

1 **The influence of target animacy and social rank on hand preference in Barbary**
2 **macaques (*Macaca sylvanus*)**

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26

27 **Abstract**

28 Brain hemispheres have different functions and control the movements of the contralateral side of
29 the body. One of these functions is the process of emotions. The right hemisphere hypothesis
30 suggests that the right hemisphere of the brain is responsible for emotional processing, and so the
31 left side of the body is activated in emotive contexts such as social interactions. In contrast, the
32 valence hypothesis proposes that both hemispheres are involved in emotional processing, with the
33 left hemisphere processing positive emotions and the right hemisphere dealing with negative
34 emotions. As sociality can influence emotional states, studying behavioral lateralization in social
35 contexts, and the effect of rank on laterality should help to clarify the role of brain hemispheres in
36 social responses. The aim of this study was to investigate whether and how target animacy
37 (interaction with inanimate and animate targets) affected manual laterality in 12 zoo-housed
38 Barbary macaques (*Macaca sylvanus*). We focused on both the direction and the strength of hand
39 preference and tested the effect of social rank on lateralization. We used continuous focal animal
40 sampling to record bouts of hand preference when interacting with inanimate targets and animate
41 targets (during social and self-directed behaviors). and recorded social interactions to measure the
42 rank. For inanimate targets, 14 15-minute sessions were done. For animate targets, 14 2-hour
43 morning sessions and 14 90-minute afternoon sessions were done. At the individual level, six of
44 nine lateralized macaques were significantly right-handed when interacting with inanimate targets,
45 whereas only three subjects showed a significant (right) lateralization when interacting with animate
46 targets. Thus, inanimate targets seem to elicit manual laterality to a greater extent than animate
47 targets. However, we found no group-level hand preference for actions directed toward inanimate or
48 animate targets in general. However, we found a group-level right-hand bias for affiliative
49 behaviors, whereas no effects of social rank on lateralization was present. Based on our results, both
50 hemispheres seem to process emotions, influencing hand preference during social interactions, as
51 suggested by the valence hypothesis. Despite the limitations due to the small sample size, these

52 findings suggest that Barbary macaques show hand preference patterns similar to those found in
53 great apes and other catarrhines in interactions with both inanimate and animate targets.

54 **Keywords:** Hand Preference, Target Animacy, Hemispheric Specialization, Emotions, *Macaca*
55 *sylvanus*

56

57 **Introduction**

58 A growing body of evidence reveals that behavioral lateralization is a shared feature across
59 the animal kingdom, including vertebrates (Rogers, Vallortigara, and Andrew 2013) and
60 invertebrates (Anfora et al. 2011; Frasnelli, Vallortigara, and Rogers 2012; Frasnelli 2013; Versace
61 and Vallortigara 2015; Niven and Frasnelli, 2018). Behavioral asymmetry in vertebrates may be
62 related to cerebral specialization (Rogers et al. 2013) and processing emotions is one of the
63 functions of the brain hemispheres. If one hemisphere is involved in the control of a behavior, the
64 contralateral side of the body is likely to perform the behavior and handedness is one of the
65 behavioral asymmetries that has been related to hemispheric specialization in primates (Hopkins
66 and Cantalupo, 2004; Hopkins et al., 2015; Marie et al., 2017; Margiotoudi et al., 2019).

67 At present, there are two hypotheses concerning the cerebral processing of emotional stimuli
68 (Davidson 1995; Demaree et al. 2005). The right hemisphere hypothesis suggests that the right
69 hemisphere is responsible for emotional processing (*e.g.*, Gainotti 1972; Tucker 1981; Borod et al.
70 1998). For example, the right brain hemisphere involvement in emotional control and perception of
71 facial expression might explain why great apes typically cradle their babies on their left side,
72 allowing the parent and the newborn to keep each other in the left visual field, processed by the
73 right hemisphere (Manning and Chamberlain, 1980; Forrester et al., 2018; Malatesta et al., 2019;
74 Boulinguez-Ambroise et al., 2020). The valence hypothesis, instead, proposes that both
75 hemispheres are involved in emotional processing, and the right hemisphere is specialized for
76 negative emotions, while the left hemisphere is specialized for positive emotions (*e.g.*, Silberman
77 and Weingartner 1986; Davidson 1995; Borod et al. 1998). Similar patterns have been reported
78 across vertebrate classes (Leliveld et al., 2013; Forrester and Todd, 2018), suggesting that human
79 social-emotional processing is consistent with an evolutionary framework (Forrester and Todd,
80 2018).

