Behavioural Processes 167 (2019) 103899

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Personality and lateralization in common marmosets (*Callithrix jacchus*)

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ARTICLE INFO

Keywords:
Personality factors
Inter-individual behavioural differences
Hand preference
Mixed-handedness
Openness
Brain lateralization

ABSTRACT

Specialization of the left and right hemispheres to control behavioural responses may represent one of the mechanisms underlying individual differences in personality structure, as well as the preferential use of one hand. The present study investigated the relationship between personality and hand preference in common marmosets (*Callithrix jacchus*), a little New World monkey that presents highly consistent and stable individual hand preferences for simple reaching. To address this issue, data on 56 different behaviours from the species' behavioural repertoire were measured in 10 different laboratory tests and during observations under social conditions on 16 adult common marmosets. Stable behavioural variables were aggregated *a priori* into 13 personality traits. Exploratory Factor Analysis (EFA) on personality traits was carried out to verify the presence of major personality factors, and their relationship with direction and strength of individual hand preferences was assessed by multiple regression, taking into account sex and age of the subjects. The largest number of species-specific behaviours so far investigated in this species was taken into account and robust temporal stability between two testing periods was verified. We confirm that common marmosets are characterized by specific and stable personality profiles. A single personality factor, accounting for about 38% of the total variance, was found by EFA, that describes the interest towards unusual and new experiences and resembles the human *Openness* domain. The strength of the hand preference was found to be predicted by this personality factor, that we named *Inquisitiveness*. Present results highlight common marmoset as a useful primate model for the study of the relationship between personality and lateralization.

1. Introduction

Animal personality is defined as an emergent property resulting from the combination and interaction of a set of stable individual-specific behavioural patterns, commonly referred to as personality traits or components (Allport, 1937). Although human personality has a long history of research, the study of personality in animals has received considerable scientific attention more recently (Carere and Maestripieri, 2013; Gosling and John, 1999; Gosling, 2001). The growing number of studies provides considerable evidence that animals, in spite of their more or less distant phylogenetic relatedness, present personality factors that can be measured and analyzed (Uher, 2011).

In spite of the increasing interest in this topic, the proximate and ultimate mechanisms of personality differences have not been clearly established (Wolf, 2009). Indeed, personality has been reported to affect fitness and survival, suggesting a role for natural selection in shaping ecologically and evolutionarily relevant intraspecific behavioural variation (Smith and Blumstein, 2008; Wolf and Weissing, 2012). Furthermore, recent evidence suggest that a complex interplay between genetic and environmental factors accounts for the phenotypic variability at species or population levels (Bulbena-Cabre et al., 2018; Gartstein and Skinner, 2018). Further studies are however needed to clarify the underlying mechanisms.

Specialization of the left and right hemispheres to process information and to control different patterns of behaviour has been proposed as one of the neurobiological underpinnings of intraspecific behavioural variation (Rogers, 2009). Functional and structural asymmetries have been in fact reported across the vertebrate lineage, with a huge number of species presenting inter-individual differences in lateral biases, such as the preferential use of the left or right eye or limb, as well as asymmetries in the nervous system (Frasnelli et al., 2012; Rogers et al., 2013; Ocklenburg and Güntürkün, 2017). Moreover, some personality traits are linked to individual differences in behavioural lateralization across different vertebrate species (Dadda et al., 2010; Hews et al., 2004; Blatchley and Hopkins, 2010; McDowell et al., 2016)

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https://doi.org/10.1016/j.beproc.2019.103899
Received 5 October 2018; Received in revised form 28 June 2019; Accepted 2 July 2019
Available online 18 July 2019
0376-6357/

and in humans (Mascie-Taylor, 1981; Canli et al., 2001). These include boldness (Irving and Brown, 2013; Byrnes et al., 2016), fearfulness (Found, 2017; Braccini and Caine, 2009; Cameron and Rogers, 1999) as well as sociability (Farmer et al., 2018; Barnard et al., 2017). Brain lateralization may thus contribute to shaping inter-individual variability in animal personality.

Hand preference is the behavioural lateralization of choice in primates and a complex trait influenced by both genetic and non-genetic factors (Bennett et al., 2008; Suzuki and Ando, 2014; Schmitz et al., 2017). Human species show a marked preference for the right hand in all those tasks requiring the use of one hand only, such as writing (Annett, 2004; Rogers, 2002). This prominent rightward hand asymmetry has been suggested to have emerged in the course of hominid evolution (Corballis, 1989) and has been related to anatomical as well as functional brain asymmetries (for an overview see Beaton, 2004). Studies in non-human primates have highlighted both individual- and population-level asymmetries in motor tasks (Merchant and McGrew, 1991; Bradshaw and Rogers, 1993), thus questioning the historical views regarding differences in the distributions of nonhuman and human primate handedness (Hopkins, 2018).

