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The Influence of Target Animacy and Social Rank on Hand Preference in Barbary Macaques (*Macaca sylvanus*)

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Abstract

Brain hemispheres have different functions and control the movements of the contralateral side of the body. One of these functions is processing emotions. The right hemisphere hypothesis suggests that the right hemisphere of the brain is responsible for emotional processing, so the left side of the body is activated in emotive contexts such as social interactions. In contrast, the valence hypothesis proposes that both hemispheres are involved in emotional processing, with the left hemisphere processing positive emotions and the right hemisphere negative emotions. We investigated whether and how interaction with inanimate and animate targets affected manual laterality in 12 zoo-housed Barbary macaques (*Macaca sylvanus*). We focused on the direction and the strength of hand preference and tested the effect of social rank on lateralization. We used continuous focal animal sampling to record bouts of hand preference when interacting with inanimate targets (fourteen 15-min samples) and animate targets (during social and self-directed behaviors, fourteen 2-h morning samples and 14 90-min afternoon samples) and recorded social interactions to measure rank. At the individual level, six of nine lateralized macaques were significantly right-handed when interacting with inanimate targets, whereas only three subjects showed a significant (right) lateralization when interacting with animate targets. Thus, inanimate targets seem to elicit manual laterality to a greater extent than animate targets. At the group level, we found no hand preference for actions directed toward inanimate or animate targets in general but we found a right-hand bias for affiliative behaviors. There was no effect of social rank on lateralization. Despite the limitations of a small sample size, our results suggest that both hemispheres influence hand preference during social interactions, supporting the valence hypothesis.

Keywords Emotions · Hand preference · Hemispheric specialization · *Macaca sylvanus* · Target animacy

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Introduction

Behavioral lateralization is a shared feature across the animal kingdom, including vertebrates (Rogers *et al.* 2013) and invertebrates (Anfora *et al.* 2011; Frasnelli 2013; Frasnelli *et al.* 2012; Niven and Frasnelli 2018; Versace and Vallortigara 2015). This lateralization may be related to cerebral specialization (Rogers *et al.* 2013), such that if one hemisphere is involved in the control of a behavior, the contralateral side of the body is likely to perform the behavior. For example, lateralized brain functioning in emotional contexts has been reported across vertebrate classes, from fish to humans, and can influence behavioral asymmetries such as hand preference (Forrester and Todd 2018; Leliveld *et al.* 2013).

At present, there are two hypotheses concerning the cerebral processing of emotional stimuli (Davidson 1995; Demaree *et al.* 2005). The right hemisphere hypothesis suggests that the right hemisphere is responsible for emotional processing (e.g., Borod *et al.* 1998; Gainotti 1972; Tucker 1981). For example, right hemisphere involvement in emotional control and perception of facial expression might explain why great apes typically cradle their babies on their left side, allowing the parent and the newborn to keep each other in the left visual field, which is processed by the right hemisphere (Boulinguez-Ambroise *et al.* 2020; Forrester *et al.* 2018; Malatesta *et al.* 2019; Manning and Chamberlain 1990). In contrast, the valence hypothesis proposes that both hemispheres are involved in emotional processing, with the right hemisphere specialized for negative emotions, and left hemisphere specialized for positive emotions (e.g., Borod *et al.* 1998; Davidson 1995; Silbermann and Weingartner 1986).

