

Research



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# Age, but not hand preference, is related to personality traits in common marmosets (*Callithrix jacchus*)

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The proximate mechanisms underlying animal personalities, i.e. consistent inter-individual differences in behaviour, are a matter of discussion. Brain lateralization, expressed as the preferred use of the contralateral limb, has been suggested as one of these mechanisms. In this study, we measured a proxy of brain lateralization in captive common marmosets ( $N = 28$ ) by testing hand preference in a simple food-reaching task and evaluated personality by coding a wide range of behaviours observed in daily situations. We explored the links between personality and both direction and strength of hand preference, as well as age and sex, using linear models. Principal component analysis revealed that the stable behavioural variables were organized in three personality dimensions: Agreeableness, Extraversion and Neuroticism. Regarding hand preference, 14 individuals were left-handed, seven were right-handed and seven were ambilateral. Contrary to our predictions, we did not find any

relationship between personality scores and hand preference or sex. Instead, age was a significant predictor of personality scores, with older individuals being more agreeable and less extraverted. The link between brain lateralization and personality seems to be equivocal and dependent on personality and brain lateralization assessment methods. Further examinations of other proximate mechanisms, such as physiology or (epi)genetics, may elucidate what drives personality variation in common marmosets.

## 1. Introduction

The research on animal personality, i.e. on consistent inter-individual differences in behaviour, has gained increasing attention in behavioural and cognitive biology in recent years [1,2]. Animal personality assumes both between-individual variation and within-individual consistency [3]. However, our understanding of its underlying proximate mechanisms is still quite limited [4,5]; while some of the personality traits seem to have a genetic or epigenetic basis [6,7], other personality traits may be governed by physiological, neuroendocrine, morphological or ontogenetic mechanisms [8–11].

Brain lateralization, i.e. asymmetry in hemispheric functions, has been hypothesized as one of the possible proximate neurophysiological mechanisms that maintain personality variation [12,13]. Brain lateralization is expressed as a preference for using the contralateral part of the body and is often measured either as a limb preference [14–18], eye dominance [19,20] or tail and body orientation [12,21,22]. Brain lateralization is present both in vertebrates and invertebrates (reviewed in [23,24]), and it provides various benefits in terms of enhanced cognition, social cohesion and better predator detection while foraging [25–27], thus directly affecting an individual's survival. Yet, population-level handedness (i.e. the tendency of the majority of the population toward using a specific hand as is known in humans) is extremely rare in animals [17]. Instead, vast individual variation in direction (i.e. preference for the left or right side of the body) and strength (i.e. magnitude of the preference irrespective of its direction) of lateralization exists within populations [28] and has been proposed to be linked with personality [13].

According to the 'approach-withdrawal hypothesis' [29], each hemisphere is specialized in processing and activating different types of behaviours. The left hemisphere controls approach-related behaviour, while the right hemisphere controls withdrawal behaviour. This general pattern has been confirmed across species and behaviours [14,30]. Individuals with right body side preference (i.e. left hemisphere dominance) are generally more explorative and bold [12] and are faster in approaching and inspecting novel objects [31]. These individuals also differ in their social interactions [28]. For example, pigs with right lateral bias were generally more sociable than their left lateral bias counterparts [12]. Right-pawed cats scored higher on playfulness [32]. Similarly, right-handed rhesus macaques received more grooming and spent more time in proximity to others than left-handed macaques, who were more frequently attacked and exhibited more submissive behaviours [33].

Personality has also been attributed to the strength of lateralization. Dogs and primates with stronger lateralization were more aggressive than their ambilateral (i.e. individuals without side preference) counterparts [31,34]. Similarly, humans with strong hand preference were rated as more extroverted than ambilateral humans, who were rated as more introverted [35]. On the other hand, ambilateral dogs tended to be more sociable, playful and bold [15].

The link between brain lateralization and personality might be species-, task- or trait-specific. For example, there was no correlation between the swimming direction and stress reactivity or docility in Port Jackson sharks [22,36]. Likewise, studies reported no association between limb preference and scores on personality dimensions in cats [32], dogs [34] or donkeys [16]. On an item level, however, limb preference significantly predicted the item 'difficult to handle' in donkeys [16] and 'playful' in cats [32]. The association of lateral bias and personality might also interact with other factors, such as sex (e.g. rhesus macaques [33,37] and humans [38], but see [35]). In cichlid fish, males with left eye dominance were more aggressive than males with right eye dominance. However, the opposite relationship was found in females [39]. Studies on humans did not report any clear pattern, and the link between lateral bias and personality seems to be equivocal [40]. While some studies confirmed personality differences between left- and right-handed individuals along the approach-withdrawal hypothesis [40,41], others found a reversed relationship [38,40] or no evidence for the link with personality [35,42]. Thus, studies on non-human primates could contribute to understanding the evolutionary mechanisms underlying the complex relationship between lateral bias and personality.

