



Preliminary investigation of foot preference for a string-pulling task in ZOO macaws

Barbara Regaiolli ^{a,*}, Sofia Bolcato ^b, Giorgio Ottolini ^a, Giorgio Vallortigara ^c, Dietelmo Pievani ^b, Caterina Spiezio ^a

^a Parco Natura Viva-Garda Zoological Park, Bussolengo, VR, Italy

^b Department of Biology, University of Padua, Padua, Italy

^c Centre for Mind/Brain Sciences, University of Trento, Rovereto, Italy

ARTICLE INFO

Keywords:

Ara spp.

Problem solving

Motor lateralization

Performance

ABSTRACT

Cognitive abilities have been found to vary widely among parrots, within and between species, and seem to be related to motor lateralization. Indeed, as shown in Australian parrots and other species, lateralized psittacines perform better in cognitive tests than non-lateralized subjects. The aim of this study was to assess foot preference of seven macaws of three different species (red-and-green macaw, *Ara chloropterus*; blue-and-yellow macaw, *A. ararauna*, scarlet macaw, *A. macao*) during two string-pulling tasks of different complexity (Experiment 1: parallel string, Experiment 2: crossed strings). We also investigated the correlation between the foot preference and the performance of the macaws (as proportion of correct choices during the first pulling-up of the string of the apparatus). Per experiment and per subject, we did ten 1-h sessions. We video-recorded all pulling-up events during the interaction with the apparatus and collected data from the videorecording using a continuous focal animal sampling. In both experiments, all macaws that interacted with the apparatus solved the tasks. The percentage of correct pulling-up responses ranged from 86 % to 100 % in Experiment 1 and from 40 % to 79 % in Experiment 2. We found foot preferences at the individual level in most of the macaws in both experiments, with the presence of right-footed, left-footed and ambi-preferent subjects. No group-level biases were found. No correlation between foot preference's indices and the percentage of correct choices emerged, suggesting that neither the direction nor the strength of lateralization seem to affect the performance of the subjects. However, as most of the macaws were lateralized and were able to solve the tasks, particularly in Experiment 1, there is a possible correlation with lateralization on the cognitive performance at individual level. Our results increase the knowledge of parrots' cognitive abilities. However, future studies should be done to increase the sample size and investigate the effect of age, sex and species on foot preference during specific tasks in macaws.

1. Introduction

Studying motor asymmetries such as limb lateralization or eye preferences during different tasks or in different contexts may represent a helpful non-invasive tool to investigate cerebral lateralization in animals. Right or left hemispheres process respectively different stimuli and situations, leading to a preferential use of the contralateral side of the body (Rogers, 2009; Rogers et al., 2013).

Research on lateralization of foot use in psittacines revealed a heterogeneous picture of their motor asymmetries, as some species show a population-level left-foot preference (Friedmann and Davis, 1938; Rogers, 1980; *Psittacula krameri*: Randler et al., 2011), whereas other

species are characterized by a right bias or by an equally proportion of left, right and ambi-preferent individuals (Australian parrots: Magat and Brown, 2009; Brown and Magat, 2011a, 2011b).

The cognitive abilities of psittacines have been found to vary within and between species (Pepperberg, 2004; Gajdon et al., 2006; Liedtke et al., 2011; Cussen and Mench, 2014) and a possible explanation can reside in their cerebral lateralization (Rogers, 1996; Magat and Brown, 2009; Brown and Magat, 2011a,b). Indeed, in Australian parrots, individuals with stronger limb and eye preferences performed better than non-lateralized subjects in problem solving tasks requiring the birds to find food among pebbles and manipulative skills, specifically the string-pulling task (Magat and Brown, 2009). Similar findings were

* Corresponding author at: Parco Natura Viva-Garda Zoological Park, Loc. Figara, 40, 37012, Bussolengo, VR, Italy.

E-mail address: barbara.regaiolli@parconaturaviva.it (B. Regaiolli).

<https://doi.org/10.1016/j.applanim.2021.105307>

Received 31 December 2020; Received in revised form 15 March 2021; Accepted 21 March 2021

Available online 26 March 2021

0168-1591/© 2021 Elsevier B.V. All rights reserved.

reported also in pigeons (*Columba livia*) (Gunturkun et al., 2000), domestic chicks (*Gallus gallus*) (Rogers et al., 2004) and across vertebrates, in which the evolution of cerebral lateralization seems to be associated with enhanced cognitive abilities (Rogers, 2000; Rogers et al., 2004). In Australian parrots, the strength rather than the direction of lateralization seems to be relevant in determining a functional advantage during problem solving (Magat and Brown, 2009). However, little is known on laterality and cognitive performance in neotropical parrots such as macaws.

