                                    | 1  | - 0.905 | 21           | 0  | - 1.000 | L        | 0.095   | -                          | -       | -                                    |
| AF1        | 1                                     | 20 | 0.905   | 0            | 21 | 1.000   | R        | 0.095   | -                          | -       | -                                    |
| AF2        | 0                                     | 21 | 1.000   | 0            | 21 | 1.000   | R        | 0.000   | 2.440                      | 4.360   | 0.282                                |
| AF3        | 0                                     | 21 | 1.000   | 1            | 20 | 0.905   | R        | 0.095   | 3.152                      | 4.420   | 0.167                                |
| AF4        | 21                                    | 0  | - 1.000 | 18           | 3  | - 0.714 | L        | 0.286   | 2.250                      | 3.890   | 0.267                                |
| AF5        | 15                                    | 6  | - 0.429 | 21           | 0  | - 1.000 | L        | 0.571   | 2.184                      | 2.960   | 0.151                                |
| AF6        | 20                                    | 1  | - 0.905 | 21           | 0  | - 1.000 | L        | 0.095   | 2.440                      | 3.147   | 0.126                                |
| AF7        | 15                                    | 6  | - 0.429 | 20           | 1  | - 0.905 | L        | 0.476   | 4.504                      | 4.960   | 0.048                                |
| AF8        | 13                                    | 8  | - 0.238 | 6            | 15 | 0.429   | R        | 0.666   | -                          | -       | -                                    |
| JF1        | 1                                     | 20 | 0.905   | 1            | 20 | 0.905   | R        | 0.000   | 1.772                      | 3.568   | 0.336                                |

0 'L' and 'R' indicate the usage of left and right hand respectively; PH and NPH indicate the preferred (i.e., maneuvering) and the nonpreferred (i.e., supporting) hand  
 1 respectively.

212 **Figure 2. Relationship between (a) the latency in food extraction using**  
213 **the preferred hand (i.e., the maneuvering hand, see mangalam et al.**  
214 **[1]) and the laterality in hand performance (LHP) in the hand-**  
215 **performance-differentiation task, and (b) the LHP in the hand-**  
216 **performance-differentiation task and the absolute difference between**  
217 **the laterality in hand usage in the unimanual and the bimanual food-**  
218 **reaching tasks. n = 10.**

219

## 220 **Discussion**

221 We examined whether the division of labor in hand usage, as described by  
222 Mangalam et al. [23], is associated with higher hand performance in free-  
223 ranging bonnet macaques. We observed negative relationships between (a) the  
224 latency in food extraction by the preferred hand in the hand-performance-  
225 differentiation task (lower latency = higher performance), the preferred hand  
226 determined using the bimanual food-reaching task, and the normalized  
227 difference between the performance of the two hands, and (b) the normalized  
228 difference between the performance of the two hands and the absolute  
229 difference between the laterality in hand usage in the unimanual and the  
230 bimanual food-reaching tasks (lesser difference = higher manual specialization).  
231 These correlations demonstrate that the division of labor between the two hands  
232 is associated with higher hand performance: the macaques that exhibit a higher  
233 manual specialization show a greater difference in the performance of the two  
234 hands, and also perform better than those that exhibit a smaller difference.  
235  
236 On the one hand, the almost ubiquitous existence of manual asymmetries in  
237 nonhuman primates is likely to have some ecological advantages, and even

238 more likely when there are underlying neurological asymmetries, as  
239 demonstrated in capuchin monkeys [24-27] and chimpanzees [28-30]. On the  
240 other hand, there may be some obvious disadvantages. Objects supposedly are  
241 randomly located with respect to the midsagittal plane of an individual (i.e.,  
242 towards the left or towards the right); this introduces difficulty in solving some  
243 tasks for individuals having a bias for one particular side. Fagot and Vauclair [8]  
244 reviewed studies on manual asymmetries in nonhuman primates and drew a  
245 distinction between hand preference and manual specialization. According to  
246 them, hand preference refers to the consistent usage of one hand to solve  
247 familiar, relatively simple, and highly practiced tasks, and may not be  
248 necessarily accompanied by an improvement in hand performance. In contrast,  
249 manual specialization refers to the consistent usage of one hand to solve novel,  
250 relatively complex, and not-practiced tasks that require peculiar action patterns,  
251 and is necessarily accompanied by an improvement in hand performance.  
252 Moreover, individuals generally exhibit manual specialization only when the tasks  
253 involve cognitively demanding manual actions. Thus, there exists a marked  
254 difference between hand preference and manual specialization in terms of the  
255 resulting differences in the performance of the two hands, which is evidently  
256 visible while considering the forms and/or functions of manual asymmetries, as  
257 described by Mangalam et al. [23]. The difference in the HI values between the  
258 unimanual and the bimanual food-reaching tasks allowed us quantifying manual  
259 specialization as an entity separate from hand preference (which an individual is  
260 likely to show because of an inherent bias) and examining whether it is  
261 associated with a higher difference in the performance between the two hands.  
262

263 In a previous study [31], captive capuchin monkeys exhibited a weak, but  
264 statistically nonsignificant, positive relationship between the strength of hand  
265 preference and the corresponding hand performance in a unimanual and a  
266 bimanual versions of the box task. The study acknowledged that the strength of  
267 hand preference could have affected the timing of the movements, and so the  
268 observed relationship. This was, however, not the case of the present study  
269 because the hand-performance-differentiation task ergonomically forced the  
270 macaques to use either the left or the right hand, which allowed measuring the  
271 hand performance independent of any ceiling effects, i.e., it was unlikely to  
272 prime any motor actions associated with the hand opposite to that of the  
273 intended one. It provided a standard setup, which could be more widely used to  
274 compare hand performance across individuals while minimizing the possibilities  
275 of confounding effects. We suggest the development of such standard and  
276 robust experimental setups which might help answering the prevailing questions  
277 on manual asymmetries in nonhuman primates.

278

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379 **Supporting Information**

380 **S1 Movie.** This footage illustrates the adult female bonnet macaque – ‘AF5’,  
381 solving the unimanual food-reaching task. Reproduced, with permission from  
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