Studies of primates have not explicitly addressed these two hypotheses. However, the right hand, and thus the left hemisphere, seems to be more involved in unimanual manipulative actions directed toward inanimate targets such as grass, sticks, objects, or food items than the left hand and the right hemisphere (Forrester *et al.* 2011, 2012). In contrast, animate targets such as conspecifics elicit no hand preference in chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) at the group level (Forrester *et al.* 2011, 2012). However, a left bias in self-touching suggests a link between emotive context and right hemisphere activation in great apes (Dimond and Harries 1983; Rogers and Kaplan 1996). In other catarrhines, particularly northern pig-tailed macaques (*Macaca leonina*) and Sichuan snub-nose monkeys (*Rhinopithecus roxellana*), there is no group-level hand preference for interactions with either inanimate and animate targets, but some authors found a trend toward greater use of the right hand for inanimate targets and the left hand for animate targets (Zhao *et al.* 2015, 2016). Together, these studies suggest a neural distinction between targets requiring functional (inanimate objects) and social (animate) manipulation in monkeys and great apes (Forrester *et al.* 2011, 2012, 2013, Zhao *et al.* 2015, 2016). According to the valence hypothesis, affiliative and agonistic interactions imply differential brain hemisphere activation related to positive (left hemisphere) and negative (right hemisphere) emotions, respectively (Forrester and Todd 2018; Leliveld *et al.* 2013). In addition, low-ranking individuals might be characterized by different emotive states to dominant individuals, as they may experience higher levels of stress and emotional tension (e.g., Feng *et al.* 2016; Qin *et al.* 2013; Shively 1998; Shively and Wallace 2001; Wascher *et al.* 2009). Thus, the type of social interaction and social group hierarchy should be considered when investigating manual laterality when interacting with animate targets. Finally, self-directed behaviors, when performed in conflict-affected social contexts, might be related to stress and anxiety, and imply emotional involvement (Leavens *et al.* 2001; Maestripieri *et al.*, 1992). Mediation of these behaviors should therefore be under control of the right hemisphere. However, to our knowledge, no studies of hand preference during interaction with animate targets have considered whether the type of interaction and the social rank of the subjects affect their manual laterality.

We investigated the effect of inanimate (e.g., food, objects) and animate (e.g., social interactions with conspecifics, self) targets on manual laterality in Barbary macaques (*Macaca sylvanus*) by observing spontaneous behaviors and social interactions. For animate targets, we also considered the type of social interaction and the social rank of the macaques. Based on the right hemisphere hypothesis, we predict that Barbary macaques use their hands differently when interacting with inanimate and animate targets and are more likely to interact with animate targets using the left hand than the right hand. Based on the valence hypothesis, we predict no overall manual lateralization when interacting with animate targets, but a bias in the case of agonistic (left bias) and affiliative interactions (right bias).

Methods

Subjects and Housing

We studied 12 Barbary macaques at Parco Natura Viva – Garda Zoological Park (Bussolengo VR, Italy). The group consisted of nine females (aged 4–13 yr) and three males (4–14 yr) (Table I). All subjects were born in zoos and parent reared. The macaques were housed in a 1560 m^2 grassy enclosure containing trees, plants, rocks, climbing structures (e.g., ropes and perches), caves, and a water pool. The group was fed with fresh fruit and vegetables twice a day at six different feeding points consisting of wire-mesh baskets. Food items such as seeds, raisins, nuts, peanuts, legumes, and primate pellets were also provided as environmental enrichment and scattered in the enclosure. Water was available *ad libitum*. The colony was involved in a daily environmental enrichment program and received different types of stimuli, consisting of foraging enrichment and manipulative devices. The zookeepers entered the enclosure only for husbandry procedures (feeding and cleaning), and direct physical interaction between humans and macaques was not allowed.

Procedure and Data Collection: Inanimate Targets

We collected data on hand preference when macaques interacted with inanimate targets through live observations of subjects in their social context, using continuous focal animal sampling (Altmann 1974; Martin and Bateson 1986). We collected fourteen 15-min sessions for each macaque with one session per day in December 2017. We collected data at 10:30–12:30 h and 14:00–15:30 h. We observed the subjects daily in a variable sequence, to balance observations across time. We recorded actions that made physical contact with inanimate targets (objects, ground, enclosure) (Forrester *et al.* 2012): retrieving food and manipulating other items. We defined retrieving food as retrieving pieces of food and bringing them to the mouth. We defined manipulation

Table I Hand preference for inanimate and animate targets in Barbary macaques at Parco Natura Viva-Garda Zoological Park (Bussolengo, VR, Italy), December 2017

					Inanimate targets					Animate targets (conspecifics, self)			
Subject	Sex	Age (yr)	Clutton-Brock Index	Handedness Index	Total number of bouts (right + left)	Z	P	Preference	Handedness Index	Total number of bouts (right + left)	Z	P	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

Preference: right: $Z > 1.96$, left: $Z < -1.96$, ambi-preferent: $-1.96 < Z < 1.96$.