81 Factors such as sociality and stress-related situations, implying an emotional involvement,
82 can determine behavioral asymmetries (Eisenberg, 2002; Eisenberg and Fabes, 2005; Clay and de
83 Waal, 2013; Malatesta et al., 2019; Boulinguez-Ambroise et al., 2020). In primates living in groups
84 (e.g. macaques), social interactions such as aggressive responses, processing of conspecifics' faces
85 or avoidance and withdrawal behaviors can lead to a high recruitment of the right hemisphere of the
86 brain (Vallortigara and Rogers, 2005; Rogers et al., 2013). Therefore, targets requiring different
87 processing skills (e.g. manipulation of objects/food) and emotional implication (social stimuli) can
88 lead to the activation of one brain hemisphere or the other one, determining behavioral
89 lateralization. Studying behavioral lateralization in social contexts might be valuable in
90 understanding brain lateralization in the emotional process.

91 Research has focused on hand preference for interaction with inanimate targets such as
92 grass, sticks, objects or food items, or with animate targets that imply emotional involvement, such
93 as physical contact with conspecifics, or with the primate's own body (self-directed behavior)
94 (Eisenberg, 2002; Eisenberg and Fabes, 2005; Clay and de Waal, 2013). The right hand, and thus
95 the left hemisphere, seems to be more involved in unimanual manipulative actions directed toward
96 inanimate targets, whereas animate targets such as conspecifics seem to elicit no hand preference in
97 chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) at the group level (Forrester et al.
98 2011; Forrester et al. 2012). On the other hand, in great apes, a left bias for self-touching underlines
99 a possible link between emotive context and right hemisphere activation (Dimond and Harries
100 1983; Rogers and Kaplan 1996). In Old World monkeys, particularly northern pig-tailed macaques
101 (*Macaca leonina*) and Sichuan snub-nose monkeys (*Rhinopithecus roxellana*), there is no group-
102 level hand preference for interactions with either inanimate and animate targets, but some authors
103 found a trend toward a greater use of the right hand for inanimate targets and left hand for animate
104 targets (Zhao et al. 2015, 2016). Together, these studies suggest a neural distinction between targets
105 requiring functional (objects) and social (conspecific, self) manipulation in monkeys and great apes
106 (Forrester et al. 2011, 2012, 2013, Zhao et al. 2015, 2016).

107 Lateralized functioning in emotional contexts has been reported across different vertebrate
108 classes, from fish to humans and can influence behavioral asymmetries such as hand preference
109 (Leliveld, Langbein and Puppe, 2013; Forrester and Todd, 2018). Thus, data on hand use for
110 different types of interactions with animate targets might help to evaluate the role of brain
111 hemispheres in processing emotions, such as in social contexts, and thus test the right-hemisphere
112 and the valence hypotheses. Non-human primates are a suitable model to investigate the evolution
113 of handedness and the influence of emotional processing on manual laterality in humans, because of
114 their phylogenetic position and manipulative abilities (Forrester et al., 2014; Versace and
115 Vallortigara 2015).

116 More studies involving a broader sample of species are needed to better understand the
117 evolutionary origin of behavioral lateralization and its correlates with neural distinction. Moreover,
118 to our knowledge, no studies of hand preference during interaction with animate targets have
119 considered whether the type of interaction and the social rank of the subjects might affect their
120 manual laterality. According to the valence hypothesis, affiliative and agonistic interactions imply
121 differential brain hemisphere activation related to positive (left hemisphere) and negative (right
122 hemisphere) emotions, respectively (Leliveld et al., 2013; Forrester and Todd, 2018). In addition,
123 low-ranking individuals might be characterized by different emotive states to dominant individuals,
124 as they may experience higher levels of stress and emotional tension (*e.g.*, Shively, 1998; Shively
125 and Wallace, 2001; Wascher et al., 2009; Qin et al., 2013; Feng et al., 2016). Thus, the type of social
126 interaction and social group hierarchy should be considered when investigating manual laterality
127 when interacting with animate targets. Finally, self-directed behaviors, when performed in conflict-
128 affected social contexts, might be related to stress and anxiety, and imply emotional involvement
129 (Maestriperi et al., 1992; Leavens et al., 2001). Mediation of these behaviors should therefore be
130 under control of the right hemisphere.