The string-pulling task is used to test the ability of individuals to reach for an item suspended from a string. The string-pulling task involves the integration of different movements in a specific sequence to successfully solve a problem and requires coordination between beak and feet as well as a series of actions involving pulling and grasping of the string to reach the reward (Heinrich, 1995; Magat and Brown, 2009; Krasheninnikova et al., 2013; Jacobs and Osvath, 2015; Gaycken et al., 2019). The ability to solve string-pulling tasks with several strings having different orientations spontaneously and on the first exposure suggests an understanding of means-end relationships between the string and the food (Heinrich, 1995; Pepperberg, 2004; Heinrich and Bugnyar, 2005; Bagozkaya et al., 2010). This ability has been found in corvids and parrots, that were able to solve these tasks spontaneously, although with interindividual and interspecific variation (Krasheninnikova & Wanker, 2010; Krasheninnikova et al., 2013). Krasheninnikova and colleagues tested spectacled parrotlets (*Forpus conspicillatus*), rainbow lorikeets (*Trichoglossus haematodus*), green-winged macaws (*Ara chloroptera*) and sulphur-crested cockatoos (*Cacatua galerita triton*) in different string-pulling tasks, including tasks with parallel and crossed strings. The authors found that 75 % of the birds solved the task with parallel strings on their first trial, whereas over 60 % of birds solved the task with crossed strings at the first trial, although macaws of the study performed less well than parrotlets, lorikeets and cockatoos (Krasheninnikova et al., 2013). Similarly, red-and-green macaws (*Ara chloropterus*) were able to solve single pull-up string tests, in which they were asked to reach for food on a single string, but failed in a pull-down apparatus, requiring non-intuitive actions with less clear or traceable visual feedback (Gaycken et al., 2019).

Regarding the use of the string-pulling task in the study of lateralization, research on different species of Australian parrots (cockatiel: *Nymphicus hollandicus*; budgerigar: *Melopsittacus undulatus*; galah: *Eolophus roseicapilla*; gang-gang cockatoo: *Callocephalon fimbriatum*; red-tailed black cockatoo: *Calyptorhynchus banksia*; sulphur-crested cockatoo: *Cacatua galerita*; king parrots: *Alisterus scapularis* and superb parrots: *Polytelis swainsonii*) revealed that strongly lateralized birds, regardless of the direction of the bias, performed better than non-lateralized subjects in solving the string-pulling task, supporting the hypothesis that laterality could enhance cognition (Magat and Brown, 2009). However, more studies on different species of parrots with distinct foraging strategies and occupying various ecological niches are needed to better understand the link between laterality and cognitive skills.

Studies on parrots' lateralization focused mainly on species such as Australian parrots (Magat and Brown, 2009; Brown and Magat, 2011a) and Amazon parrots (*Amazona* spp.) (Cussen and Mench, 2014).

The aim of this study was to assess the foot preference of three species of zoo macaws in two string-pulling tasks of different complexity. We also investigated the relationship between the foot preference and the performance of the macaws, scored as the proportion of correct choices during the first interactions (pulling up of the string) with the apparatus. We gave the string-pulling tasks to red-and-green macaws (*Ara chloropterus*), scarlet macaws (*A. macao*) and blue-and-yellow macaws (*A. ararauna*), housed together in a mixed-species aviary. We recorded the foot used to pull the string (pulling up) and noted whether the choice of the string was correct (string with peanut) or not (empty string). Little is known on individual-level and group-level biases in foot use in macaws. However, based on previous research on other

parrots, we expected that: 1) most of the individuals would show a foot preference to solve the task; 2) lateralized macaws would have an advantage in solving both string-pulling tasks.

2. Material & methods

2.1. Study subjects and area

Subjects of this study were seven adult macaws of different species: four red-and-green macaws (*Ara chloropterus*), one blue-and-yellow macaw (*Ara ararauna*) and two scarlet macaws (*Ara macao*) (Fig. 1). All subjects were born in zoos and parent reared. Macaws of the study were housed together in a 400 m² mixed-species free-flight aviary built on a sloping area, containing a variety of trees and shrubs, rocks, several perches, a small waterfall and a pool. An old female blue-and-yellow macaw was housed in the aviary with the study macaws but was not involved in the study due to the lack of interaction with the apparatus. Visitors could see the macaws from a window on one side of the aviary. The main meal of the macaws was made of seeds, fresh fruits, vegetables and legumes, whereas food items such as peanuts, nuts, cornflakes, corn, crackers and carobs were provided as environmental enrichments. Food was provided once a day in three feeding points in the middle of the aviary. Macaws were involved in an environmental enrichment program and received different types of enrichment devices five to seven times a week. Enrichment devices could be paper cup or cloth bundles filled with food rewards, whole (or big pieces of) fruit hung around in the aviary and fresh browse. Water was available ad libitum. The zookeepers entered the enclosure only for husbandry procedures (feeding and cleaning) and direct physical interaction between humans and macaws was not allowed.

2.2. Apparatus and experiments

The study apparatus was a bamboo rod (approximately 25 cm long, with a diameter of approximately 1 cm) with two strings on the

Subject	Species	Total N interactions
A	Red-and-green Macaw	60
B	Red-and-green Macaw	70
C	Red-and-green Macaw	50
D	Red-and-green Macaw	24
F	Blue-and-yellow Macaw	44
G	Scarlet Macaw	11
H	Scarlet Macaw	20

Fig. 1. Study macaws. For each macaw of the study, the figure reports the identification letter, the species and the total number of interactions (pulling up) with the apparatuses.