Numerous studies on non-human primate species demonstrate an association between intraspecific behavioural variation and individual differences in the direction (left *vs* right) of hand preference (Rogers, 2009, 2018). Left-handed common marmosets (*Callithrix jacchus*) have been in fact reported to be less active in exploring novel objects, show less social facilitation of behaviour, have a negative cognitive bias, and express higher levels of fear and stress responses (Cameron and Rogers, 1999; Gordon and Rogers, 2010; Rogers, 2018). Moreover, right-handed chimpanzees appear to be more curious than left-handed ones (Hopkins and Bennet, 1994) and in Geoffroy's marmoset (*Callithrix geoffroy*), right-handed individuals are faster in approaching and sniffing novel food than left-handed ones (Braccini and Caine, 2009). Furthermore, the strength (strong *vs* weak) of hand preference has been linked to individual differences in the ability to perform two tasks at once in common marmosets (detection of a predator while searching for food) (Piddington and Rogers, 2013).

Altogether, these evidences suggest that a close association between hand preference and some personality traits may ensue in non-human primates and involve complex aspects of the personality structure of a particular individual. To test this hypothesis, in the present study we carried out a comprehensive evaluation of the personality of common marmosets (*Callithrix jacchus*), a little New World monkey widely used in biomedical research as laboratory model (Mansfield, 2003), and tested the association of personality factors with the strength and direction of unskilled individual hand preference.

Common marmosets were chosen for two reasons: first, individuals present highly consistent and stable hand preferences for simple reaching, defined as the hand used to pick up pieces of food and bring them to the mouth (Hook and Rogers, 2000; Gordon and Rogers, 2015). In fact, although the strength of hand preference is influenced by task demands in this species, highlighting the relevance of methodological issues when assessing hand preference in nonhuman primates (Hopkins, 2018), common marmosets use the same preferred hand for simple reaching across their lifetime (Hook and Rogers, 2000). Secondly, several specific personality traits [*e.g.* Curiosity (Kaplan and Rogers, 2006); Boldness and Exploratory Behaviour (Koski and Burkart, 2015); Playfulness (Chalmers and Locke-Haydon, 1984)] and personality domains (Koski et al., 2017) have been extensively investigated in this species. Moreover, recent, more comprehensive studies suggest that personality in common marmosets could be described by five dimensions as observed in humans (Iwanicki and Lehmann, 2015) and its reliability through the criteria of temporal stability has been demonstrated in this species (Šlipogor et al., 2016).

To assess the personality of 16 adult common marmosets, data on 56 different behaviours were collected in 10 different tests and during observations under social conditions within two non-overlapping periods and standardized. Temporal stability and individual differences were verified by Intraclass Correlations analyses (ICCs). Temporally stable behavioural variables were then aggregated to obtain measures of 13 personality traits. Exploratory Factor Analysis (EFA) on traits was performed to verify the presence of major personality factors. In addition, to establish the individual hand preference, the hand used to pick up pieces of food and bring them to the mouth was recorded as previously described by Hook and Rogers (2000; 2008). Regression analyses were carried out to verify the relationship between direction and strength of individual hand preferences (Hook and Rogers, 2000; 2008) with the personality factors identified by EFA.

2. Method

2.1. Study subjects

The subjects of this study were 16 adult common marmosets (*Callithrix jacchus*), 9 females and 7 males, aged between 4 and 14 years (mean age 7 years), housed at the Istituto Superiore di Sanità (Rome, Italy). The animals belonged to five family groups of different compositions.

2.2. Housing and husbandry

Each family was housed in a stainless steel cage (220 × 150 × 80 cm). The five families were all housed in the same room, thus being in constant olfactory and auditory contact with each other. Curtains partially prevented visual contact, so that monkeys were allowed to choose whether to maintain visual contact with the neighbours or not. All tests and observations were carried out in a test room provided with two experimental cages with plexiglass front doors (220 × 150 × 80 cm), to allow the recording of high quality videos during test sessions. Monkeys could reach the test room by PVC tunnels, a system of sliding windows allowed to selected subjects the access to the experimental cages. All experimental animals were familiar with the experimental cages because each family normally used them as extra space one day per week. All cages were provided with enrichments consisting of branches, nests, platforms, plastic nets, plastic objects of various shapes and dimensions. The facility was maintained at a fixed temperature of 22 °C degrees and humidity of 50%. Lighting conditions were programmed with a 12 h light/dark cycle starting at 7 a.m. Monkeys were fed in the morning with fresh fruits and a commercial cream rich in vitamins and mineral salts balanced on the specific needs of this species (Mucedola srl, Milan, Italy). Two times per week monkeys also received either boiled eggs, wax worms (*Galleria mellonella*) or arabic gum. Water and pellets were available *ad libitum*. All procedures were formally approved by Italian Ministry of Health (D. Lgs. 26/2014, transposition of Directive 2010/63/UE). Animals were kept following the guidelines from the International Primatological Society and Associazione Primatologica Italiana.