131 We investigated the effect of inanimate (*e.g.*, food, objects) and animate (*e.g.*, social
132 interactions with conspecifics, self) targets on manual laterality in Barbary macaques (*Macaca*

133 *sylvanus*) by observing spontaneous behaviors and social interactions. For animate targets, we also
134 considered the type of social interaction and the social rank of the macaques. Based on previous
135 literature and according to the right hemisphere hypothesis, we predict that Barbary macaques will
136 use the hands differently when interacting with inanimate and animate targets and will be more
137 likely to interact animate targets using the left hand. Based on the valence hypothesis, we predict no
138 overall manual lateralization when interacting with animate targets, but rather a differential bias in
139 the case of agonistic (left bias) and affiliative interactions (right bias).

140

141 **Methods**

142 *Subjects and housing*

143 The subjects of the study were 12 Barbary macaques, housed at Parco Natura Viva - Garda
144 Zoological Park (Bussolengo VR, Italy). The colony consisted of nine adult females and three males
145 of different ages (Table 1). All subjects were born in zoos and parent-reared. The macaques were
146 housed in a 1560 m² semi-naturalistic grassy enclosure containing trees, plants, rocks, climbing
147 structures (*e.g.*, ropes and perches), caves, and a water pool. The colony was fed with fresh fruit and
148 vegetables twice a day at six different feeding points consisting of wire-mesh baskets. Food items
149 such as seeds, raisins, nuts, peanuts, legumes and primate pellets were also provided as
150 environmental enrichment and scattered in the enclosure. Water was available *ad libitum*. The
151 colony was involved in a daily environmental enrichment program and received different types of
152 stimuli, consisting of foraging enrichment and manipulative devices. The zookeepers entered the
153 enclosure only for husbandry procedures (feeding and cleaning) and direct physical interaction
154 between humans and macaques was not allowed.

155

156 *Ethical Note*

157 We carried out the study through behavioral observation of the macaques, using non-invasive
158 techniques. The study procedure was in accordance with the EU Directive 2010/63/EU and the Italian

159 legislative decree 26/2014 for Animal Research. No special permission to use animals in the current
160 ethological non-invasive study is required, as zoological gardens in Italy are expected to carry out
161 behavioral observations of the individuals in their care (D. Lgs.73/2005).

162

163 *Procedure and data collection: inanimate targets*

164 We collected data on hand preference when interacting with inanimate targets through live
165 observations of subjects in their social context, using continuous focal animal sampling (Altmann
166 1974; Martin and Bateson 1986). We collected fourteen 15-minute sessions for each macaque with
167 one session per day in December 2017. We collected data 10.30-12.30 and 14.00-15.30. We
168 observed the subjects daily in a variable sequence, to balance observations across time. We recorded
169 actions that made physical contact with inanimate targets (objects, ground, enclosure) (Forrester et
170 al., 2012): retrieving food and manipulating other items. We defined retrieving food as retrieving
171 pieces of food and bringing them to the mouth. We defined manipulation as reaching for, holding,
172 touching or moving non-food items, including straw, environmental enrichment devices, branches,
173 rocks, and the soil or grass. We focused on bouts of hand preference for inanimate targets, recording
174 the first occurrence in a series of the same action (*e.g.*, McGrew and Marchant 1997; Hopkins et al.
175 2001; Schnoell et al. 2014; Regaiolli et al. 2016, 2018). We did not record a response if it was not
176 separated from a previous action by a different behavioral event or postural change by the subject.
177 We considered only actions performed with one hand and starting from a symmetrical posture and
178 discarded data if the subject was in a position or situation that constrained the use of a particular
179 hand (*e.g.*, retrieving bouts in which macaques were already holding something in one hand and
180 those performed when macaques were laying on their side) (Regaiolli et al., 2018).

181

182 *Procedure and data collection: animate targets*

183 We collected data on animate targets during the same period. We video-recorded all
184 observation sessions, and obtained data by observing the recording, using continuous focal animal
185 sampling. We mounted a digital video camera (Sony Handycam FDR-AX53) on a tripod and
186 recorded 10.30-12.30 and 14.00-15.30 for 14 non-consecutive days. The camera was fixed and wide
187 angle, covering the central area (approximately 75%) of the enclosure. The macaques were used to
188 the presence of observer and camera as the observer stayed on the zoo visitor path during a
189 preliminary observation period for approximately one month before the study and introduced the
190 camera in the last two weeks. We obtained 14 2-hour morning recordings and 14 90-minute
191 afternoon recordings. We analyzed each session for each macaque giving 210 minutes of recordings
192 per day per subject. We used all-occurrences sampling for interactions with animate targets
193 (Altmann, 1974; Martin and Bateson, 1994) and recorded bouts of hand preference (McGrew and
194 Marchant 1997; Hopkins et al. 2001; Schnoell et al. 2014; Regaiolli et al. 2016, 2018) during social
195 interactions observing the video-recorded sessions. We recorded actions that were directed toward
196 and made physical contact with conspecifics and self (Forrester et al., 2012). We considered only
197 unimanual actions performed when the focal subject was in a symmetrical posture.