extremities. The strings were approximately 30–35 cm long and each string was fastened to one extremity of the rod (Fig. 2). All strings consisted of natural hemp twines. We fixed a peanut at the end of only one of the two strings, while the other end was empty. We tied the apparatus on the underside of horizontal bamboo perches and branches placed in the central area of the aviary through a natural hemp twine string fixed in the middle of the bamboo rod. In almost all cases, macaws could only access the apparatus by landing on the top of it, while the peanut was hanging down. However, if macaws were able to access the apparatus from the side or in different ways, data on foot preference were discarded. We carried out the experiment in the study aviary and all macaws could decide freely whether to interact with the apparatus or not. To avoid competition between individuals, for each session, we provided 24 bamboo rods to the macaws (approximately three rods per subject) and to each rod a piece of apparatus was attached. The minimum distance between two rods was one meter. Rarely, two birds decided to interact with the same apparatus. As this interaction could affect their choices of the string and their performance, we did not score data in these ambiguous circumstances. In Experiment 1 (E1), the two strings were parallel (Fig. 2A) whereas in Experiment 2 (E2) the strings were crossed (Fig. 2B). To reach for the suspended peanut, macaws had to pull up the correct string with the foot and/or with the beak to get closer to it. The position of the peanut (on the right or on the left string) was randomized across apparatus. The experimental equipment was provided in the morning before the feeding time. However, macaws were not starving as bowls with remaining fruits/vegetable and seeds of the day before the experiment were removed only when new food was provided.

2.3. Procedure and data collection

The study was carried out in June and July 2018. Experiment 1 was carried out in June, Experiment 2 in July. Both experiments took place in the same aviary and bamboo rods were placed in the same area (long perches and branches). All sessions were video-recorded and we obtained data from the recordings using a continuous focal animal sampling (Altmann, 1974). We used a digital video camera (Sony Handycam FDR-AX53) on a tripod that was fixed and wide angle, with a view of the central area of the aviary with the experimental equipment (approximately 75 % of the aviary). Only one observer (S.B.) carried out the data collection in both experiments. The observer and the camera were placed at the main window of the aviary, on the visitors' path, in front of the perches with the experimental equipment. Thus, we collected data on all birds that interacted with the apparatus. The macaws were used to the presence of the camera and the observer thanks to a preliminary observation period of approximately one month, so that the data

collection did not interfere with the spontaneous activities of the macaws. During this preliminary observation period, the observer learned to recognize the study macaws through live observation and through the observation of the video-recordings. For each experiment (E1 in June and E2 in July), we did ten 1-h sessions, one session per day for non-consecutive random ten days, recording from 11.00–12.00. All experimental equipment was removed at the end of each session. We analyzed each session for each macaw and collected 600 min of recordings per subjects per period. We recorded the foot use for all actions directed toward the apparatus, specifically manipulation of the rod or the string, pulling up the string (thereafter referred simply to "pulling up") and reaching for the peanut (when present). However, we recorded enough data for analyses only for pulling up, and that was therefore the only action considered to assess foot preference in the current study. We did not score foot preference in situations in which the foot work was not clearly observable (e.g., when a bird turned its back to the observer/camera). Macaws could also use the beak to pull the string, but we only scored events performed with the foot. Foot preference was evaluated considering two measures: 1) *all interactions*: that is the number of right- and left-foot pulling-up events over all sessions; 2) *first interactions*: that is the number of right- and left-foot pulling-up events during the first interaction only with each of the apparatus explored by each macaw, over all sessions. In other words, if a macaw approached an apparatus and pulled the string on its right and immediately after pulled the other string, only the first pulling-up event was considered for this measure. First interactions were collected every time a macaw started to pull up the string of a different apparatus, so that more pulling-up interactions per session could be collected. The comparison of foot preference during *first interactions* and *all interactions* would allow verification of whether and how practice could affect the foot use in the study macaws.

To assess the performance of the macaws, per subject and per experiment, we also recorded the frequency of correct (and incorrect) choices, scored as the number of times each macaw used one foot to pull up the string with or without the peanut. As for foot preference during *first interactions*, we considered correct choices only those choices made during the first pulling-up event with each apparatus (consecutive choices on the same apparatus were not included). Hereafter "correct choice" refers to the individual bird choosing the right string that carries a peanut. To evaluate whether a macaw solved the task, we used the Binomial sign test to compare the number of correct choices with the total number of choices, to be sure that correct choices were not due to chance. Thus, only macaws scoring the number of correct choices significantly higher than the number of incorrect choices were considered successful in solving the string-pulling task. First choices were recorded every time each macaw pulled up a string of a different apparatus. We decided to consider only first choices between the two strings to evaluate the performance of the macaws as previous studies using the string-pulling task suggested that birds which successfully complete this problem on first exposure demonstrate cognitive skill and are more likely to show means-end comprehension, especially in the crossed-string paradigm (Pepperberg, 2004; Heinrich and Bugnyar, 2005; Magat and Brown, 2009; Jacobs and Osvath, 2015). The same observer (S.B.) collected data during both experiments.

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 non-invasive study is required, as zoological gardens in Italy are expected to carry out behavioral observations of individuals in their care (D. Lgs.73/2005).