2.3. Procedure

2.3.1. Behavioural tests and observations of social behaviour

The study was carried out between May and July 2012. To assess the personality of adult common marmosets, 10 behavioural tests and observations under social conditions were carried out, as previously described by Uher et al. (2008), with some modifications to adapt it to the species under investigation (Table 1). Behavioural tests were repeated several times (number of repetitions per test are reported in Table 1), apart from the "*Masked human test*" which was conducted only twice for ethical reasons.

To assess temporal stability of the individual differences and to test if they can be interpreted as reflecting personality, behavioural tests were carried out in the same order and with the same number of repetitions, during two 15-days long periods (P_1 and P_2), separated by a

Table 1
Behavioural Tests and Observation under Social Condition.

Paradigm	Description	Behavioural variables
FOOD BOX TEST (FB)	Different kinds of food were placed inside a plexiglass box (10x4x4 cm), fixed on a wooden platform. The test consisted of four trials, in the first one the box was empty, in successive trials it was baited with a biscuit piece, banana piece and one monkey pellet. If the monkey didn't open the box, the bait was removed after 1 minute. **Duration:** max 1 minute per trial. **N° of repetitions (P_1– P_2):** 3-3	FB Touch box (Latency) FB Eat rewards (Percentage) FB Open box (Frequency) FB Deal with box (Duration)
BLOCKED FOOD BOX TEST (BFB)	A piece of biscuit was positioned in plexiglass box (same used in the previous test), which was closed with transparent adhesive tape. Monkeys could see the reward inside the box, but they couldn't reach it. **Duration:** 2 min. **N° of repetitions (P_1– P_2):** 2-2	BFB Touch box (Latency) BFB Try to open box (Duration) BFB Attempts to open box (Frequency) BFB Deal with box (Duration) BFB Vocalize (Frequency)
CAGE INTRUDER TEST (CI)	The experimenter entered in the cage adjacent to the one where the subject was, searching persistently for visual contact for one minute. Then, for two minutes the experimenter offered some biscuit pieces through the mesh of the cage. **Duration:** 2 min. **N° of repetitions (P_1– P_2):** 2-2	CI Agonistic behaviours (Frequency) CI Vocalize (Frequency) CI Take biscuit (Latency) CI Eat biscuit (Percentage) CI Proximity to intruder (Latency) CI Proximity to intruder (Duration)
HIDDEN FOOD TEST (HF)	The experimenter hid ten rewards consisting of banana and biscuit pieces inside the cage. To induce seeking behaviour, one piece of a biscuit was left in sight. **Duration:** 5 min. **N° of repetitions (P_1– P_2):** 3-3	HF Find rewards (Percentage) HF Locomotion (Scan sampling) HF Rest (Scan sampling) HF Actively searching (Duration)
BABY FOOD TEST (BF)	A plexiglass panel (20x50 cm) smeared with meat baby food was placed 2 cm away from the cage. Subjects could reach baby food through the mesh with their hand or tongue. After the subject began to eat, the experimenter placed behind him at a distance of 60cm,knocking continuously on the plexiglass front doors of the cage and producing a moderate noise. **Duration:** 5 min. **N° of repetitions (P_1– P_2):** 3-3	BF Touch panel (Latency) BF Eat baby food (Duration) BF Look at experimenter (Frequency)
MASKED HUMAN TEST (MH)	The experimenter came in the testing room wearing a raincoat with the hood covering the head, a pair of rain boots, sunglasses and coloured latex gloves. For 1 minute the experimenter remained motionless and stared at monkeys continuously, then she offered them some pieces of a biscuit. Because of the intensity of the stimulus, this test was carried out only two times in total. **Duration:** 2 min. **N° of repetitions (P_1– P_2):** 1-1	MH Pilo-erection (Latency) MH Pilo-erection (Duration) MH Agonistic behaviours (Frequency); MH Take biscuit (Latency) MH Fear behaviours (Frequency) MH Vocalize (Frequency)
NOVEL FOOD TEST (NF)	The experimenter put inside a bowl alternatively four little pieces of banana and four different food items, unknown to animals. The subject had 1 minute to reach the bowl, take food, eat or reject it. We used banana alternately to novel food to understand if subjects were hungry and exclude that the curiosity may have been affected by this confounding factor. **Duration:** max 8 min (max 1 minute per trial). **N° of repetitions (P_1– P_2):** 2-2	NF Touch novel food (Latency) NF Deal with novel food (Duration); NF Eat novel food (Latency) NF Eat novel food (Percentage)
NOVEL OBJECT TEST (NO)	In each session, the experimenter put inside the cage a small object (max 10 cm), unknown to animals. A plastic tablespoon, red cockade, fishing float and a plastic ball were used. The subject had 2 min to reach the object and interact with it, smelling, touching or playing with it. **Duration:** 5 min. **N° of repetitions (P_1– P_2):** 2-2	NO Touch novel object (Latency) NO Interact with novel object (Duration) NO Return to interact with n.o. (Frequency)
PILE OF FOOD TEST (POF)	During the 2 min session, the experimenter cut a banana, an apple and pear in slices on a wood table leaned against the Plexiglas front door of the cage. Animals could get very close to the food but they couldn't reach it. **Duration:** 2 min. **N° of repetitions (P_1– P_2):** 3-3	POF Proximity to food (Latency) POF Proximity to food (Duration) POF Return in proximity of food (Frequency) POF Attempts to grab food (Frequency) POF Change position (Frequency)
FOOD OUT OF REACH (FOR)	Slices of a apple, a pear and a banana were put outside the experimental cage, so that monkeys could stay very close to it but they couldn't take it. Differently from the "pile of food test", the experimenter was far from the cage during the test, in order not to influence the behaviour of monkeys with her close presence. **Duration:** 2 min. **N° of repetitions (P_1– P_2):** 2-2	FOR Proximity to food (Latency) FOR Proximity to food (Duration) FOR Return in proximity of food (Frequency) FOR Attempts to grab food (Frequency) FOR Vocalize (Frequency) FOR Try to grab food (Duration)