198 We included all unimanual affiliative (grooming events performed with one hand, side
199 embraces, touching, unimanual genital inspection), agonistic physical contact (unimanual
200 aggressive contacts such as pushing or holding away, pulling, grabbing, and cuffing) (Deag, 1974;
201 Thierry et al., 2000; Sandri et al., 2017) between individuals. We also recorded agonistic
202 interactions to construct a dominance hierarchy.

203 The same observer (MB) collected all data. While the camera recorded the whole group, the
204 observer collected data on the interaction with inanimate targets and on self-directed behaviors
205 (self-grooming, self-touching and scratching).

206

207 **Data analysis**

208 To assess hand preference at the individual level, we calculated a Handedness Index (HI)
209 following the formula: (right hand bouts – left hand bouts)/(right hand bouts + left hand bouts). The
210 HI varies between -1.00 (left-hand preference) and +1.00 (right-hand preference) (Hopkins 1999).
211 We used the absolute values of the HI (ABS-HI) to assess the strength of the hand preference
212 (Hopkins 1999, 2013; Meunier et al. 2011). The HI has been widely used in laterality studies and is
213 a useful tool to manage an unbalanced sample of data across subjects (Hopkins 1999, 2013). In
214 addition, we used binomial *z-scores* to classify the subjects as left-handed ($z \leq -1.96$), right-handed
215 ($z \geq 1.96$) or ambi-preferent ($-1.96 < z < 1.96$) (McGrew and Marchant 1997; Michel, Sheu and
216 Brumley 2002). To assess lateralization at the individual level, we considered only subjects that
217 performed a minimum of 10 bouts per each type of target (inanimate and animate) and per each
218 type of interaction (self, affiliative and agonistic interactions) (Meguerditchian and Vauclair, 2009;
219 Meguerditchian et al., 2010; Spiezio et al., 2016). We used a chi-squared test to compare the
220 proportion of lateralized macaques between inanimate targets and animate targets.

221 For group-level analysis, Shapiro-Wilk goodness-of-fit tests revealed that not all data were
222 normally distributed, so we used non-parametric statistical tests. To evaluate the symmetry of the HI
223 distribution and the presence of group-level biases, we used one-sample Wilcoxon signed-rank tests
224 with HI as the dependent variable (*e.g.*, Meunier et al. 2011; Spinozzi, Castorina, and Truppa 1998).
225 We used Wilcoxon tests to assess the effect of target animacy on manual laterality, by comparing
226 the HI and the ABS-HI for interacting with inanimate and animate targets. For animate targets, we
227 performed the analysis considering all actions together and also focusing on self-directed behaviors,
228 affiliative interactions and agonistic interactions separately. We included only the HI of subjects that
229 performed a minimum of five bouts per each type of target (inanimate and animate) as well as per
230 each type of interaction (self, affiliative and agonistic interactions) in analyses.

231 To evaluate whether the rank of the macaques was related to their hand preference for
232 interacting with animate targets, we used the Clutton-Brock index (CBI, Clutton-Brock et al., 1979)
233 to determine the hierarchy (Clutton-Brock et al., 1979; Bang et al., 2010). The CBI for each

234 macaque was given by the formula $CBI = (B + b + 1)/(L + l + 1)$, in which “B = number of
235 individuals whom the subject dominates, b = number of individuals who those dominated by the
236 subject in turn dominate, L = number of individuals who dominate the subject, l = number of
237 individuals who dominate those dominating the subject” (Bang et al., 2010, p. 632). The higher the
238 CBI of an individual, the higher the rank in the social group. We tested the correlation between CBI
239 and HI for all animate targets, and for affiliative interactions and self-directed behaviors using
240 Spearman correlations.

241 We carried out statistical analysis in the R 3.5.0 environment (R Core Team, 2013). All tests
242 were two-tailed, and we set the significance level at $p < 0.05$. We report the interquartile ranges
243 (IQR) in brackets.

244

245 **Results**

246 *Inanimate vs. animate targets*

247 The median HI for interaction with inanimate targets was 0.15 (0.23) and the median ABS-
248 HI was 0.22 (0.14). The median HI for interaction with animate targets was 0.13 (0.41) and the
249 median ABS-HI was 0.26 (0.25) (Fig. 1).