2.4. Data analysis

We used non-parametric statistical tests to perform all the analyses and all tests were two tailed. To evaluate the performance of the macaws between the two tasks, we compared the % of correct choices between

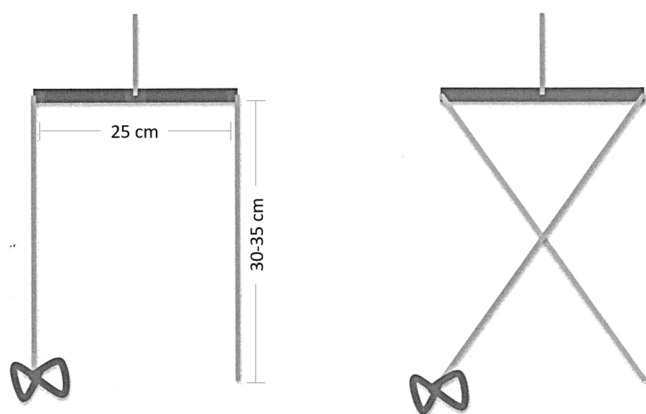


Fig. 2. schematic representation of the string-pulling tasks provided to the study macaws. On the left: the apparatus used in Experiment 1 (parallel strings). On the right: the apparatus used in Experiment 2 (crossed strings).

the two experiments using the Wilcoxon test.

At the individual level, we assessed foot preference using the Laterality Index (LI) given by the formula (right foot events – left foot events)/(right foot events + left foot events). The LI is similar to the Handedness Index used in the study of hand preference and ranges between -1.00 (left preference) and +1.00 (right preference) (Hopkins, 1999). The absolute values of the LI (ABS-LI) indicate the strength of the foot preference (Hopkins, 1999, 2013). To classify the macaws based on the foot use, we used binomial z-scores to classify the subjects as left-foot preferent ($z \leq -1.96$), right-foot preferent ($z \geq 1.96$) or ambi-preferent ($-1.96 < z < 1.96$) (McGrew and Marchant, 1997; Michel et al., 2002). For the individual-level analyses, for both first interactions and all interactions, we calculated the z-score only for macaws that performed a minimum of ten pulling-up interactions (Meguerditchian and Vaclair, 2009; Meguerditchian et al., 2010; Spiezio et al., 2016). We used this criterion to analyze data of both experiments pooled together (overall foot preference) and within each experiment.

To verify whether and how practice could affect the foot preference of macaws, we used Spearman correlations to compare the LI values relative to the first interactions with the LI values relative to all interactions. We used the one-sample sign-test to test the symmetry of the LI distribution for overall foot preference and in each experiment (e.g., Meunier et al., 2011; Spinozzi et al., 1998). We used Spearman correlations to assess the degree of concordance among different foot preference measures (overall vs. per experiment). Bonferroni adjustment was used to correct the p-value for multiple comparisons (adjusted p-value for three comparisons: $p = 0.017$).

To test whether foot lateralization could be related to the problem-solving ability of the macaws, for each experiment, we correlated the LI and the ABS-LI of first interactions with the % of correct choices (N° of pulling-up events on the string with a peanut/total number of pulling-up events) using Spearman correlations. We performed the same analysis with data of both experiments pooled together (overall LI and ABS-LI and overall number of correct choices). Significance level was set at $p < 0.05$. In the Results, we reported medians and interquartile ranges (IQR).

3. Results

In Experiment 1, all macaws (N = 7) interacted with the apparatus and solved the task. The percentage of correct choices during the first interaction ranged from 86 % to 100 % (median [IQR]: 100 [0]) (Table 1). In Experiment 2, all macaws except for G (N = 6) interacted with the apparatus and three of them successfully solved the tasks. The percentage of correct choices ranged from 40 % to 79 % (65 [25.5]) (Table 1). Overall, regardless of the experiment, the percentage of correct choices ranged from 68 % to 92 % (86 [14]) (Table 1). When comparing the % of correct choices between the two experiments, we found that macaws chose the correct string more in Experiment 1 than in Experiment 2 (Wilcoxon test: $W = 0, p < 0.05, N = 6$).

The LI for all interactions were positively correlated with the LI for first interactions, indicating that the first foot used to fish for the string was representative of further interactions (Overall: $r = 0.964, p = 0.0005$; E1: $r = 0.857, p = 0.014$; E2: $r = 0.829, p = 0.042$). Thus, all analyses to determine foot preference were done considering all interactions with the apparatus.

3.1. Foot preference in macaws

When pooling together data of Experiment 1 and 2 (overall foot preference), the median (IQR) LI was -0.26 (1.02) and the median ABS-LI was 0.44 (0.64). At the individual level, 5 of 7 macaws showed a significant foot preference: the *A. chloropterus* (2 left-foot and 2 right-foot-preferent) and one *A. macao* (left-foot preferent), whereas the *A. ararauna* was ambi-preferent (Table 2). The one-sample sign-test revealed no group-level bias in overall foot preference ($p = 0.1$).

Table 1
Foot preference for first interactions in the study macaws.