Here, both aspects of laterality, strength and direction, should be investigated as potential underpinnings of consistent individual variation in behaviour.

Brain lateralization expressed as hand preference has been already studied in common marmosets (*Callithrix jacchus*) [43–46], New World primates, that are due to their size and ease of breeding one of the most common primate species in the laboratory [47,48]. Hand preference develops early in marmosets' life (5–8 months) and strengthens with time, stabilizing after the second year of life [49]. Hand preference in marmosets correlates with other motor preferences like mouth use [44] but not with sensory preferences [44,50]. Studies on marmosets found no population-level bias, yet they report vast individual variation in hand preference [44,45,49–53, cf. 54]. This individual variation is not, however, related to sex or age differences [46,51–53,55], but is likely due to other factors, like body posture and visual demands of the task [43,49,52], relatedness or social facilitation [49,54], or basal cortisol levels [53].

Behavioural studies of common marmosets confirmed the link between hand preference and reactions to novel or threatening stimuli in experimental settings [30,46,56,57]. Across studies, right-handed marmosets exhibited more explorative, active, approach-prone and less fearful behaviours than the left-handed marmosets (reviewed in [30]). Specifically, right-handed marmosets touched more objects, were faster to enter a novel room or to approach novel food [46], emitted more vocalizations when confronted with novel food [57], reacted to predator vocalizations with less freezing behaviour [56], and exhibited more social behaviours [53]. However, none of the mentioned studies directly tested the relationship between hand preference and personality measured as repeated behavioural reactions, on a broader construct level.

Personality of common marmosets has already been assessed with a variety of methods, including trait rating as well as experimental and common behaviour coding [58–62]. The resulting personality structures show considerable cross-method and ecological validity [63,64], and individual personality scores exhibit short- and long-term stability [59,60,63]. To our knowledge, only one captive study has assessed the potential links between hand preference and personality in common marmosets so far [55]. Combining experiments and common behaviour coding, a single broad personality dimension labelled as Inquisitiveness was revealed, describing individuals' interest in food, novelty and friendliness to conspecifics. Inquisitiveness was not related to the direction of hand preference, but rather to the strength of hand preference, with more strongly lateralized individuals being more inquisitive than weakly lateralized individuals [55]. To fully understand the complex associations between brain lateralization and personality, it is necessary to explore the hand preference and its links with a broad range of personality dimensions (i.e. other than just Inquisitiveness).

Thus, the main objective of this study was to investigate the relationship between personality traits, measured by common behaviour coding, and brain lateralization, measured as hand preference in a simple food-reaching task, in captive common marmosets. We expected that the marmosets will show consistent differences in their hand use and that the handedness will be related to their personality type. Specifically, we predicted that right-handed individuals will be more extraverted, agreeable and assertive than left-handed individuals [33,55,59]. We also predicted that more strongly lateralized individuals will be more extraverted than weakly lateralized individuals [55].

## 2. Material and methods

### 2.1. Subjects

The subjects of this study were common marmosets housed in the Animal Care Facility of the Department of Behavioural and Cognitive Biology, University of Vienna, Austria. Marmosets were housed in social groups in indoor-outdoor enclosures equipped with branches, shelves, sleeping baskets and enrichment that was frequently changed. They were fed twice a day, in the morning with New World monkey pellets and around lunchtime with a varied diet consisting of fruits, vegetables, yoghurt, marmoset gum and jelly, and protein sources like insects or cooked chicken. Water was available ad libitum. More information on animal husbandry can be found in Šlipogor *et al.* [63].

### 2.2. Personality assessment

We assessed personality through common behaviour coding [65], which refers to the recording of the behaviour of animals in their social groups during everyday situations. In total, 33 marmosets older than 12 months ( $F = 12$ ,  $M = 21$ ) were observed in three study periods: in 2015 ( $n = 17$ ), in 2016 ( $n = 7$ )

and in 2020/2021 ( $n=9$ ) (see electronic supplementary material, table S1). In 2015 and 2016, each marmoset was followed for a total of 10 h (i.e. 240 h in total) over a period of 8 to 31 days. In 2020/2021, we collected 7 h of observation per individual instead (i.e. 63 h in total) over a period of 25 to 62 days (for details, see electronic supplementary material, table S1), because 5 to 7 h were found to be sufficient to capture personality in another callitrichid species [65].