250 At the individual level, nine of the 12 subjects were lateralized when considering hand
251 preference for inanimate targets: six subjects showed a significant right-hand preference, three
252 showed a significant left-hand preference, and three were ambi-preferent, although all of these had
253 positive HI values (Table 1).

254 When considering hand preference for animate targets three subjects were significantly
255 lateralized and showed a right-hand preference, whereas all the other subjects (9) were ambi-
256 preferent (Table 1): five had positive HI and four had negative HI values (Table 1).

257 **Table 1: Hand preference for inanimate and animate targets in Barbary macaques at Parco Natura Viva-Garda Zoological Park,**
 258 **(Bussolengo, VR, Italy), December 2017.** (Preference: Right: z -score > 1.96 , Left: z -score < -1.96 , ambi-preferent: $-1.96 < z$ -score < 1.96). *
 259 indicates $p < 0.05$.

Subject	Sex	Age (years)	Clutton-Brock Index	Handedness Index	Inanimate targets				Animate targets (conspecifics, self)				
					Total number of bouts (right + left)	Z	p-value	Preference	Handedness Index	Total number of bouts (right + left)	Z	p-value	Preference
Belinda	F	12	0.13	0.70	202	9.92*	0	Right	0.31	35	1.69	0.091	Ambi
Belle	F	4	0.33	-0.29	169	-3.69*	< 0.001	Left	0.08	24	0.20	0.841	Ambi
Berta	F	6	1	0.11	249	1.65	0.099	Ambi	-0.25	40	-1.42	0.156	Ambi
Buddha	F	13	22	0.14	187	1.90	0.057	Ambi	0.54	13	1.66	0.097	Ambi
Elly	F	5	2.13	-0.24	196	-3.36*	0.001	Left	-0.06	49	-0.29	0.772	Ambi
Emma	F	5	4.67	0.25	171	3.21*	0.001	Right	0.17	60	1.16	0.246	Ambi
Fanny	F	8	0.38	0.83	241	12.88*	< 0.001	Right	0.43	53	3.02*	0.003	Right
Jack	M	4	1	0.19	221	2.83*	0.005	Right	0.33	66	2.58*	0.009	Right
Milly	F	10	0.51	0.29	217	4.21*	< 0.001	Right	0.05	40	0.16	0.873	Ambi
Lazzarino	M	4	0.67	-0.16	198	-2.20*	0.028	Left	0.37	79	3.15*	0.002	Right
Lucky	M	14	30	0.15	194	2.08*	0.038	Right	-0.28	47	-1.75	0.080	Ambi
Lucrezia	F	9	3	0.10	242	1.48	0.139	Ambi	-0.10	31	-0.36	0.719	Ambi

260

261

262 **Table 2: Hand preference for animate targets based on self-directed, affiliative and agonistic behaviors in Barbary macaques at Parco**
 263 **Natura Viva-Garda Zoological Park, (Bussolengo, VR, Italy), December 2017.** (Preference: Right: z -score > 1.96 , Left: z -score < -1.96 , ambi-
 264 preferent: $-1.96 < z$ -score < 1.96). * indicates $p < 0.05$, # insufficient number of datapoints.

Subject	Sex	Age (years)	Clutton-Brock Index	Self-directed behaviors					Affiliative behaviors					Agonistic behaviors				
				Handedness Index	Total number of bouts (right + left)	Z	p-value	Preference	Handedness Index	Total number of bouts (right + left)	Z	p-value	Preference	Handedness Index	Total number of bouts (right + left)	Z	p-value	Preference
Belinda	F	12	0.13	0.25	16	0.75	0.453	Ambi	0.37	19	1.38	0.167	Ambi	#	0	#	#	#
Belle	F	4	0.33	0.00	8	#	#	#	0	14	0	1	Ambi	1	2	#	#	#
Berta	F	6	1	-0.23	13	-0.55	0.582	Ambi	-0.33	24	-1.43	0.153	Ambi	0.33	3	#	#	#
Buddha	F	13	22	0.50	8	#	#	#	0.60	5	#	#	#	#	0	#	#	#
Elly	F	5	2.13	-0.38	13	-1.11	0.267	Ambi	0	30	0	1	Ambi	0.33	6	#	#	#
Emma	F	5	4.67	0.17	41	0.9	0.347	Ambi	0.29	14	0.80	0.424	Ambi	-0.20	5	#	#	#
Fanny	F	8	0.38	0.47	34	2.57*	0.010	Right	0.44	18	1.65	0.099	Ambi	-1	1	#	#	#
Jack	M	4	1	0.33	15	1.03	0.303	Ambi	0.42	45	2.68*	0.007	Right	-0.33	6	#	#	#
Milly	F	10	0.51	-0.13	23	-0.42	0.674	Ambi	0.43	14	1.34	0.180	Ambi	-0.33	3	#	#	#
Lazzarino	M	4	0.67	0.73	22	3.20*	0.001	Right	0.48	46	3.10*	0.002	Right	-0.82	11	-2.41*	0.016	Left
Lucky	M	14	30	-0.29	28	-1.32	0.187	Ambi	-0.20	15	-0.52	0.603	Ambi	-0.50	4	#	#	#
Lucrezia	F	9	3	-0.43	7	#	#	#	0.18	17	0.49	0.624	Ambi	-0.43	7	#	#	#