	Overall (Exp 1 + Exp 2)																		
	Experiment 1					Experiment 2													
	N	LI	z-score	p-value	Pref.	% correct choices	N	LI	z-score	p-value	Pref.	% correct choices							
A	<i>A. chloropterus</i>	25	-0.60	-2.80	0.004	Left	100*	14	-1.00	-3.47	$p < 0.001$	Left	79*	39	-0.74	-4.48	$p < 0.001$	Left	92*
B	<i>A. chloropterus</i>	37	0.62	3.62	0.000	Right	100*	10	1.00	2.85	0.002	Right	60	47	0.70	4.67	$p < 0.001$	Right	91*
C	<i>A. chloropterus</i>	23	-0.57	-2.50	0.011	Left	100*	36	-0.22	-1.17	0.243	Ambi	69*	59	-0.36	-2.60	0.009	Left	81*
D	<i>A. chloropterus</i>	11	0.82	2.41	0.012	Right	100*	27	0.85	4.23	$p < 0.001$	Right	56	38	0.84	5.03	$p < 0.001$	Right	68*
F	<i>A. ararauna</i>	19	-0.05	0.00	1.000	Ambi	100*	13	0.69	2.22	0.022	Right	77*	32	0.25	1.24	0.215	Ambi	91*
G	<i>A. macao</i>	7	-1.00	#	#	#	86*	0	#	#	#	#	#	7	-1.00	#	#	#	86*
H	<i>A. macao</i>	8	-0.50	#	#	#	100*	5	0.20	#	#	#	40	13	-0.23	-0.55	0.581	Ambi	77*

For each macaw (*Ara spp.*), the table reports the identification letter and the species. For each experiment and for each subject, the table reports the total number of first interactions collected (N), the Laterality Index (LI), the z-score and p-value from Binomial tests, the preference (Pref.) (Right: z-score > 1.96, Left: z-score < -1.96, ambi-preferent: -1.96 < z-score < 1.96) and the percentage of correct choices (string with the peanut) during the first interactions with the apparatuses. # insufficient number of data.

* Correct choice significantly more than wrong choice (Sign test: $p < 0.05$).

Table 2
Foot preference in the study macaws.

		Experiment 1				Pref.	Experiment 2				Pref.	Overall (Exp 1 + Exp 2)				Pref.
		N	LI	z-score	p-value		N	LI	z-score	p-value		N	LI	z-score	p-value	
A	<i>A. chloropterus</i>	42	-0.48	-2.93	0.003	Left	29	-0.72	-3.71	<0.001	Left	71	-0.58	-4.75	0.000	Left
B	<i>A. chloropterus</i>	50	0.36	2.40	0.016	Right	18	0.67	2.59	0.010	Right	68	0.44	3.52	0.000	Right
C	<i>A. chloropterus</i>	39	-0.59	-3.52	<0.001	Left	56	-0.04	-0.13	0.897	Ambi	95	-0.26	-2.46	0.014	Left
D	<i>A. chloropterus</i>	14	0.86	2.94	0.003	Right	45	0.91	5.96	<0.001	Right	59	0.90	6.77	<0.001	Right
F	<i>A. ararauna</i>	31	-0.23	-1.08	0.280	Ambi	19	0.68	2.75	0.006	Right	50	0.12	0.71	0.478	Ambi
G	<i>A. macao</i>	10	-1.00	-2.85	0.004	Left	0	#	#	#	#	10	-1.00	-2.85	0.004	Left
H	<i>A. macao</i>	12	-0.67	-2.02	0.043	Left	7	0.14	#	#	#	19	-0.37	-1.38	0.168	Ambi

For each macaw (*Ara* spp.), the table reports the identification letter and the species. For each experiment and for each subject, the table reports the total number of interactions with the apparatuses (all interactions) collected (N), the Laterality Index (LI), the z-score and p-value from Binomial tests, the preference (Pref.) (Right: z-score > 1.96, Left: z-score < -1.96, ambi-preferent: -1.96 < z-score < 1.96) and the percentage of correct choices (string with the peanut) during the first interactions with the apparatuses. # insufficient number of data.

In Experiment 1, the median (IQR) LI was -0.48 (1.03) and the median ABS-LI was 0.59 (0.50) (Fig. 3). At the individual level, 6 of 7 macaws showed a significant foot preference: the *A. chloropterus* (2 left-foot and 2 right-foot preferent) and both *A. macao* (left-foot preferent) whereas the *A. ararauna* was ambi-preferent (Table 2). The one-sample sign-test revealed no group-level bias in foot preference ($p = 0.453$) (Fig. 3).

In Experiment 2, the median (IQR) LI was 0.40 (0.95) and the median ABS-LI was 0.68 (0.95) (Fig. 3). At the individual level, 6 of 7 macaws interacted with the apparatus. The only *A. macao* that interacted with the apparatus did not perform enough events to be included in the individual-level analysis. Thus, 4 of 5 macaws showed a significant foot preference: 3 *A. chloropterus* (2 right-foot, 1 left-foot preferent) and the *A. ararauna* (right-foot preferent) whereas 1 *A. chloropterus* was ambi-preferent (Table 2). The one-sample sign-test revealed no group-level bias in foot preference ($p = 0.688$) (Fig. 3).

When focusing on the degree of concordance among different foot preference measures (overall vs. per experiment), we found that the LI for overall foot preference were positively correlated with the LI of Experiment 1 (Spearman corr.: $r = 0.893$, $p = 0.007$, $N = 7$, Bonferroni adjusted p -value: 0.017) but not with the LI of Experiment 2 ($r = 0.886$, $p = 0.019$, $N = 6$, Bonferroni adjusted p -value: 0.017). No correlation was found between the LI of Experiment 1 and 2 ($r = 0.714$, $p = 0.111$, $N = 6$).