In 2015 and 2016, MM used a voice recorder (Olympus VN-8700PC Digital Voice Recorder) to capture the behavioural observations, and afterward transcribed them into Microsoft Excel (Microsoft Office Professional Plus 2019). In 2020/2021, the behaviour was filmed by GM with a video camera (Canon LEGRIA HF R806), and the recordings were afterwards coded from a video player (Kakao PotPlayer v. 2002004 1.7.21126; 5KPlayer v. 6.8) into Microsoft Excel by GM (84 videos) and MM (42 videos). Before starting observations and coding videos, MM trained GM to ensure sufficient inter-rater reliability.

We used a combination of focal continuous and instantaneous sampling [66]. The focal period lasted 30 min with a sampling interval each 2 min. The focal periods for each individual were equally distributed during the day (from 7:30 AM to 5:00 PM). We observed a wide range of behaviours as defined in a previously published ethogram [59] (for details see electronic supplementary material, table S2). From these, we calculated 22 behavioural indices following Masilkova *et al.* [59] (electronic supplementary material, table S3). They comprised three types of variables: frequencies e.g. *Scratching*<sup>F</sup>—frequency of scratching per hour), proportions of time (e.g. *Affiliation*<sup>P</sup>—the proportion of time focal subject spent in affiliative behaviours such as contact, proximity, social play and allogrooming), and diversity indices (e.g. *Activity diversity*<sup>S</sup>—Shannon diversity index of activity types; Shannon diversity index, computed according to Shannon & Weaver [67], describes the variation in behavioural diversity, low value = no behavioural diversity, high value = high behavioural diversity). Because of the different nature of indices (i.e. frequencies, proportions and Shannon diversity indices) and their range of possible values, we transformed the indices into z-scores (i.e. re-scaled them, so the mean value of index = 0 and s.d. = 1).

### 2.3. Hand preference test

We assessed hand preference using a simple food-reaching task in 28 marmosets ( $F=10$ ,  $M=18$ ) in 2019 and 2021. Marmosets were tested individually in the experimental cage ( $72 \times 42 \times 110$  cm). For the food-reaching task, we used a closed semi-transparent plastic box ( $9 \times 9$  cm) with a hole in one of the lid's corners (diameter: 2.5 cm). The box contained five small pieces of banana (diameter: 1 cm): four placed in the corners and one placed in the middle of the box. We noted the number of times and which hand an individual used to access a piece of food through the hole (figure 1). Tests lasted until the marmosets collected all five banana pieces, and not more than 8 min. The experiment was recorded with a video camera (Canon LEGRIA HF R806). The experimental enclosure was thoroughly cleaned with a vinegar–water solution between different individuals.

Each individual was tested between 2 and 6 times (i.e. 10–30 hand preferences scores, depending on the age-criterion and availability in different testing periods) in two different periods (two trials in March 2019 by MH, four trials in February 2021 by GM, see electronic supplementary material, table S1) and with a minimum interval of 48 h between each trial. We calculated the direction and strength of the hand preference only once all the behavioural observations were done to prevent any possible involuntary influences on the personality assessments.

### 2.4. Data analyses

All analyses were conducted in R studio (v. 1.2.5019 [68]). To control for inter-rater reliability, a subset of videos from 2020/2021 (10%) was coded by both observers (GM and MM) and the Intra-Class Correlation Coefficients (3,1; two-way, agreement, single) and associated 95% confidence intervals were computed in package *irr* [69], independently for substrate and behaviour instances in the instantaneous sampling, and behaviour instances in the continuous recording.

Subsequently, we calculated the repeatability estimates of the behavioural indices, which reflect the proportion of behavioural variation attributed to differences between individuals [70]. Because the overall length and method of observation differed between the first two and the third study periods, we assessed the repeatability of behavioural indices for the first two study periods, for which we had the same observation length ( $n=24$ ). We split the observations into two 5-h blocks per individual and computed the repeatability between them. The repeatability was calculated using linear mixed models



**Figure 1.** A marmoset performing a food-reaching task. Drawn by VŠ.

with an individual as a random factor in package *rptR* [71]. The  $p$  values and 95% confidence intervals were calculated from 1000 permutation and 1000 bootstrap runs [70].

Only significantly repeatable behavioural indices entered the personality analyses. We checked the sampling adequacy using the Keiser–Meyer–Olkin test (KMO) and Bartlett’s Test of Sphericity, both as functions of package *psych* [72]. To determine the number of personality dimensions in the data, we ran Horn’s parallel analysis [73] and inspected scree plots [74] using package *paran* [75]. We then conducted the Principal Component Analysis (PCA) in package *psych* [72] to identify the personality components. Next, we rotated the resulting component structure using oblique (Promax) and orthogonal (Varimax) rotations, the former enabling intercorrelations among components. We interpreted the Varimax rotated structure if the correlations were negligible and the resulting structures similar. Loadings  $\geq |0.4|$  were considered salient [58,76,77].