*$P < 0.05$.

as reaching for, holding, touching, or moving nonfood items, including straw, environmental enrichment devices, branches, rocks, and the soil or grass. We focused on bouts of hand preference for inanimate targets, recording the first occurrence in a series of the same action (e.g., Hopkins *et al.* 2001; McGrew and Marchant 1997; Schnoell *et al.* 2014; Regaiolli *et al.* 2016, 2018). We did not record a response if it was not separated from a previous action by a different behavioral event or postural change by the subject. We considered only actions performed with one hand and starting from a symmetrical posture and discarded data if the subject was in a position or situation that constrained the use of a particular hand (e.g., retrieving bouts in which macaques were already holding something in one hand and those performed when macaques were laying on their side) (Regaiolli *et al.*, 2018).

Procedure and Data Collection: Animate Targets

We collected data on animate targets during the same period. We video-recorded all observation sessions and obtained data by observing the recording, using continuous focal animal sampling. We mounted a digital video camera (Sony Handycam FDR-AX53) on a tripod and recorded at 10:30–12:30 h and 14:00–15:30 h for 14 nonconsecutive days. The camera was fixed and wide angle, covering the central area (*ca.* 75%) of the enclosure. The macaques were used to the presence of observer and camera as the observer stayed on the zoo visitor path during a preliminary observation period for *ca.* 1 mo before the study and introduced the camera in the last 2 weeks. We obtained fourteen 2-h morning recordings and fourteen 90-min afternoon recordings. We analyzed each session for each macaque giving 210 min of recordings per day per subject. We used all-occurrences sampling for interactions with animate targets (Altmann 1974; Martin and Bateson 1986) and recorded bouts of hand preference (Hopkins *et al.* 2001; McGrew and Marchant 1997; Regaiolli *et al.* 2016, 2018; Schnoell *et al.* 2014) during social interactions observing the video-recorded sessions. We recorded actions that were directed toward and made physical contact with conspecifics and self (Forrester *et al.*, 2012). We considered only unimanual actions performed when the focal subject was in a symmetrical posture.

We included all unimanual affiliative (grooming events performed with one hand, side embraces, touching, unimanual genital inspection), agonistic physical contact (unimanual aggressive contacts such as pushing or holding away, pulling, grabbing, and cuffing) (Deag 1974; Sandri *et al.* 2017; Thierry *et al.* 2000) between individuals.

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

Data Analysis

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

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

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

We collected data on dyadic agonistic encounters, focusing on behaviors that involve a clear winner (e.g., slapping, grabbing, chasing, dominance mount), with an animal directing an aggressive behavior toward another individual (the receiver/victim), which flees or moves away (Norscia and Palagi 2015). We recorded actor's and receiver's identity and entered the outcomes of such dyadic interactions in a matrix to calculate the CBI (see Electronic Supplementary Material). The CBI for each macaque was given by the formula CBI = (B + b + 1)/(L + l + 1), in which B = number of individuals that the subject dominates, b = number of individuals that those dominated by the subject in turn dominate, L = number of individuals that dominate the subject, l = number of individuals that dominate those dominating the subject (Bang *et al.*, 2010, p. 632). The higher the CBI of an individual, the higher the rank in the social group. We tested the correlation between CBI and HI for all animate targets, and for affiliative interactions and self-directed behaviors using Spearman correlations.

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

Ethical Note

We carried out the study through behavioral observation of the macaques, using noninvasive techniques. The study procedure was in accordance with the EU Directive

2010/63/EU and the Italian legislative decree 26/2014 for Animal Research. No special permission to use animals in the current ethological noninvasive study is required, as zoological gardens in Italy are expected to carry out behavioral observations of the individuals in their care (D. Lgs.73/2005). The authors declare that they have no conflict of interest.