(*continued on next page*)

Table 1 (*continued*)

Paradigm	Description	Behavioural variables
OBSERVATIONS UNDER SOCIAL CONDITIONS (SB)	Subjects' behaviours were observed in their natal group for 15 min per day, each minutes was divided in four 15 - second time intervals in which behaviours of all members was registered with scan sampling (Altmann, 1974). **Duration:** 15 min. **N° of repetitions (P_1– P_2):** 6-6	SB Agonistic behaviours (Scan sampling) SB Scratching (Scan sampling) SB Foraging behaviours (Scan sampling) SB Proximity to group members (Scan sampling) SB Allogrooming (Scan sampling) SB Locomotion (Scan sampling) SB Rest (Scan sampling) SB Social play (Scan sampling) SB Scent marking (Scan sampling) SB Interact with enrichment (Scan sampling)

break of 15 days. During each test period, each family group was subjected to two different tests per day according to a rotation scheme. Subjects within each family were tested in a random order. The selection of tests to be performed on each testing day was done to specifically avoid collecting data from related behaviours on the same day. This was done to reduce the effects of temporary fluctuations of behaviour on the aggregated data.

During the tests, subjects were isolated in the plexiglass experimental cage for no more than 10 consecutive minutes. To reduce the distress due to the unavoidable isolation, the experimental subjects were kept in visual contact with their family during test sessions.

To collect data on behaviours that occur mainly in social context, social group observations were also carried out during two 6 days long periods (P_1 and P_2), separated by a 7 days long break. According to a rotation scheme, every day each family was observed in the plexiglass experimental cage and behaviours were recorded for 15 min divided in 15 s intervals using scan sampling (Altmann, 1974). At the beginning of social group observations, a female subject was expulsed from her natal group and transferred to another colony, so data on social behaviour from this subject are missing.

Tests were videotaped and the videos were subsequently scored with the Observer XT software (v. 10.5., www.noldus.com; Noldus Information Technology) to obtain latencies, frequencies, durations and percentages measures. Vocalizations were also recorded during the execution of tests. A total of 56 behavioural variables was recorded (Table 1).

Throughout tests and social group observations, animals were fed at 8.15 a.m. with commercial cream. Fresh fruit was provided at the end of behavioural testing, at about 2.30 p.m. Water was provided *ad libitum*.

2.3.2. Hand preference

To determine the hand preference for simple reaching of the experimental subjects, we considered the hand used to pick up pieces of food and bring them to the mouth during three of the personality tests: Food box test, Hidden food test and Novel food test (Table1), according to the methods described by Hook and Rogers (2000; 2008). Briefly, repeated taking of the same item to the mouth using the same hand was recorded as only one score. If the food item was brought to the mouth, put down into the cage or switched to the other hand, and then it was brought to the mouth again, one additional right or left score was recorded.

2.4. Data analysis

All statistical analyses were carried out using SPSS software (v. 20, IBM SPSS Statistics).