265 We found no group-level biases in the HI distributions for inanimate (one-sample Wilcoxon
266 signed-rank test: $V = 56.5$, $p = 0.182$, 95% CI [-0.047, 0.429], $N = 12$) or animate targets ($V = 59$, p
267 $= 0.129$, 95% CI [-0.061, 0.333], $N = 12$) (Fig. 1).

268 We found no significant differences in hand preference between inanimate and animate
269 targets for HI (Wilcoxon test: $W = 73$, $p = 0.977$, 95% CI [-0.234, 0.336], $N = 12$) or ABS-HI ($W =$
270 74 , $p = 0.931$, 95% CI [-0.144, 0.162], $N = 12$) (Fig. 1). The number of lateralized macaques for
271 inanimate targets was significantly higher than the number of lateralized subjects for animate
272 targets (chi-squared test: $X^2(1, 12) = 6$, $p = 0.014$).

273

274 *Interaction with animate targets and effect of social rank*

275 The median HI for self-directed behaviors was 0.09 (0.61) and the median ABS-HI was 0.31
276 (0.22). We found no group-level bias in hand preference (one-sample Wilcoxon signed-rank test: V
277 $= 42$, $p = 0.450$, 95% CI [-0.258, 0.402], $N = 12$) (Table 2). The median HI for affiliative
278 interactions was 0.33 (0.44). We found a group-level right bias in hand preference ($V = 49$, $p =$
279 0.032 , 95% CI [0.045, 0.460], $N = 12$) (Table 2). We did not analyze agonistic interactions as they
280 were rarely performed by the subjects (median -0.33, IQR 0.91, $N = 10$).

281 We found no significant correlations between rank (CBI) and HI for animate targets
282 (Spearman correlation.: $\rho = 0.277$; $p = 0.384$), self-directed behaviors ($\rho = 0.284$; $p = 0.372$) or
283 affiliative interactions ($\rho = -0.172$; $p = 0.593$). Similarly, we found no significant correlations
284 between rank and ABS-HI for animate targets ($\rho = 0.067$; $p = 0.837$), self-directed behaviors (ρ
285 $= 0.263$; $p = 0.410$) or affiliative interactions ($\rho = -0.112$; $p = 0.728$).

286

287 **Discussion**

288 We found that: (1) individual-level differences in hand preference depend on target animacy,
289 with a greater number of lateralized individuals when interacting with inanimate than animate
290 targets; (2) macaques showed no group-level hand preference for actions directed toward inanimate

291 or animate targets; (3) macaques showed a group-level right hand preference for affiliative
292 interactions; (4) there were no effects of rank on the hand used to interact with animate targets. We
293 interpret these results with caution due to the small sample size. At the individual level, nine of 12
294 subjects were significantly lateralized, six were right-handed and three were left-handed when
295 interacting with inanimate targets, including retrieving food and object manipulation. Considering
296 all animate targets (conspecifics and self), three of 12 subjects were lateralized, all of which were
297 right handed. However, we did not find a significant bias in hand use at the group level for both
298 inanimate or animate targets, possibly due to the small sample size. These results add to the
299 literature that found no hand preferences at the group level in monkeys, suggesting individual
300 variability in hand preference patterns for different tasks involving functional manipulation
301 (inanimate targets) (Fitch and Braccini, 2013) and social manipulation (animate targets) (Zhao et al.
302 2015, 2016).