Data Availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Results

Inanimate vs. Animate Targets

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

At the individual level, 9 of the 12 subjects were lateralized when considering hand preference for inanimate targets: six subjects showed a significant right-hand preference, three showed a significant left-hand preference, and three were ambi-preferent, although all of these had positive HI values (Table I).

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

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

We found no significant differences in hand preference between inanimate and animate targets for HI (Wilcoxon test: $W = 73$, $P = 0.977$, 95% CI [−0.234, 0.336],

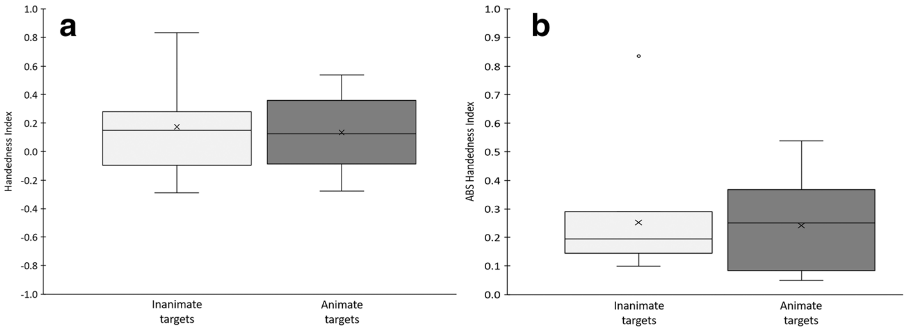

Fig. 1 Manual laterality in interactions with inanimate and animate targets in Barbary macaques ($N = 12$) at Parco Natura Viva-Garda Zoological Park, (Bussolengo, VR, Italy), December 2017. Horizontal lines within boxes indicate the medians, boundaries of the boxes indicate the first and third quartile,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

$N = 12$) or ABS-HI ($W = 74$, $P = 0.931$, 95% CI [−0.144, 0.162], $N = 12$) (Fig. 1). The number of lateralized macaques for inanimate targets was significantly higher than the number of lateralized subjects for animate targets (chi-squared test: $\chi^2(1, 12) = 6$, $P = 0.014$).

Interaction with Animate Targets and Effect of Social Rank

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

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

Discussion

We found that 1) individual-level differences in hand preference depend on target animacy, with a greater number of lateralized individuals when interacting with inanimate than animate targets; 2) macaques showed no group-level hand preference for actions directed toward inanimate or animate targets; 3) macaques showed a group-level right-hand preference for affiliative interactions; and 4) there were no effects of rank on the hand used to interact with animate targets. We interpret these results with caution due to the small sample size. At the individual level, 9 of 12 subjects were significantly lateralized, 6 were right-handed, and 3 were left-handed when interacting with inanimate targets, including retrieving food and object manipulation. Considering all animate targets (conspecifics and self), 3 of 12 subjects were lateralized, all of which were right-handed. However, we did not find a significant bias in hand use at the group level for inanimate or animate targets. Although this may be due to the small sample size, these results reflect the lack of hand preferences at the group level in other monkey species, suggesting individual variability in hand preference patterns for different tasks involving functional manipulation (inanimate targets) (Fitch and Braccini 2013) and social manipulation (animate targets) (Zhao *et al.* 2015, 2016).