3.2. Foot preference and problem-solving performance

When pooling together data of both experiments, we found no significant correlation between the LI and the percentage of correct choices (Spearman corr.: $r = -0.342$, $p = 0.452$, $N = 7$). We found the same result considering the ABS-LI ($r = 0.036$, $p = 0.939$, $N = 7$).

In Experiment 1, we found no significant correlation between the LI and the percentage of correct choices (Spearman corr.: $r = 0.612$, $p = 0.144$, $N = 7$). We found the same result considering the ABS-LI ($r = 0.612$, $p = 0.144$, $N = 7$).

In Experiment 2, we found no significant correlation between the LI and the percentage of correct choices (Spearman corr.: $r = -0.486$, $p = 0.329$, $N = 6$). We found the same result considering the ABS-LI ($r = 0.464$, $p = 0.354$, $N = 6$).

4. Discussion

The string-pulling task has been extensively used for studies of cognitive function and motor lateralization in avian species, including psittacines (Magat and Brown, 2009; Jacobs and Osvath, 2015; Krasheninnikova, 2013; Gaycken et al., 2019), but there are few if any investigations on this topic in macaws. All macaws of the study interacted with the apparatus and solved the string-pulling task with parallel strings (Experiment 1), choosing to pull the correct string on average 98 % of the times. In Experiment 2, in which the strings were crossed and the difficult to solve the task increased, not all macaws interacted with the apparatus (6 out of 7) and half of them successfully solved the task,

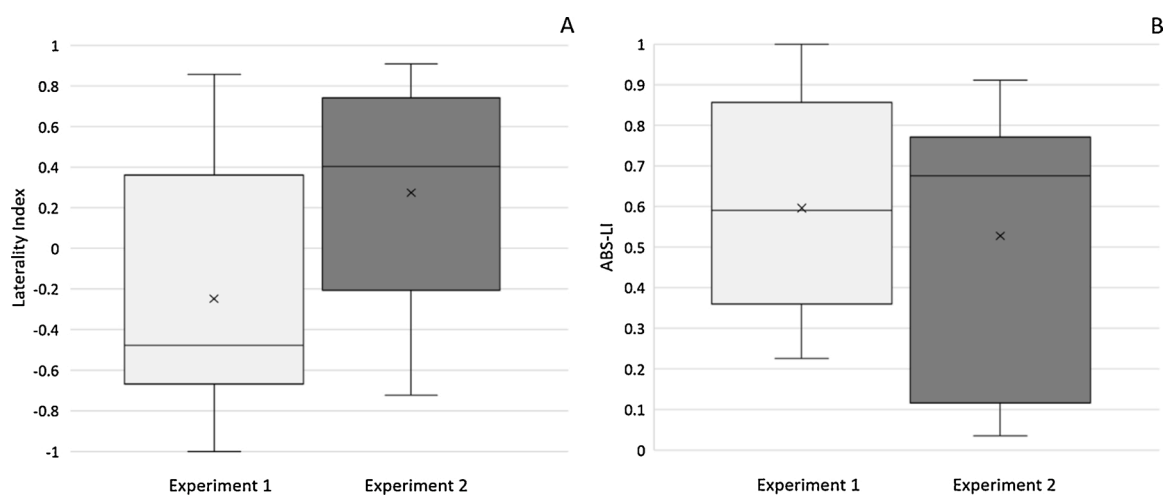


Fig. 3. Foot preference (LI) (A) and strength of the foot preference (ABS-LI) (B) of the study macaws in the two experiments. Horizontal lines within boxes indicate the medians, boundaries of the boxes indicate the first and third quartile, crosses indicate the mean. Whiskers extend up from the top of the box to the largest data element that is less than or equal to 1.5 times the interquartile range (IQR) and down from the bottom of the box to the smallest data element that is larger than 1.5 times the IQR. Values outside this range are outliers and are drawn as points.

pulling the correct string. In this experiment, macaws varied in their performance and chose the correct string on average 63 % of the times, with the number of correct choices above chance level ($p < 0.05$). The percentage of correct choices was significantly higher in Experiment 1 than in Experiment 2, indicating that macaws needed a greater number of trials to solve the crossed-string task ($p < 0.05$). These results suggest that macaws have more difficulty to understand the relation between the string and the reward and have a higher failure rate in the crossed-string condition. Our results add to previous research on avian cognition suggesting that these neotropical parrots share similar cognitive abilities with other birds, particularly corvids and psittacines (Schuck-Paim et al., 2009; Taylor et al., 2009, 2010; Krasheninnikova et al., 2013; Jacobs and Osvath, 2015; Gaycken et al., 2019).

Since the foot used by macaws in the study in the first interactions with the apparatus was the same used in all other interactions, it seems that they chose the preferred foot at first and this can become a well-defined action pattern (Goldberg and Costa, 1981; Regaioli et al., 2015).

When considering the overall foot preference (all interactions, Table 2), we found individual-level biases, with approximately 86 % of the macaws showing a preferential use of one foot when interacting with the apparatus. At the group level, no foot preference was reported as both right-footed and left-footed individuals were present in the study sample. Our results are not consistent with studies highlighting a population level foot preference in parrots (Friedmann and Davis, 1938; *Psittacula krameri*: Randler et al., 2011) but this could be due to our small sample size.