2.4.1. Personality structure

The behavioural tests and the social observations were scored to analyse the expression of 56 behaviours. Data measured during replicates of the same behavioural test from each testing period were then averaged to obtain a single mean value for each individual representing the propensity for each individual to manifest a particular behaviour. Two mean values, one for each testing period (t_{P1} and t_{P2}), measured as latencies, frequencies, durations and percentages, were thus obtained and then further transformed to obtain z- scores. The z-score of behavioural variables related to a specific trait and measured in different behavioural tests and social group observations for each testing period were then aggregated *a priori* into 13 personality traits according to the method described by Uher and colleagues (Uher et al., 2008) (Table 2). Intraclass correlations (ICCs) were then applied to assess the temporal stability of each behavioural variable or trait under investigation (between-subject approach). To assess the stability of the individual behavioural profiles, the ICC was calculated for each subject, taking into account all 56 behavioural variables (within-subject approach).

To investigate whether and how personality traits were associated with each other, Explorative Factor Analysis (EFA) was conducted on the values of stable traits obtained by averaging values from the two non-overlapping testing periods. The Bartlett's test was determined to be $\chi^2 = 83.57$ (df = 45, $p < 0.001$), thus confirming the suitability of the data for factor analysis (Bartlett, 1950). Horn's Parallel Analysis (PA) was applied to determine the optimal number of factors to retain (Horn, 1965). Absolute factor loadings ≥ 0.55 were considered as salient (Tabachnick et al., 2007). For each experimental subject, an individual factor score relative to the significant factor identified by EFA was calculated considering the contribution of each trait under investigation to the factor of interest (sum score method: Comrey and Lee, 1992).

2.4.2. Strength and direction of hand preferences

Individual hand preference was assessed through the binomial test, performed on the proportion of use of the right (Rp) and the left hand (Lp), respectively defined as $Rp = R/(R + L)$ and $Lp = L/(R + L)$, where R = Total number of occurrences with the right hand and L = Total number of occurrences with the left hand. A marmoset was considered to have a significant hand preference if the binomial test highlighted a z-score ≥ 1.96 or ≤ -1.96 ($p < 0.05$). We also calculated its absolute value (ABS-z score), and considered it as an index of the strength of the preference.

2.4.3. Sex and age effects

To verify whether sex and age affected the expression of the personality factor identified by EFA and strength and direction of hand preference, three multiple regressions were carried out (Koski et al., 2017). The personality factor or the strength or the direction of hand

Table 2
Temporal stability of behavioural variables and personality traits.

Trait	ICC	p-value	Behaviours	ICC	p-value
AGGRESSIVENESS	**0.88**	**p < 0.01**	**CI Agonistic behaviours**	**0.81**	**p < 0.01**
			CI Vocalize	**0.91**	**p < 0.01**
			MH Agonistic behaviours	**0.45**	**p = 0.04**
			MH Vocalize	**0.87**	**p < 0.01**
			SB Agonistic behaviours	**0.99**	**p < 0.01**
ANXIOUSNESS	0.39	p = 0.19	BF Look at experimenter	0.28	p = 0.15
			CI Take biscuit	**0.56**	**p = 0.01**
			CI Eat biscuit	**0.73**	**p < 0.01**
			MH Take biscuit	0.03	p = 0.46
			SB Scratching	**0.61**	**p < 0.01**
AROUSABILITY	**0.56**	**p = 0.01**	**BFB Vocalize**	**0.56**	**p = 0.01**
			FOR Vocalize	0.33	p = 0.11
CURIOSITY	**0.85**	**p < 0.01**	**BFB Touch box**	**0.81**	**p < 0.01**
			FB Touch box	**0.82**	**p < 0.01**
			NF Eat novel food (L)	**0.57**	**p < 0.01**
			NF Eat novel food (P)	**0.80**	**p < 0.01**
			NF Touch novel food	**0.64**	**p < 0.01**
			NF Deal with novel food	**0.48**	**p = 0.03**
			NO Touch novel object	−0.05	p = 0.56
			NO Interact with novel object	0.19	p = 0.25
			NO Return to interact with n.o.	−0.16	p = 0.71
			SB Interact with enrichment	0.36	p = 0.09
ATTENTIVENESS	**0.48**	**p = 0.03**	**BF Eat baby food**	**0.48**	**p = 0.03**
FEARFULNESS	**0.68**	**p < 0.01**	**MH Pilo-erection (L)**	**0.85**	**p < 0.01**
			MH Pilo-erection (D)	**0.82**	**p < 0.01**
			MH Fear behaviours	**0.60**	**p < 0.01**
FOOD ORIENTATION	**0.71**	**p < 0.01**	BF Touch panel	0.03	p = 0.45
			FB Eat rewards	**0.89**	**p < 0.01**
			FB Open box	**0.90**	**p < 0.01**
			FOR Proximity to food (L)	0.39	p = 0.07
			FOR Proximity to food (D)	**0.56**	**p = 0.05**
			FOR Return in proximity of food	**0.58**	**p = 0.01**
			POF Proximity to food (L)	**0.76**	**p < 0.01**
			POF Proximity to food (D)	**0.83**	**p < 0.01**
			POF Return in proximity of food	**0.51**	**p = 0.02**
			SB Foraging behaviours	**0.99**	**p < 0.01**
FRIENDLINESS TO CONSPECIFICS	**0.82**	**p < 0.01**	**SB Proximity to group members**	**0.96**	**p < 0.01**
			SB Allogrooming	**0.99**	**p < 0.01**
CAUTION TOWARDS HUMANS			CI Proximity to intruder (L)	0.25	p < 0.13
			CI Proximity to intruder (D)	0.31	p < 0.12
PERSISTENCY	**0.85**	**p < 0.01**	**BFB Attempts to open box**	**0.68**	**p < 0.01**
			BFB Deal with box	**0.56**	**p < 0.01**
			BFB Try to open box	**0.77**	**p = 0.01**
			FB Deal with box	**0.62**	**p < 0.01**
			FOR Attempts to grab food	**0.46**	**p = 0.04**
			FOR Try to grab food	**0.70**	**p < 0.01**
			HF Find rewards	**0.44**	**p = 0.05**
			POF Attempts to grab food	**0.91**	**p < 0.01**
			POF Change position	**0.84**	**p < 0.01**
PHYSICAL ACTIVITY			HF Locomotion	0.29	p = 0.14
			HF Rest	−0.05	p = 0.57
			HF Actively searching	0.25	p = 0.17
			SB Locomotion	0.17	p = 0.25
			SB Rest	0.34	p = 0.12
PLAYFULNESS	**0.84**	**p < 0.01**	**SB Social play**	**0.84**	**p < 0.01**
TERRITORIALITY	**0.54**	**p = 0.02**	**SB Scent marking**	**0.54**	**p = 0.02**