303 We found no significant differences in the direction (HI) or strength (ABS-HI) of hand
304 preference between inanimate and animate targets. At the individual level, our results are in line
305 with studies of great apes, Sichuan snub-nose monkeys and northern pig-tailed macaques, which
306 also report a lack of lateralization when interacting with animate targets (Forrester et al., 2011,
307 Forrester et al., 2012; Forrester et al., 2013; Zhao et al., 2015). The lack of hand preference in the
308 presence of animate targets suggests that both hemispheres are involved in emotive situations that
309 could be both positive or negative, such as social interactions (Eisenberg, 2002; Eisenberg and
310 Fabes, 2005; Clay and de Waal, 2013). More studies focusing on lateralization in the presence of
311 different types of social interactions (e.g., affiliative and agonistic encounters) are needed to assess
312 the role of brain hemispheres in processing positive and negative emotions.

313 We investigated whether the macaques used their right or the left hand in the presence of
314 different social stimuli (and therefore in different emotive contexts), focusing on the type of social
315 interaction and rank of the subjects involved. We found a right bias in hand preference for affiliative
316 interactions. This finding supports the valence hypothesis suggesting that the left hemisphere is

317 dominant for positive emotions, such as those resulting from affiliative behavior and both
318 hemispheres of the brain seem to be involved in emotional and social control (Leliveld et al., 2013;
319 Forrester and Todd, 2018). A possible explanation for the ambi-preferent use of the right and left
320 hand in the presence of animate targets is that both manipulative and emotive processes are
321 involved in the interaction with social partners. For example, when grooming a conspecific,
322 macaques may be emotionally involved in the affiliative social interaction, but they are also
323 performing a manual activity requiring manipulation of the fur and reaching actions. If this is the
324 case, both the left and the right hemispheres would be involved, leading to an overall lack of hand
325 preference (Forrester et al., 2011). Future research should investigate side biases in social behaviors
326 of different complexity, comparing, for example, side embraces, body placement (Karenina et al.,
327 2017) and approach to conspecifics with more complex behaviors like grooming. Moreover, more
328 data on lateralization during agonistic interactions are needed to test the valence hypothesis in
329 Barbary macaques and other non-human primates.

330 In primates living in groups such as macaques, individuals may have a high recruitment of
331 the right hemisphere. Social interactions like aggressive responses, processing of conspecifics' faces
332 or avoidance and withdrawal behaviors can activate the right side of the brain (Vallortigara and
333 Rogers, 2005; Rogers et al., 2013). Although both high-ranking and low-ranking individuals are
334 involved in these social functions, low-ranking individuals might experience higher stress level and
335 social tension (Shively, 1998; Shively and Wallace, 2001; Wascher et al., 2009; Qin et al., 2013;
336 Feng et al., 2016). However, the lack of a significant correlation between the Handedness Index and
337 the Clutton-Brock Index does not support this hypothesis. This result is in agreement with research
338 on domestic horses (*Equus caballus*), which showed no effect of rank on behavioral laterality
339 (Farmer et al., 2018). In the wild, Barbary macaques live in groups with an average size of 40
340 individuals with a polygynandrous mating system (Modolo et al., 2005; MPC Foundation, 2012). In
341 the study macaques, group size and composition differed from that reported in the wild, food was
342 always available and social tension and competition were kept to a minimum by keepers. These

343 factors might explain the lack of correlation between social rank and hand preference reported in
344 the study, suggesting that future research on larger population of macaques, possibly in wild
345 contexts, are needed to better understand the relationship between sociality and manual laterality.

346 Finally, we examined hand preference for self-directed behaviors, specifically self-
347 grooming, scratching, and self-touching. It has been proposed that these behaviors, when performed
348 in conflict-affected social contexts, might be related to stress and anxiety, and imply emotional
349 involvement (Maestriperi et al., 1992; Leavens et al., 2001). Mediation of these behaviors should
350 therefore be under control of the right hemisphere. Self-directed behaviors show a left-hand
351 preference in humans (Forrester et al., 2014) and non-human primates (Dimond and Harries 1983;
352 Rogers and Kaplan 1996; Wagner, Hopper and Ross, 2016). Because self-directed behaviors are
353 considered behavioral indicators of emotional situations, we predicted that these behaviours would
354 be lateralized in the macaques. However, we found no group-level bias in hand preference for self-
355 directed behaviors and only two of 12 subjects were significantly lateralized (right-handed) for
356 these behaviours. Our results suggest that self-directed behaviors are not under the control of one of
357 the hemispheres when unrelated to stressful situations but are processed as spontaneous (routine and
358 familiar) behaviors. Further research investigating manual laterality for self-directed behaviors
359 should compare hand preference for these actions in contexts with different level of psychological
360 and social stress.