We found no significant differences in the direction (HI) or strength (ABS-HI) of hand preference between inanimate and animate targets. At the individual level, our results are in line with studies of great apes, Sichuan snub-nose monkeys, and northern pig-tailed macaques, which also report a lack of lateralization when interacting with animate targets (Forrester *et al.* 2011, 2012, 2013; Zhao *et al.* 2015). The lack of hand preference in the presence of animate targets suggests that both hemispheres are

Table II Hand preference for animate targets based on self-directed, affiliative and agonistic behaviors in Barbary macaques at Parco Natura Viva-Garda Zoological Park (Bussolengo, VR, Italy), December 2017

						Self-directed behaviors				
Subject	Sex	Age (yrs)	Clutton-Brock Index	Handedness Index	Total number of bouts (right + left)	*Z*	*P*	Preference	Handedness Index	Total number of bouts (right + left)
Belinda	F	12	0.13	0.25	16	0.75	0.453	Ambi	0.37	19
Belle	F	4	0.33	0.00	8	[a]	[a]	[a]	0	14
Berta	F	6	1	−0.23	13	−0.55	0.582	Ambi	−0.33	24
Buddha	F	13	22	0.50	8	[a]	[a]	[a]	0.60	5
Elly	F	5	2.13	−0.38	13	−1.11	0.267	Ambi	0	30
Emma	F	5	4.67	0.17	41	0.9	0.347	Ambi	0.29	14
Fanny	F	8	0.38	0.47	34	2.57*	0.010	Right	0.44	18
Jack	M	4	1	0.33	15	1.03	0.303	Ambi	0.42	45
Milly	F	10	0.51	−0.13	23	−0.42	0.674	Ambi	0.43	14
Lazzarino	M	4	0.67	0.73	22	3.20*	0.001	Right	0.48	46
Lucky	M	14	30	−0.29	28	−1.32	0.187	Ambi	−0.20	15
Lucrezia	F	9	3	−0.43	7	[a]	[a]	[a]	0.18	17

Table II (continued)

	Affiliative behaviors					Agonistic behaviors		
Subject	Z Affiliative behaviors	P	Preference	Handedness Index	Total number of bouts (right + left)	Z Agonistic behaviors	P	Preference
Subject	Z	P	Preference	Handedness Index	Total number of bouts (right + left)	Z	P	Preference
Belinda	1.38	0.167	Ambi	[a]	0	[a]	[a]	[a]
Belle	0	1	Ambi	1	2	[a]	[a]	[a]
Berta	−1.43	0.153	Ambi	0.33	3	[a]	[a]	[a]
Buddha	[a]	[a]	[a]	[a]	0	[a]	[a]	[a]
Elly	0	1	Ambi	0.33	6	[a]	[a]	[a]
Emma	0.80	0.424	Ambi	−0.20	5	[a]	[a]	[a]
Fanny	1.65	0.099	Ambi	−1	1	[a]	[a]	[a]
Jack	2.68*	0.007	Right	−0.33	6	[a]	[a]	[a]
Milly	1.34	0.180	Ambi	−0.33	3	[a]	[a]	[a]
Lazzarino	3.10*	0.002	Right	−0.82	11	−2.41*	0.016	Left
Lucky	−0.52	0.603	Ambi	−0.50	4	[a]	[a]	[a]
Lucrezia	0.49	0.624	Ambi	−0.43	7	[a]	[a]	[a]

Preference: right: $Z > 1.96$, left: $Z < -1.96$, ambi-preferent: $-1.96 < Z < 1.96$.

[a] Insufficient number of datapoints.

*$P < 0.05$.

involved in emotive situations that could be both positive or negative, such as social interactions (Clay and de Waal 2013; Eisenberg 2002; Eisenberg and Fabes 2005).

We investigated whether the macaques used their right or the left hand in the presence of different social stimuli (and therefore in different emotive contexts), focusing on the type of social interaction and rank of the subjects involved. We found a right bias in hand preference for affiliative interactions. This finding supports the valence hypothesis, suggesting that the left hemisphere is dominant for positive emotions, such as those resulting from affiliative behavior, and both hemispheres of the brain are involved in emotional and social control (Forrester and Todd 2018; Leliveld *et al.* 2013). A possible explanation for the ambi-preferent use of the right and left hand in the presence of animate targets is that both manipulative and emotive processes are involved in the interaction with social partners. For example, when grooming a conspecific, macaques may be emotionally involved in the affiliative social interaction, but they are also performing a manual activity requiring manipulation of the fur and reaching actions. If this is the case, both the left and the right hemispheres would be involved, leading to an overall lack of hand preference (Forrester *et al.* 2011). Future research should investigate side biases in social behaviors of different complexity, comparing, for example, side embraces, body placement (Karenina *et al.* 2017), and approach to conspecifics with more complex behaviors such as grooming. Moreover, more data on lateralization during agonistic interactions are needed to test the valence hypothesis in Barbary macaques and other nonhuman primates.