Note: Boldface indicates significant outcomes ($p < 0.05$).

preference were the dependent variable, and the independent variables were sex (1 for females, −1 for males) and age (−1 for adults; 1 for aging) and a product term representing the Sex x Age interaction. Based on previous studies demonstrating that in this species the average age at which aging signs start appearing is 8 years and the average lifespan in captivity is 16 years, marmosets with < 8 years were classified as adults, while marmosets having ≥ 8 years as aging (Abbott et al., 2003).

2.4.4. *Regression model*

Multiple regression was used to examine the effect of the personality factor identified by EFA on the strength and direction of hand preference, taking into account sex and age of the subjects. Variance inflation factors (VIF) were computed to check for multi-collinearity among explanatory variables. VIF value of 5 was considered as threshold.

Table 3
Temporal stability of individual behavioural profiles.

Subject	Sex	Age	ICC	p-value
Chiara	F	4	**0.42**	**p = 0.04**
Chiwi	M	5	**0.74**	**p < 0.01**
Cocco	M	5	**0.75**	**p < 0.01**
Dosso	M	8	**0.89**	**p < 0.01**
Edera	F	8	**0.85**	**p < 0.01**
Elena	F	14	**0.70**	**p < 0.01**
Elettra	F	8	**0.58**	**p < 0.01**
Emilia	F	7	**0.67**	**p < 0.01**
Epi	M	4	**0.53**	**p < 0.01**
Ernesto	M	9	**0.77**	**p < 0.01**
Gianni	M	14	**0.66**	**p < 0.01**
Ginevra	F	10	**0.59**	**p < 0.01**
Vega	F	4	**0.70**	**p < 0.01**
Vento	M	4	**0.73**	**p < 0.01**
Virginia	F	3	**0.80**	**p < 0.01**
Wisconsin	F	3	**0.85**	**p < 0.01**

Note: Boldface indicates significant outcomes ($p < 0.05$).

Table 4
Loadings of the personality factor extracted by EFA.

Traits	Factor loadings
Persistency	**0.87**
Curiosity	**0.73**
Food orientation	**0.72**
Attentiveness	**0.66**
Friendliness to conspecifics	**0.57**
Arousability	−0.53
Fearfulness	−0.44
Territoriality	−0.38
Playfulness	0.31
Aggressiveness	−0.03
Eigenvalue	3.82
Proportion of variance explained	38.20

Note: Analysis based on correlation matrix (N = 16).
Extraction method: Principal axis factoring.
Only loadings with absolute values ≥ 0.55 are considered as salient.

Table 5
Age and Sex effects on personality factors and strength and direction of hand preference.

Response variable	Predictors	Beta	t value	p value	Adjusted R square
Personality factor (Inquisitiveness)	Age	−0.238	−0.847	0.413	−0.165
	Sex	0.073	0.260	0.799	
	Age x Sex	−0.050	−0.178	0.862	
Direction of hand preference	Age	0.219	0.814	0.665	−0.065
	Sex	0.079	0.293	0.432	
	Age x Sex	−0.324	−1.197	0.775	
Strength of hand preference	Age	0.225	0.840	0.418	−0.055
	Sex	0.155	0.58	0.573	
	Age x Sex	0.274	1.018	0.329	

Note: Boldface indicates significant outcomes ($p < 0.05$).