After that, we computed a unit-weighted personality score for each marmoset on each resulting personality component. The unit-weighted scores are the sum of all indices that loaded saliently on a dimension. Indices that loaded positively are weighed by plus one, and indices that loaded negatively are weighed by minus one [78].

The direction of hand preference was calculated with the following formula:  $HI = (R - L) / N$ . Here, ‘HI’ stands for the handedness index, ‘R’ for the number of right-hand instances, ‘L’ for the number of left-hand instances and ‘N’ for the total number of instances [56]. HI ranges from  $-1$  to  $+1$ . Zero on the index indicates no hand preference, a positive index value indicates a right-hand preference and a negative index value signifies a left-hand preference. To obtain a statistically significant indication of hand preference, we calculated  $z$ -score using the formula:  $z = (R - 0.5N) / \sqrt{(0.25N)}$  (for abbreviations, see above). The values of  $z > 1.96$  were considered the statistically significant indication of the right-hand preference,  $z < -1.96$  the indication of the left-hand preference, and values between  $-1.96$  and  $1.96$  the indication of no-hand preference [57]. In addition to direction, we calculated the strength of hand preference as an absolute value of HI (hereafter absHI). The absHI ranges from 0 (no or weak hand preference) to 1 (strong hand preference regardless the side).

To further explore the hand preference in common marmosets and to assess the consistency of HI between the two study periods (2019 versus 2021), we calculated the Spearman rank-order correlations. Two linear models were run with age (in months) and sex (M, F) as fixed factors and HI or absHI as a response to assess the effect of age and sex on handedness measures. Finally, we used the Chi-Squared test to determine the bias in the distribution of left, right and ambilateral preferences at the population level.

Linear models were used to assess the relationship between personality scores, direction and strength of hand preference, sex and age. The appropriateness of model parameters was visually checked using *plot* function, and the collinearity of the predictors was checked using variance inflation factors (*vif* function, all less than 1.29). We ran three separate models for each personality dimension (Agreeableness, Extraversion, Neuroticism) with HI, absHI, age (at the time of personality data collection, in months) and sex (M, F) as fixed predictors.

**Table 1.** The repeatability of behavioural indices across two five-hour long blocks of observation.

behavioural index	$R \pm SE$	95% CI	$p$
<i>activity diversity</i> <sup>S</sup>	0.24 ± 0.17	[0, 0.58]	0.13
<i>affiliation</i> <sup>P</sup>	<b>0.71</b> ± 0.11	[0.44, 0.87]	0.001
<i>approaches</i> <sup>F</sup>	<b>0.61</b> ± 0.14	[0.29, 0.81]	0.001
<i>carrying food away</i> <sup>F</sup>	0.34 ± 0.17	[0, 0.62]	0.05
<i>contact aggression</i> <sup>F</sup>	<b>0.91</b> ± 0.04	[0.80, 0.96]	0.001
<i>departures</i> <sup>F</sup>	<b>0.68</b> ± 0.12	[0.41, 0.85]	0.002
<i>exploration</i> <sup>F</sup>	<b>0.83</b> ± 0.07	[0.67, 0.92]	0.001
<i>grooming(in)</i> <sup>F</sup>	<b>0.52</b> ± 0.15	[0.16, 0.76]	0.009
<i>grooming(rec)</i> <sup>F</sup>	<b>0.69</b> ± 0.12	[0.38, 0.85]	0.001
<i>invite grooming(in)</i> <sup>F</sup>	<b>0.61</b> ± 0.14	[0.28, 0.82]	0.007
<i>invite grooming(rec)</i> <sup>F</sup>	0.19 ± 0.16	[0, 0.54]	0.21
<i>monitoring</i> <sup>P</sup>	<b>0.62</b> ± 0.13	[0.32, 0.80]	0.002
<i>object sniffing</i> <sup>F</sup>	<b>0.79</b> ± 0.08	[0.58, 0.91]	0.001
<i>passive affiliation</i> <sup>P</sup>	<b>0.40</b> ± 0.18	[0, 0.70]	0.03
<i>resting</i> <sup>P</sup>	<b>0.35</b> ± 0.17	[0, 0.65]	0.04
<i>scent marking</i> <sup>F</sup>	<b>0.84</b> ± 0.07	[0.68, 0.93]	0.001
<i>scratching</i> <sup>F</sup>	<b>0.78</b> ± 0.09	[0.56, 0.90]	0.001
<i>self-grooming</i> <sup>F</sup>	<b>0.77</b> ± 0.09	[0.55, 0.88]	0.001
<i>substrate diversity</i> <sup>S</sup>	<b>0.51</b> ± 0.16	[0.14, 0.76]	0.005
<i>terminate grooming</i> <sup>F</sup>	<b>0.50</b> ± 0.15	[0.13, 0.74]	0.009
<i>threats</i> <sup>F</sup>	<b>0.95</b> ± 0.02	[0.89, 0.98]	0.001
<i>vigilance</i> <sup>F</sup>	<b>0.88</b> ± 0.05	[0.73, 0.94]	0.001

Note. <sup>F</sup> = frequency of behaviour per hour, <sup>P</sup> = proportion of time, <sup>S</sup> = Shannon diversity index [67]. The significantly repeatable indices are in bold.

