Personality, Subjective Well-Being, and the Serotonin 1a Receptor Gene in Common Marmosets (*Callithrix jacchus*)

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Abstract

Unlike many species, common marmosets (*Callithrix jacchus*), perhaps because they are cooperative breeders, appear to possess a personality domain that captures individual differences in directedness, focus, and perseverance, that resembles human Conscientiousness. However, one study of common marmosets personality did not find this domain. This difference between studies may have come about because, in the study that failed to find a Conscientiousness domain, many markers of that domain were excluded because of low interrater reliability. We increased the number of common marmosets that were rated, bringing it up to 128 from 77. We also gathered new data on subjective well-being and genetic data related to serotonin 1a receptor polymorphisms. Factor analysis revealed evidence for an Openness domain and a domain labeled "Impulsiveness" that combined low Conscientiousness and high emotional instability. The other domains included Sociability, Dominance, and Negative Affect, and resembled those found in previous studies of common marmosets. Correlations between these factors were higher than expected and a second-order factor analysis indicated the presence of a domain, Pro-Sociality, related to high Sociability, low Dominance, and low Impulsiveness, and a domain, Boldness, related to high Openness and low Negative Affect. Further analyses could not determine whether Pro-Sociality and Boldness were artifacts or represented a higher-level of personality organization. Statistically significant correlations were found between the domains and the subjective well-being measures. There were no statistically significant associations between personality and genotype of serotonin 1a receptor. New analytic methods and larger samples may help to better understand personality in common marmosets.

Keywords: higher-order, assessment, temperament, behavioral syndrome, callitrichid

Personality, Subjective Well-Being, and the Serotonin 1a Receptor Gene in Common Marmosets (*Callithrix jacchus*)

Common marmosets (*Callithrix jacchus*) are small New-World monkeys found in South America where they inhabit a wide range of habitats (1, 2). Their small size, fast life history, and other physical and physiological characteristics make common marmosets an increasingly popular animal model in biomedical research (3), although there has been some criticism of this trend (e.g., 4).

Comparative psychologists and behavioral ecologists are also coming to appreciate common marmosets as research subjects. This is in part due to findings from studies that are finding that common marmosets display behaviors and capabilities that were once believed to be the domain of humans and great apes. For example, common marmosets exhibit high levels of spontaneous cooperative behavior (5, 6) and are capable of discriminating between third parties that do and do not reciprocate (7). These behaviors and capabilities are believed to be the products of the unique (among nonhuman primates) reproductive system of common marmosets (see 8 for a review). Specifically, like other callitrichids, are cooperative breeders, and so, rather than disperse and mate, the adult siblings and offspring of mating pairs often stay within the family unit to help raise offspring, and so delay or even forego reproduction (9).

Researchers have also been examining the extent to which common marmoset personality resembles and differs from that of other species. As in other species, behavioral experiments have revealed the presence of stable traits in common marmosets (10, 11). However, there is also evidence, at least for personality traits in this species, for plasticity, either via social facilitation or via social group effects (12). There also appears to be mixed evidence for the construct validity of common marmoset personality traits, that is, for convergent and discriminant validity between personality ratings, behavioral observations,

and responses to behavioral tests (13). Finally, studies of common marmoset personality that relied on behavioral measures have revealed an association between a factor labeled "Inquisitiveness" and the strength of laterality (14), and various associations between factors labeled "Sociability", "Aggressiveness", and "Social Anxiety" and the binding potential of serotonin transporters in the brain (15).