3. Results

We found that 40 out of 56 of behavioural variables (71%) and 10 out of 13 personality traits (77%) were stable over the 2 testing periods (Table 2). All the subjects showed stable individual behavioural profiles (Table 3).

The EFA highlighted a single factor with eigenvalue > 2.01, the threshold identified by PA (Horn, 1965). This factor, which accounted for about 38% of the variability, included high positive loadings of traits related to the propensity to promptly approach (*curiosity* and *attentiveness*) and persistently interact (*persistency* and *food orientation*) with stimuli presented under challenging situations (Table 4). As such, this factor reflected the interest for unusual and new experiences, thus resembling the inquisitiveness component found by Koski et al. (2017) and the openness domain identified by Iwanicki and Lehmann (2015). We named this factor *Inquisitiveness*.

Table 6
Individual Hand Preference.

Subjects	Total reaches	% Right	Z score	Hand Preference
Chiara	50	14	−4.95	Left
Chiwi	37	32	−2.30	Left
Cocco	98	11	−7.78	Left
Dosso	37	51	0.00	None
Edera	69	97	7.70	Right
Elena	95	26	−4.51	Left
Elettra	103	81	6.11	Right
Emilia	112	53	0.47	None
Epi	25	12	−4.00	Left
Ernesto	119	98	10.45	Right
Gianni	37	38	−1.32	None
Ginevra	76	5	−7.69	Left
Vega	41	61	1.25	None
Vento	82	66	2.76	Right
Virginia	94	88	7.32	Right
Wisconsin	88	69	3.52	Right

Table 7
Multiple regression analyses predicting direction or strength of hand preference from personality factors.

Response variable	Predictors	Beta	t value	p value	Adjusted R square
Direction of hand preference	*Inquisitiveness*	−0.129	−0.446	0.664	−0.172
	Sex	0.130	0.465	0.650	
	Age	0.146	0.505	0.623	
Strength of hand preference	***Inquisitiveness***	**0.595**	**2.604**	**0.023**	0.267
	Sex	0.073	0.327	0.749	
	Age	0.405	1.778	0.101	

Note: Boldface indicates significant outcomes ($p < 0.05$).

No sex or age differences on the expression of the personality factor were found (Table 5).

The analysis of individual hand preference found that six subjects preferred the right hand for simple reaching, six preferred the left hand, four showed no preference (Table 6). No sex or age differences on the strength or the direction of hand preference were found (Table 5).

Table 7 reports the results of the multiple regression analysis. The personality component was not associated with the direction of hand preference. However, we found that it accounted for a significant amount of the variance in the strength of hand preference ($B = 0.595$, $t = 2.604$, $p = 0.023$). Strong left- and right-handers were thus more inquisitive than individuals with weak preferences (Fig. 1).

4. Discussion

The present study confirms that common marmosets are characterized by stable and consistent personality profiles (Iwanicki and Lehmann, 2015; Šlipogor et al., 2016). Robust temporal stability of inter-individual differences between two test periods was in fact confirmed, with just a few of the behavioural variables under investigation showing inconsistency over time. Such high repeatability values exceed earlier findings in marmosets as well as in most other animals (Bell et al., 2009). They are however consistent with previous studies adopting the same methodology by Uher and colleagues (Uher et al., 2008, 2013a, 2013b, Uher and Visalberghi, 2016), in which the propensity for each individual to manifest a particular behaviour is estimated by averaging data measured during replicates of the same behavioural test. Present results thus suggest that the application of a high

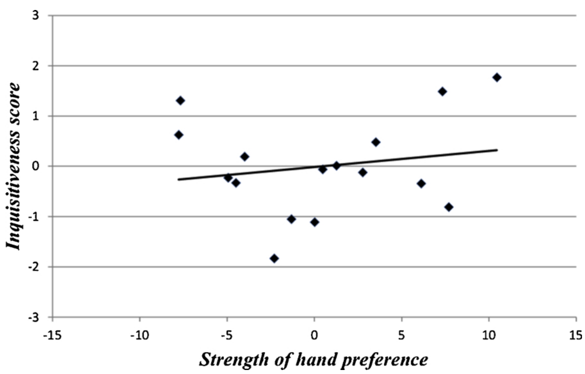

Fig. 1. Personality differences are associated with hand preference in common marmosets. The strength of individual hand preference (Abs-z score) correlates with the personality factor *Inquisitiveness*, identified by EFA. Individuals whose personality profiles are characterized by more marked interest towards unusual and new experiences (higher *Inquisitiveness* score) presents a stronger preference for the use of one of the two hands (higher *strength of preference*).

number of tests and repetitions may increase the probability to obtain reliable estimates in personality investigations.