### 3. Results

#### 3.1. Personality

The inter-observer reliability of personality observations was excellent for substrate types (ICC (3,1) = 0.985, 95% CI [0.976, 0.991]) and behaviour instances (ICC (3,1) = 0.927, 95% CI [0.897, 0.949]) in instantaneous sampling and behaviour instances (ICC (3,1) = 0.969, 95% CI [0.957, 0.978]) in continuous recording. In terms of repeatability of behavioural measures, from 22 behavioural indices, only three were not repeatable across two time points within 2015 and 2016 study periods: *Activity diversity*<sup>S</sup> ( $R = 0.24$ ,  $p = 0.13$ ), *Carrying food away*<sup>F</sup> ( $R = 0.34$ ,  $p = 0.05$ ) and *Invite grooming(rec)*<sup>F</sup> ( $R = 0.19$ ,  $p = 0.21$ ). The remaining 19 indices were repeatable (mean  $R \pm s.d.$ :  $0.68 \pm 0.17$ ) and thus were considered for further personality analyses. Among repeatable indices, *Threats*<sup>F</sup> had the highest repeatability ( $R = 0.95$ ). Two indices (*Resting*<sup>P</sup> and *Passive affiliation*<sup>P</sup>) with the lowest repeatabilities ( $R = 0.34$  and  $R = 0.40$ , respectively) contained zero in the confidence interval but we nevertheless considered them repeatable (due to  $p < 0.05$ ). For details, table 1.

The KMO measure of PCA sampling adequacy was 0.4, below the recommended level of 0.6 [79,80]. On the other hand, Bartlett's test of sphericity indicated that the sampling is adequate for PCA ( $\chi^2 = 459.05$ , d.f. = 171,  $p < 0.01$ ) [79,81]. Horn's parallel analysis and visual inspection of the scree plot suggested retaining four components in the data. Because the Promax- and Varimax-rotated four-component structures did not differ considerably, and inter-component correlations were low, we interpreted the Varimax-rotated structure, which explained 61% of the variance (Promax solution in electronic supplementary material, table S4, Varimax solution in electronic supplementary material, table S5). Yet, its fourth component was difficult to interpret meaningfully.

**Table 2.** The Varimax-rotated principal component structure.

	agreeableness	extraversion	neuroticism	$h^2$
<i>terminate grooming</i> <sup>F</sup>	<b>0.76</b>	0.01	−0.05	0.59
<i>grooming(in)</i> <sup>F</sup>	<b>0.74</b>	0.03	−0.07	0.55
<i>threats</i> <sup>F</sup>	<b>−0.67</b>	0.30	0.19	0.58
<i>contact aggression</i> <sup>F</sup>	<b>−0.58</b>	−0.05	−0.20	0.38
<i>grooming(rec)</i> <sup>F</sup>	<b>0.54</b>	−0.32	<b>0.41</b>	0.56
<i>monitoring</i> <sup>P</sup>	−0.39	−0.02	−0.02	0.16
<i>departures</i> <sup>F</sup>	−0.07	<b>0.79</b>	0.20	0.68
<i>approaches</i> <sup>F</sup>	−0.28	<b>0.76</b>	0.31	0.75
<i>exploration</i> <sup>F</sup>	−0.02	<b>0.73</b>	0.00	0.54
<i>passive affiliation</i> <sup>P</sup>	−0.27	<b>−0.71</b>	−0.11	0.58
<i>affiliation</i> <sup>P</sup>	0.28	<b>−0.49</b>	<b>−0.45</b>	0.52
<i>substrate diversity</i> <sup>S</sup>	<b>0.42</b>	<b>0.45</b>	−0.30	0.47
<i>resting</i> <sup>P</sup>	0.04	−0.29	0.20	0.13
<i>object sniffing</i> <sup>F</sup>	0.01	−0.02	<b>0.84</b>	0.71
<i>scent marking</i> <sup>F</sup>	−0.33	0.06	<b>0.73</b>	0.65
<i>invite grooming(in)</i> <sup>F</sup>	<b>0.42</b>	−0.03	<b>0.63</b>	0.58
<i>scratching</i> <sup>F</sup>	−0.16	0.18	<b>0.59</b>	0.41
<i>vigilance</i> <sup>F</sup>	0.09	−0.01	<b>0.45</b>	0.21
<i>self-grooming</i> <sup>F</sup>	0.12	0.26	<b>0.40</b>	0.24
explained variance	16%	17%	16%	

Note. <sup>F</sup> = frequency of behaviour per hour, <sup>P</sup> = proportion of time, <sup>S</sup> = Shannon diversity index [67],  $h^2$  = communalities. Salient loadings  $\geq |0.4|$  in bold.