Lateralization has been linked to cognition in different animal species (Rogers, 2000), including parrots tested on the string-pulling tasks similarly to those adopted in the current study (Magat and Brown, 2009). We did not find relationships between the foot preference (LI) and its strength (ABS-LI) and the performance of the macaws when choosing the correct string and retrieving the suspended reward suggesting that the strength and the direction of laterality might be shaped also by ecological variables (Brown and Magat, 2011b). However, macaws of the current study were generally able to solve the tasks, especially in Experiment 1, with a high proportion of correct choices (98 % and 63 % in Experiment 1 and 2, respectively) and were also significantly lateralized, so that the presence of individual-level lateralization, regardless to the direction of biases, could have played a role in the success of the macaws in the two experiments (Magat and Brown, 2009; Cussen and Mench, 2014). Our findings seem to support the evolutionary hypothesis suggested by results from studies on Australian psittacines, according to which laterality in these species could have been shaped by few events in their history. In particular, the authors suggested that cerebral lateralization might provide a fitness benefit to larger bodied species that extract seeds from seedpods using coordinated foot-beak actions and this seem to be also the case of *Ara* parrots, too (Brown and Magat, 2011b).

In conclusion, when interacting with string-pulling tasks of different complexity, most macaws of the study were able to solve the simple task, half of them were able to also solve the complex task and they showed a foot preference at the individual level. Thus, the ability to solve a task and the lateralization of the individual seem to be linked. The direction of lateralization seemed not to affect the performance of the subjects as right and left-footed birds were randomly distributed within each experiment. Despite the small number of macaws, our findings improve the knowledge on macaws' cognition and motivate future research on lateralization and cognitive performance in macaws, investigating the effect of factors such as age, sex, and species.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

Acknowledgements

We would like to thank Dr. Cesare Avesani Zaborra and Camillo Sandri for allowing this study to take place in Parco Natura Viva. Special thanks should be given to Giuseppe Alampi and Victor Orozco Buides for their support during the provision of the apparatuses and the husbandry of the macaws. We gratefully acknowledge the anonymous reviewers for their useful revisions that improved notably the form, precision, and contents of the manuscript. We would finally like to thank Prof. Lesley J. Rogers Ed. for giving us the opportunity to publish on this special issue and to contribute to the fascinating debate on lateralization in animals.

References

- Altmann, J., 1974. Observational study of behaviour: sampling methods. *Behaviour* 49, 227–266.
- Bagozkaya, M.S., Smirnova, A.A., Zorina, Z.A., 2010. Comparative study of the ability to solve a string-pulling task in Corvidae. *Zh Vyssh Nerv Deyat* 60, 321–329.
- Brown, C., Magat, M., 2011a. Cerebral lateralization determines hand preference in Australian parrots. *Biol. Lett.* 7, 496–498.
- Brown, C., Magat, M., 2011b. The evolution of lateralized foot use in parrots: a phylogenetic approach. *Behav. Ecol.* 6, 1201–1208.
- Cussen, V.A., Mench, J.A., 2014. Performance on the Hamilton search task, and the influence of lateralization, in captive orange-winged Amazon parrots. *Anim. Cogn.* 17, 901–909.
- Friedmann, H., Davis, M., 1938. 'Left-handedness' in Parrots. *Auk* 55, 478–480.
- Gajdon, G.K., Fijn, N., Huber, L., 2006. Limited spread of innovation in a wild parrot, the kea (*Nestor notabilis*). *Anim. Cogn.* 9, 173–181.
- Gaycken, J., Picken, D.J., Pike, T.W., Burman, O.H., Wilkinson, A., 2019. Mechanisms underlying string-pulling behaviour in green-winged macaws. *Behaviour* 156, 619–631.
- Goldberg, E., Costa, L., 1981. Hemisphere differences in the acquisition and use of descriptive systems. *Brain Lang.* 14, 144–173. [https://doi.org/10.1016/0093-934X\(81\)90072-9](https://doi.org/10.1016/0093-934X(81)90072-9).
- Gunturkun, O., Diekamp, B., Manns, M., Nottelmann, F., Prior, H., Schwarz, A., Skiba, M., 2000. Asymmetry pays: visual lateralization improves discrimination success in pigeons. *Curr. Biol.* 10, 1079–1081.
- Heinrich, B., 1995. An experimental investigation of insight in common ravens (*Corvus corax*). *Auk* 112, 994–1003.
- Heinrich, B., Bugnyar, T., 2005. Testing problem solving in ravens: string-pulling to reach food. *Ethology* 111, 962–976. <https://doi.org/10.1111/j.1439-0310.2005.01133.x>.
- Hopkins, W.D., 1999. On the other hand: statistical issues in the assessment and interpretation of hand preference data in non-human primates. *Int. J. Primatol.* 20, 852–866.
- Hopkins, W.D., 2013. Independence of data points in the measurement of hand preferences in primates: statistical problem or urban myth? *Am. J. Phys. Anthropol.* 151, 151–157. <https://doi.org/10.1002/ajpa.22248>.
- Jacobs, I.F., Osvath, M., 2015. The string-pulling paradigm in comparative psychology. *J. Comp. Psychol.* 129, 89–120.
- Krasheninnikova, A., 2013. Patterned-string tasks: relation between fine motor skills and visual-spatial abilities in parrots. *PLoS One* 8, e85499. <https://doi.org/10.1371/journal.pone.0085499>.
- Krasheninnikova, A., Bräger, S., Wanker, R., 2013. Means-end comprehension in four parrot species: explained by social complexity. *Anim. Cogn.* 16, 755–764.
- Liedtke, J., Werdenich, D., Gajdon, G.K., Huber, L., Wanker, R., 2011. Big brains are not enough: performance of three parrot species in the trap-tube paradigm. *Anim. Cogn.* 14, 143–149.
- Magat, M., Brown, C., 2009. Laterality enhances cognition in Australian parrots. *Proc. R. Soc. B Biol. Sci* 276, 4155–4162.
- McGrew, W.C., Marchant, L.F., 1997. On the other hand: current issues and metaanalysis of the behavioral laterality of hand function in non-human primates. *Yearb. Physic. Anthropol.* 40, 201–232.
- Meguerditchian, A., Vauclair, J., 2009. Contrast of hand preferences between communicative gestures and non communicative actions in baboons: implications for the origins of hemispheric specialization for language. *Brain Lang.* 108, 167e174.
- Meguerditchian, A., Vauclair, J., Hopkins, W.D., 2010. Captive chimpanzees use their right hand to communicate with each other: implications for the origin of the cerebral substrate for language. *Cortex* 46, 40–48.
- Meunier, H., Blois-Heulin, C., Vauclair, J., 2011. A new tool for measuring hand preference in non-human primates: adaptation of Bishop's quantifying hand preference task for olive baboons. *Behav. Brain Res.* 218, 1–7. <https://doi.org/10.1016/j.bbr.2010.11.011>.
- Michel, G.F., Sheu, C., Brumley, M.R., 2002. Evidence of a right-shift factor 682 affecting infant hand-use preference from 7 to 11 months of age as revealed by latent class analysis. *Dev. Psychobiol.* 40, 1–13.
- Pepperberg, I.M., 2004. "Insightful" string-pulling in grey parrots (*Psittacus erithacus*) is affected by vocal competence. *Anim. Cogn.* 7, 263–266.
- Randler, C., Braun, M., Lintker, S., 2011. Foot preferences in wild-living ring-necked parakeets (*Psittacula krameri*, Psittacidae). *Laterality* 16, 201–206.