Other studies of common marmosets have focused on the question of how personality traits are organized (personality structure), that is, the number of domains these traits represent and what these domains represent. Comparative studies of members of the genus *Macaca* (16) and *Pan* (17), the genera *Saimiri*, *Sapajus*, and *Cebus* (18-20), and of the family Callitrichidae (21) indicate that species socioecology influences personality structure evolution. This appears to also be true for common marmosets, that is, cooperative breeding appears to have influence how personality traits are organized in this species. For example, a study of ratings and behavioral observations revealed rating-based domains that the authors labeled Extraversion—similar domains have been labeled "Dominance" and "Assertiveness" in other studies of common marmosets—and Agreeableness, Conscientiousness, and Openness, and domains based on behavioral observations, which the authors labeled Agreeableness, Neuroticism, and Perceptual Sensitivity (22). A later study (23) that used ratings found five domains, four of which resembled those found by Iwanicki and Lehmann; these domains were labeled Conscientiousness, Agreeableness, Assertiveness, and Inquisitiveness. The remaining domain, Patience, was thought to perhaps be a ratings-based analogue of Perceptual Sensitivity (23). Thus, traits related to, for instance, perseverance, predictability, and distractibility, are correlated in such a way to suggest the presence of one or two broad domains, those being labeled "Conscientiousness", "Patience", and perhaps "Perceptual Sensitivity" in these studies (22, 23).

These findings in common marmosets are remarkable in that, although many primate and non-primate species exhibit individual differences in these traits (24, 25), the only other primate species in which they reflect the presence of one or two broad personality domains include chimpanzees *Pan troglodytes* (26-31), bonobos *Pan paniscus* (17), and both brown *Sapajus apella* (32) and perhaps golden-bellied capuchin monkeys *Sapajus xanthosternos* (20), and humans *Homo sapiens* (e.g., 33). Cooperative breeding therefore appears to have led to the evolution of a domain that, until now, has only been found in larger brained primate species.

The first goal of our study was to follow-up an earlier study of personality in 77 common marmosets that were housed in the Kobe, Japan campus of the Institute of Physical and Chemical Research (RIKEN), a Japanese research organization for basic and applied science. This earlier study did not find evidence for a Conscientiousness or Patience domain; this study also did not find evidence for an Openness domain (34). Because Conscientiousness, Openness, and possibly Patience, were found in previous studies (22, 23), the failure to find one or more of these domains in the RIKEN sample is puzzling. One possible reason for these differences with regards to Conscientiousness or Patience is that, of the items that Inoue-Murayama, Yokoyama (34) removed because they had interrater reliability estimates that were less than zero, two (reckless and unperceptive) were associated with Conscientiousness and three (inventive, persistent, and quitting) were associated with Patience in Koski et al.'s (23) study (note that only two of these items were examined in Iwanicki and Lehmann's study, those being reckless, which was associated with Extraversion and inventive, which was associated with Openness). The negative interrater reliabilities of these items suggest that there was either very little between-subject variance in ratings of these items or that there was a large amount of error variance (35). A low level of between-subject variance may reflect unmeasured influences related to the way in which the subjects

were housed or bred. It may also have come about because the personality of individual common marmosets can conform to that of their group (12).

A second goal of this study was to examine the associations between the personality domains and subjective well-being. Previous studies in humans (36, 37) and in nonhuman primate species, including chimpanzees (29, 38, 39), orangutans *Pongo* spp. (40), rhesus macaques *Macaca mulatta* (41), brown capuchin monkeys (42), and common marmosets (34), show similar relationships between personality domains and measures of subjective well-being and/or welfare. Across these species, personality domains associated with greater degrees of gregariousness, assertiveness, activity, and other traits associated with Extraversion (43), were related to higher subjective well-being and personality domains made up of traits associated with greater vigilance, fearfulness, anxiety, and other traits associated with Neuroticism (44), were associated with lower subjective well-being. We therefore tested for associations between the personality domains and subjective well-being as measured by a reliable, well-validated scale (38). We examined correlations between the personality domains and the items from this scale, too, for by doing so we could assess the degree to which personality domains were measures of distinct psychological constructs.

A third goal of this study was to further investigate whether genetic polymorphisms were associated with personality. In a previous, we found that lower Dominance and lower Neuroticism in common marmosets were associated with a single nucleotide polymorphism (SNP), the AA genotype of the μ-opioid receptor gene; lower Neuroticism was additionally associated with the short form of the arginine vasopressin receptor 1A gene (34). For the present study we focused on polymorphisms of the serotonin receptor 1a gene. A previous study of chimpanzees identified a SNP (rs25209664: C743A) causing a proline to glutamine substitution at the 248th amino acid of the serotonin receptor 1a gene. This polymorphism was associated with aggression and sociability: chimpanzees who possessed two C alleles

engaged in less social grooming and were rated as being more anxious (45). This study also found evidence for some interactions: males with the CC genotype displayed more and, of chimpanzees with the AC genotype, mid-ranking individuals had lower proximity scores (45).