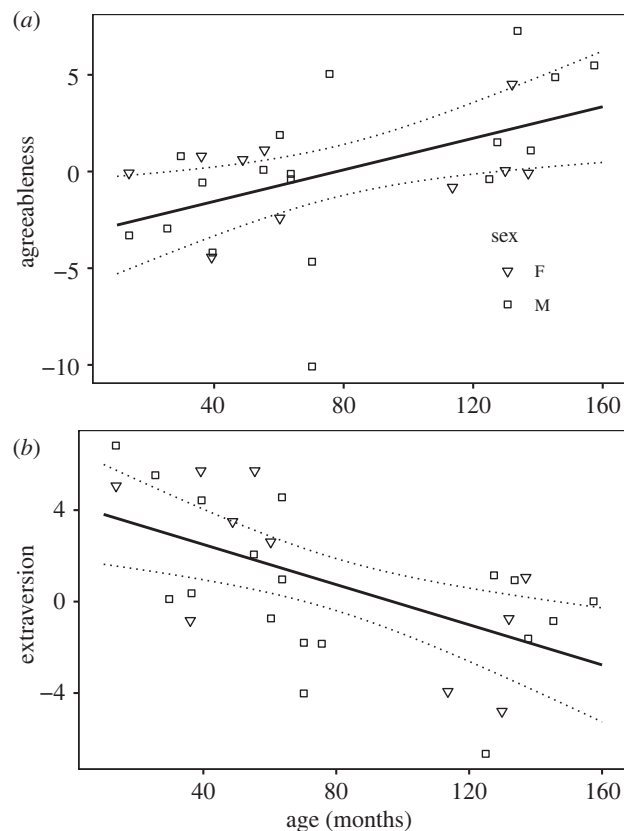
Thus, we retained the three-component solution instead. Because Promax- and Varimax-rotated three-component solutions were almost identical (Promax solution in electronic supplementary material, table S6), we interpreted the Varimax solution, which explained 49% of the variance (table 2). The first component included positive loadings of grooming-related indices (e.g. *Grooming(in)*<sup>F</sup>) and negative loadings of aggression-related indices (e.g. *Contact aggression*<sup>F</sup>). Therefore, we labelled it as Agreeableness. The second component was defined by indices related to the social activity (e.g. *Approaches*<sup>F</sup>) and exploration (e.g. *Exploration*<sup>F</sup>). We thus named it Extraversion. The third component included positive loadings of indices such as *Scratching*<sup>F</sup>, *Vigilance*<sup>F</sup> and *Scent marking*<sup>F</sup>, so we labelled it as Neuroticism. From 19 repeatable indices, two indices (*Monitoring*<sup>P</sup> and *Resting*<sup>P</sup>) did not load saliently on any component.

### 3.2. Hand preference

According to the HI z-score, 14 individuals (F = 7, M = 7) were left-handed, seven individuals (F = 2, M = 5) were right-handed and seven individuals (F = 1, M = 6) were ambilateral (electronic supplementary material, table S7). The direction of hand preference was consistent (Spearman's rank-order correlation:  $r_s = 0.94$ ,  $p < 0.001$ ) across two study periods (2019 versus 2021). There was no effect of age and sex on either the direction (all  $p > 0.18$ ) or the strength (all  $p > 0.35$ ) of hand preference. For the full results of the linear models, see electronic supplementary material, table S8. The observed distribution of hand preference did not significantly differ from that expected by chance ( $\chi^2 = 3.5$ ,  $p = 0.17$ ); hence, there was no population-level bias in hand preference in our study population.

### 3.3. The link between personality, hand preference, sex and age

Agreeableness was significantly related only to age, as older individuals had higher Agreeableness scores (slope mean  $\pm$  SE =  $0.041 \pm 0.015$ ,  $p = 0.013$ ; figure 2a). The relationships with sex, absHI and HI were



**Figure 2.** The relationship between age (in months) and Agreeableness (a) and Extraversion (b) personality z-scores from linear model. The area represented by dotted lines depicts 95% confidence interval.

non-significant (all  $p > 0.88$ ). The results were qualitatively similar for Extraversion, as older individuals had significantly lower scores on Extraversion (slope mean  $\pm$  SE =  $-0.044 \pm 0.013$ ,  $p = 0.003$ ; figure 2b), and the other three relationships were not significant (all  $p > 0.42$ ). The Neuroticism scores were not significantly predicted by any of the four predictor variables (all  $p > 0.50$ ; see electronic supplementary material, table S9 for details; see electronic supplementary material, figure S1 for the relationship between personality and HI and absHI).