Social interactions such as aggressive responses, processing of conspecifics' faces, or avoidance and withdrawal behaviors can activate the right side of the brain (Rogers *et al.* 2013; Vallortigara and Rogers 2005). Although both high-ranking and low-ranking individuals are involved in these social functions, low-ranking individuals might experience higher stress level and social tension (Feng *et al.* 2016; Qin *et al.* 2013; Shively 1998; Shively and Wallace 2001; Wascher *et al.* 2009;). However, the lack of a significant correlation between the Handedness Index and the Clutton-Brock Index does not support this hypothesis. This result is in agreement with research on domestic horses (*Equus caballus*), which showed no effect of rank on behavioral laterality (Farmer *et al.* 2018). The size and composition of our study group differed from that reported in the wild, where Barbary macaques live in groups with an average size of 40 individuals with a polygynandrous mating system (Modolo *et al.* 2005; MPC Foundation 2012). Moreover, food was always available and social tension and competition were kept to a minimum by keepers. These factors might explain the lack of correlation between social rank and hand preference reported in the study, suggesting that future research on a larger sample of macaques, possibly in wild contexts, is needed to better understand the relationship between sociality and manual laterality.

Finally, we examined hand preference for self-directed behaviors, specifically self-grooming, scratching, and self-touching. These behaviors, when performed in conflict-affected social contexts, are proposed to be related to stress and anxiety and imply emotional involvement (Leavens *et al.* 2001; Maestripieri *et al.* 1992). Mediation of these behaviors should therefore be under control of the right hemisphere, so we predicted that these behaviors would be lateralized in the macaques. However, we found no group-level bias in hand preference for self-directed behaviors and only 2 of 12 subjects were significantly lateralized (right-handed) for these behaviors. Our results suggest that self-directed behaviors are not under the control of one of the hemispheres. This differs from findings that self-directed behaviors show a left-hand preference in humans (Forrester *et al*. 2014) and other nonhuman primates (Dimond and Harries 1983; Rogers and Kaplan 1996; Wagner *et al.* 2016). A potential explanation for this difference may be that self-directed behaviors, when unrelated to stressful situations, are processed as spontaneous (routine and familiar) behaviors. Thus, further research investigating manual laterality for self-directed behaviors should compare hand preference for these actions in contexts with different levels of psychological and social stress.

In conclusion, interactions with inanimate targets were more likely to elicit a right-hand preference, at least at the individual level, than interaction with animate targets. Animate targets, which may be linked to emotional involvement, are not associated with specific manual lateralization when considering both affiliative and agonistic interactions. However, the group-level right-hand preference for affiliative interactions highlights the possible contribution of the left hemisphere in the management of social responses with positive connotations. Thus, in these Barbary macaques, both hemispheres seem to be involved in processing emotions, as suggested by the lack of motor lateralization, particularly in the presence of social stimuli. Our findings reflect those for other mammalian species, suggesting that both brain hemispheres play significant roles in social responses (Giljov and Karenina 2019; Giljov *et al*. 2019; Roberts *et al.* 2019). Finally, the social rank of the subjects was not related to hand preference, although more data on agonistic interactions are needed to investigate the effect of hierarchy on behavioral laterality in macaques. Studies of a greater sample of monkeys are needed, to further examine the effect of target animacy on primate lateralization and to better investigate the influence of different social interactions (e.g., agonistic contacts) on primate handedness. Finally, our study highlights the importance of research investigating hand preference as well as other behavioral asymmetries to better understand cognitive and emotional functions of the primate brain.

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