361 In conclusion, interactions with inanimate targets were more likely to elicit a right-hand
362 preference, at least at the individual level, than interaction with animate targets. We found that
363 animate targets, which are possibly linked to emotional involvement, are not associated with
364 specific manual lateralization when considering both affiliative and agonistic interactions. However,
365 the group-level right-hand preference for affiliative interactions highlights the possible contribution
366 of the left hemisphere in the management of social responses with positive connotations. Thus, in
367 these Barbary macaques, both hemispheres seem to be involved in processing emotions, as
368 suggested by the lack of motor lateralization, particularly in the presence of social stimuli. Our

369 findings reflect those for other mammalian species, suggesting that both brain hemispheres play
370 significant roles in social responses (Giljov and Karenina, 2019; Giljov, Malashichev and Karenina,
371 2019; Roberts et al., 2019). Finally, the social rank of the subjects was not related to hand
372 preference, although more data on agonistic interactions are needed to investigate the effect of
373 hierarchy on behavioral laterality in macaques. Studies of a greater sample of monkeys are needed,
374 to further examine the effect of target animacy on primate lateralization and to better investigate the
375 influence of different social interactions (*e.g.*, agonistic contacts) on primate handedness. Finally,
376 our study highlights the importance of research investigating hand preference as well as other
377 behavioral asymmetries to better understand cognitive and emotional functions of the primate brain.

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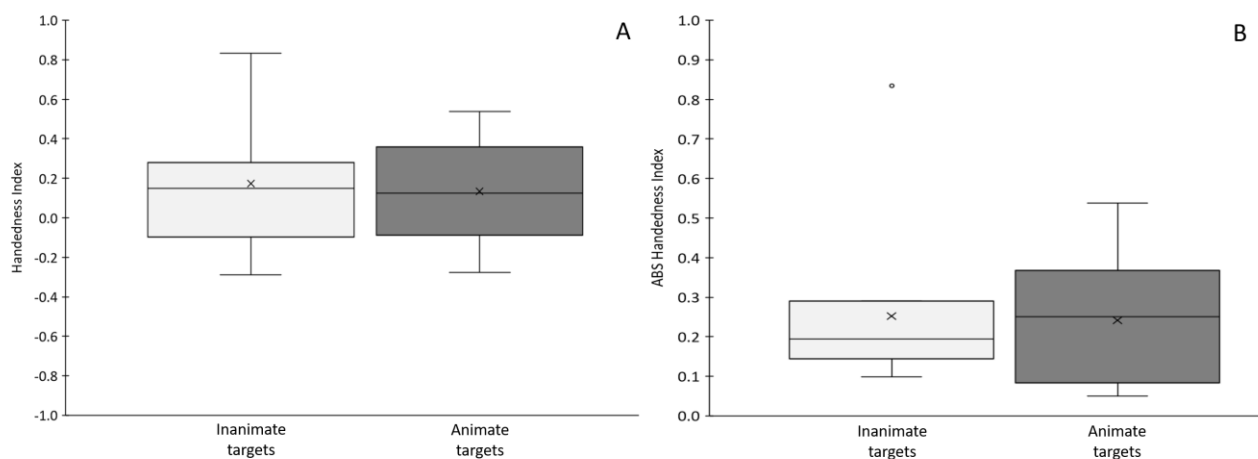
652 **Conflicts of Interest:** The authors declare that they have no conflict of interest.

653

654 **Ethical Statement:** The study was carried out through the behavioral observation of the macaques,
655 using non-invasive techniques. The study procedure was in accordance with the EU Directive
656 2010/63/EU and the Italian legislative decree 26/2014 for Animal Research. No special permission to
657 use animals in the current ethological non-invasive study is required, as zoological gardens in Italy are
658 expected to carry out behavioral observations of the individuals in their care (D. Lgs.73/2005).

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663 Fig. 1 Manual laterality in interactions with inanimate and animate targets in Barbary macaques (N = 12) at
664 Parco Natura Viva-Garda Zoological Park, (Bussolengo, VR, Italy), December 2017. Horizontal lines within
665 boxes indicate the medians, boundaries of the boxes indicate the first and third quartile, and crosses indicate
666 the mean. Whiskers extend up from the top of the box to the largest data element that is ≤ 1.5 times the
667 interquartile range (IQR) and down from the bottom of the box to the smallest data element that is > 1.5 times
668 the IQR. Values outside this range are considered to be outliers and are drawn as points.