## 4. Discussion

Personality structure in common marmosets, evaluated by behavioural observations in daily situations, comprised three personality dimensions (Agreeableness, Extraversion and Neuroticism). We also detected individual differences in right-, left- and ambilateral hand preference in a simple food-reaching task. Contrary to our predictions, neither direction nor strength of hand preference were linked to individual scores on personality dimensions. The personality variation was instead explained by age differences, with older individuals being more agreeable and less extraverted than younger ones.

The resulting personality dimensions were broadly comparable to the personality dimensions previously described in common marmosets using the same [62] as well as different methods of personality evaluation such as trait rating [48,58,62,82,83] and experimental coding [60,63,64]. The personality structure was also comparable but not completely identical to the structure reported in our previous study based on the same method of personality assessment and a subset of individuals ( $N = 17$ ) [59]. Therefore, the observed individual behavioural variation reflected well the existing personality variation in this species.

Agreeableness, defined by high levels of grooming and low levels of aggression, resembles Sociability [58,83] and Agreeableness [62,82] assessed by trait rating and characterized by adjectives such as affectionate, sociable and friendly. Moreover, Agreeableness is similar to Agreeableness reported in our previous study [59] evaluated by common behaviour coding. Extraversion, depicting the exploration



and physical activity of individuals, broadly resembles questionnaire-derived Openness [58,62] and Inquisitiveness [82] and experimentally derived Exploration-Avoidance [60]. In addition, Extraversion in our study is also defined by indices related to social activity, such as *Departures<sup>F</sup>* and *Approaches<sup>F</sup>*, which might, to some extent, reflect the general level of an individual's activity. Compared to our previous study [59], Extraversion was more narrowly specified. Neuroticism, defined by high levels of vigilance, scratching and self-grooming, resembles Neuroticism in the study using the same method of personality evaluation [62]. It also broadly resembles the questionnaire-derived Impulsiveness dimension [58] and Conscientiousness [82] that loaded items such as irritable or excitable. In our previous study [59], we detected Assertiveness that had positive loadings of *Threats<sup>F</sup>*, *Scent marking<sup>F</sup>* and *Invite grooming(in)<sup>F</sup>*—behaviours indicative of dominance [84]. Yet, the dimension in the current study did not load *Threats<sup>F</sup>* but had positive loadings of *Vigilance<sup>F</sup>* and *Self-grooming<sup>F</sup>*. In other words, an individual scoring high on this dimension exhibits frequent scratching, self-grooming, scent-marking and vigilant behaviour. These changes in the item content led us to the decision to label this dimension Neuroticism instead of Assertiveness. Indeed, several studies have confirmed the connection between scent marking, scratching, and stress in common marmosets [85,86].

In our study population, age was a strong predictor of Agreeableness and Extraversion personality scores (cf. [60]). In particular, older individuals were more agreeable and less extraverted than younger ones which corresponds to previous finding in the same species [82]. Nonetheless, the positive relationship between age and Agreeableness is surprising, as in white-faced capuchins, another New-World monkey species, the directionality of the link was reversed so that the older individuals were less agreeable [77]. Our results thus more resemble the results in chimpanzees and humans [87–89]. A possible explanation for the similar trend in humans and marmosets might be their socio-ecologies, particularly similarities in terms of cooperative breeding and living in family units (e.g. [47]). The negative relationship between age and Extraversion, i.e. that older individuals become less extraverted, reflects a general pattern found in New World monkeys and apes, including humans [77,87–90]. Studies on Old World monkeys, in contrast, reported positive relationship between age and Extraversion [91,92]. This similarity in age effect between our marmoset population and captive great ape populations is unexpected and perhaps driven by a particular composition of our individuals that included some quite old marmosets (mean = 78.4 mo), which is also often the case in the studied captive great ape populations.

Although some studies report sex-specific variation in primate personality (frequently in Dominance or Neuroticism related dimensions, e.g. [76,77,93]), we did not detect any sex effects on personality scores which is consistent with the general pattern found across animal taxa [94], and due to their cooperative breeding and biparental care of infants, should not be expected in common marmosets. Indeed, available marmoset personality studies either did not evaluate the sex effects [59,62–64,83,95] or did not find any statistically significant differences [60,61]. Koski *et al.* [82] found a significant interaction between sex and age in Agreeableness. We, however, could not test for this interaction due to the uneven distributions of individuals in the sex and age categories. To sum up, sex differences in personality in primates might have evolved independently in different species and might be connected to species' social or mating system [93].