- Regaiolli, B., Spiezio, C., Vallortigara, G., 2015. Manual lateralization in macaques: handedness, target laterality and task complexity. *Laterality* 20, 1–8. <https://doi.org/10.1080/1357650X.2015.1076834>.
- Rogers, L.J., 1980. Lateralisation in the avian brain. *Bird Behav* 2, 1–12.
- Rogers, L.J., 1996. Behavioral, structural and neurochemical asymmetries in the avian brain: a model system for studying visual development and processing. *Neurosci. Biobehav. Rev.* 20, 487–503.
- Rogers, L.J., 2000. Evolution of hemispheric specialization: advantages and disadvantages. *Brain Lang.* 73, 236–253.
- Rogers, L.J., 2009. Hand and paw preferences in relation to the lateralized brain. *Proc. R. Soc. B* 364, 943–954.
- Rogers, L.J., Zucca, P., Vallortigara, G., 2004. Advantages of having a lateralized brain. *Proc. R. Soc. Lond. B* 271, S420–S422. <https://doi.org/10.1098/rsbl.2004.0200>.
- Rogers, L.J., Vallortigara, G., Andrew, R.J., 2013. *Divided Brains: the Biology and Behaviour of Brain Asymmetries*. Cambridge University Press.
- Schuck-Paim, C., Borsari, A., Ottoni, E.B., 2009. Means to an end: neotropical parrots manage to pull strings to meet their goals. *Anim. Cogn.* 12, 287–301. <https://doi.org/10.1007/s10071-008-0190-z>. PubMed: 18766389.
- Spiezio, C., Regaiolli, B., Vallortigara, G., 2016. Motor and postural asymmetries in marsupials: forelimb preferences in the red-necked wallaby (*Macropus rufogriseus*). *Behav. Proc.* 128, 119–125. <https://doi.org/10.1016/j.beproc.2016.04.019>.
- Spinozzi, G., Castorina, M.G., Truppa, V., 1998. Hand preferences in unimanual and coordinated-bimanual tasks by tufted capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* 112, 183–191. <https://doi.org/10.1037/0735-7036.112.2.183>.
- Taylor, A.H., Hunt, G.R., Roberts, R., Gray, R.D., 2009. Causal reasoning in New Caledonian crows: ruling out spatial analogies and sampling error. *Comm. Integ. Bio* 2, 311–312.
- Taylor, A.H., Medina, F.S., Holzhaider, J.C., Hearne, L.J., Hunt, G.R., Gray, R.D., 2010. An investigation into the cognition behind spontaneous string pulling in new caledonian crows. *PLoS One* 5, e9345. <https://doi.org/10.1371/journal.pone.0009345>.