We found that most of the inter-individual variability in our sample was explained by one major factor. This factor, we named *Inquisitiveness*, strongly resembles those found by previous studies that investigated the personality structure of common marmosets adopting different methodologies, involving either provision of questionnaires to caregivers (Koski et al., 2017) or the simultaneous use of questionnaires and focal observations in the home cages (Iwanicki and Lehmann, 2015). By contrast, in the present study the behavioural coding of marmoset personality was achieved through the implementation of a varied battery of behavioural tests, that included observations under social conditions and the exposure to neutral as well as challenging situations. Our results thus support the generalizability of at least one personality component in common marmosets across different samples and suggest that *Inquisitiveness* is a high reliable and relevant personality factor for this species. This finding is consistent with the hypothesis that feeding ecology, that is based in this species on strategies that takes time and efforts (insectivory and gum feeding), may have favoured the evolution of traits related to openness towards novel experiences (Stevens et al., 2005; Koski et al., 2017).

Another major conclusion of this study concerns the demonstration that the strength of individual hand preference is linked to a personality factor that accounts for about 38% of variability. Interestingly, this personality factor describes the propensity to promptly approach and persistently interact with novel stimuli in common marmosets, thus resembling the *openness* domain found in humans and in other non-human primates (Manson and Perry, 2013; Morton et al., 2013). Thus, an individual whose personality profile is characterized by more marked interest towards unusual and new experiences presents a stronger preference for the use of one of the two hands.

Our study is, to the best of our knowledge, the first one reporting an association between a personality factor and the degree of hand preference in non-human primates. Interestingly, mixed-handedness for unskilled activity has been previously linked to lower levels of *Openness to experience* in a human sample (Bryson et al., 2009), suggesting that an evolutionary conserved biological mechanism may underlie these two phenomena. This suggestion is fascinating given that mixed-handedness has been associated with several mental disorders (Ocklenburg et al., 2015; Paracchini et al., 2016; Sommer et al., 2001), such as schizophrenia (Annett and Moran, 2006; Hirnstein and Hugdah, 2014) and post-traumatic stress disorder (Goetz et al., 2016), suggesting it may represent a vulnerability factor. Moreover, mixed-handers have been found to differ from both left- and right-handers in other domains, such as magical ideation, episodic memory and intelligence (Propper et al., 2005; Nicholls et al., 2010). A better understanding of this association may thus provide translationally relevant information.

Even though further studies are needed to evaluate whether a common biological mechanism might explain the association between the strength of hand preference and *Inquisitiveness*, available literature points to dopamine as an intriguing candidate. This neurotransmitter is in fact centrally involved in reward, approach behaviour, exploration, and various aspects of cognition (Scaplen and Kaun, 2016). Moreover, variations in dopaminergic function have been associated with personality differences (DeYoung, 2013), and studies in rodents demonstrate that an hyperdopaminergic state, an hallmark of schizophrenia that has been linked to positive schizophrenic symptoms, impairs the degree of lateralization without affecting the direction (Cabib et al., 1995; Morice et al., 2005). Future studies addressing this possibility are however necessary.

In the present study we did not find any relationship between the direction of hand preference and the personality factors identified by EFA. Such a lack of association is indeed surprising. A large number of studies in common marmosets have in fact highlighted consistent behavioural differences between left and right-handers in domains, such as exploration, sociability and fear-related behaviours, potentially relevant for the personality factors herein identified (Cameron and Rogers, 1999; Gordon and Rogers, 2010; Rogers, 2018). Even though it is conceivable that the direction of hand preference may be linked to individual behavioural differences not caught by our approach (*e.g.* differences in coping styles, see Rogers, 2009), we cannot exclude that this discrepancy may be ascribable to the sample under investigation that was indeed characterized by a higher number of mixed handers than could be expected based on available literature on this topic (Rogers, 2018).

In conclusion, the present study provides a comprehensive characterization of the personality of common marmosets. Although this species is highly represented in biomedical research centres and its behavioural repertoire is well known, the studies focused on its personality are relatively recent (Koski and Burkart, 2015; Iwanicki and Lehmann, 2015; Šlipogor et al., 2016; Koski et al., 2017). Furthermore, evidence is provided that the strength of individual hand preference in common marmosetsis linked to *Inquisitiveness*, a personality domain that resembles the *Openness* domain described in humans and describes the individual interest towards new experiences. Even though further studies are needed to understand the nature of this relationship, we argue here that an evolutionary conserved biological mechanism may underlie these two phenomena and stress the need for future studies aimed at a better understanding of the underpinnings of this association.

Acknowledgements

We would like to thank Dr. Jana Uher for discussion of the data and for providing a critical reading to an early draft of the manuscript and Luigia Cancemi for her precious and empathic care of the marmosets.

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