In terms of hand preference, 50% of individuals were left-handed, 25% right-handed and 25% ambilateral. As in other studies on hand use in marmosets [49,51–53], we did not detect any population-level bias in hand preference. The individual hand preference was, however, highly consistent (across the time span of two years), but neither strength nor direction of hand preference were explained by individual's sex or age—a general pattern commonly reported for marmosets [51–53,55].

Although we detected stable individual differences in observed behaviour, this variation was not attributable to observed individual variation in hand use in marmosets. Contrary to our prediction, neither direction nor strength of hand preference in a food-reaching task were linked to personality, as found also in humans and other species [16,34,35,42]. For instance, Extraversion and Agreeableness were not associated with the direction of limb preference in donkeys [16], lateral bias did not correlate with docility in sharks [22], and most of the personality dimensions did not show a link with paw preference in dogs [34]. There are several possible explanations for this result. First, perhaps brain lateralization is not the proximate mechanism responsible for maintaining personality variation in the common marmoset and other species, including humans [35,42]. One of the possible suggested explanations for personality differences between left-handers and right-handers in humans stems from a different experience of left-handers as a minority group in a right-handed majority society. This experience includes possible negative prejudice and also difficulties while

operating equipment designed for the right-handed population [41]. To sum up, other proximate mechanisms, such as genetics or hormone levels [83], may play a more significant role in the development of personality differences.

Second, even though Tomassetti *et al.* [55] reported more strongly lateralized marmosets being more inquisitive, we did not find a link between a similar personality dimension, Extraversion, and hand preference in our study. This is perhaps due to the different personality assessment methods used in these studies. Measuring personality differences as repeatable reactions to certain experimental stimuli, e.g. novel object or space, might target more specific dimensions related to approach-withdrawal reactions that are perhaps better reflected in brain lateralization, as demonstrated in common marmosets [55], pigs [12] or cichlids [19]. Trait rating and common behaviour coding, in contrast, yield broadly defined personality dimensions in which several seemingly not related behaviours might be correlated, such as social activity and tendency to explore (i.e. Extraversion in our study). As a result, these methods might not be sensitive enough to detect the positive association with brain lateralization [34]. This is further supported by the fact that trait rating studies failed to find a link between brain lateralization and individual scores on personality dimensions (e.g. impulsiveness). Instead, they report positive links between brain lateralization and single personality items (e.g. playful), such as, for instance, in donkeys and cats [16,32]. Future studies should, thus, use methods that describe narrowly specified personality traits.

Third, the preference for using one hand over the other in a particular task does not necessarily involve using a specific hemisphere and, as a result, may not reflect the general brain lateralization. Laterality is often viewed as a multifactorial phenomenon in which not all lateral biases are necessarily in the same direction, an issue frequently discussed also in the human literature [40]. In fact, in a study that compared the hand preference in a normal feeding situation and in a reaching task using an apparatus, almost half of the marmosets displayed opposite preferences in these two tasks [96]. The direction of hand preference was, however, retained when comparing hand preference during simple feeding and other tests. Therefore, the individual's universal hand preference may differ based on the complexity of the task, as well as their postural and visuospatial demands [52,97].

To conclude, even though there has been previous evidence that right-handed and left-handed marmosets behave differently [46,56], we did not find a link between hand preference and personality differences, assessed with behavioural observations. Instead, we detected a strong effect of age on personality scores, whereby older marmosets were more agreeable and less extraverted than the younger ones, which corresponds to the general pattern found in other primates. The association between hand preference and personality thus remains ambiguous. To tackle this ambiguity, future studies should employ methods targeting personality traits related to approach-withdrawal and tasks that can better reveal brain lateralization. Finally, it is possible that other proximate mechanisms, such as development, (epi)genetics or physiology, might instead underpin the personality variation in common marmosets, as well as other primate and mammalian species.

**Ethics.** The study was approved by the Animal Ethics and Experimentation Board, Faculty of Life Sciences, University of Vienna (licence number 2015-013) and adhered to the legal requirements of Austria. We followed all applicable institutional, national and international guidelines for the care and use of animals.

**Data accessibility.** The datasets and code supporting this article have been uploaded as part of the supplementary material [98].

**Authors' contributions.** M.M.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, writing—original draft, writing—review and editing; V.Š.: funding acquisition, methodology, project administration, resources, visualization, writing—original draft, writing—review and editing; G.H.L.M.S.: investigation, writing—review and editing; M.H.: conceptualization, funding acquisition, investigation, methodology, writing—review and editing; S.L.: conceptualization, writing—review and editing; T.B.: conceptualization, resources, supervision, writing—review and editing; M.K.: conceptualization, formal analysis, funding acquisition, methodology, project administration, supervision, visualization, writing—original draft, writing—review and editing.

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