For the present study, to address the questions about personality and subjective well-being, we asked three individuals to complete personality and subjective well-being questionnaires for 51 common marmosets at RIKEN and pooled these with ratings of the 77 subjects from the original study (34). To address questions about the genetic bases of personality in this species, we surveyed the polymorphism of the serotonin receptor 1a gene around the reported region in chimpanzees and genotyped all 128 subjects and tested for associations between personality and polymorphisms of the serotonin 1a receptor gene.

Method

Subjects

The common marmosets used in this study were recruited in three waves. The subjects from the first wave had taken part in a previous similar study (see 34 for details) and included 68 males and 9 females ranging in age from 1.5 to 15.1 years (mean=6.0, SD=2.6). The subjects from the second and third waves were born at RIKEN. These subjects included 17 males and 7 females ranging in age from 1.7 to 4.5 years (mean = 2.6, SD = 0.7), and 14 males and 13 females ranging in age from 2.0 to 4.9 years (mean = 3.0, SD = 0.8), respectively. The total sample therefore comprised 128 subjects (99 males, 29 females) ranging in age from 1.6 to 15.1 (mean = 4.8, SD = 2.7).

Animal Housing and Husbandry

Subjects were housed in the RIKEN Center for Biosystems Dynamics Research in Kobe, Japan. Of the total sample, 112 were born at the center, 6 were supplied by CLEA Japan Inc. (Tokyo, Japan), and 10 were supplied by Japan Wild Animal Laboratory Limited

(Amami, Japan). Subjects sourced from other facilities had lived in the center for at least three years prior to this study.

At RIKEN, subjects were housed in breeding rooms that had a 12-h light-dark cycle (light: 08:00–20:00). Enclosures (1630 × 760 × 831 mm for families, 660 × 650 × 600 or 660 × 450 × 600 mm for pairs or individuals) had wooden perches, a plastic cube-shaped shelter, a food tray, and a water dispenser. There were around twenty cages in each breeding room and so even animals that were individually housed were exposed to visual and auditory stimulation from conspecifics. The temperature and humidity in the breeding room were maintained at approximately 28°C and 50%, respectively. In the morning and afternoon, subjects received solid food (CMS-1, CLEA Japan, Inc., Tokyo, Japan) mixed with an appropriate amount of water to soften, powdered milk formula, honey, gluconic acid, calcium, vitamin C, and lactobacillus probiotic. The food in the afternoon was softened into a paste by soaking it in water and then stirring it. Once a week subjects' diets were supplemented with chopped and boiled eggs or bananas.

Animal Rearing

Animals were normally reared by their parents or their family members including parents and 1-5 elder brothers or sisters in the family cages. At around 14 days after birth, these infants were fed a food paste that was given to them in the afternoon. When these individuals were between 6 and 12 months old, they left their family cages and began living with mixed-age peers in one of the home cages. Some individuals, because they were to be used in some experiments or because they did not get along with their partners, were housed individually.

Animals that were not reared by their parents, for example in the event of a triplet birth or parental neglect, were hand-reared in climate-controlled rearing cages by human caregivers. This procedure has been described in detail elsewhere (34). In short, these animals

were housed in a thermal insulation box and a towel roll from 1 to 21 days after birth. From 21 days after birth to weaning, these animals were housed in a wire-mesh box sized 390 × 230 × 300 mm furnished with a hammock, perches, a towel roll, a feeding dish, and a water bottle. The animals were breastfed on the day of birth, and then bottle-fed until weaning. A food paste was introduced at around 28 days and they were weaned fully 50 to 70 days after birth. After weaning, animals were housed in one of home cages with peers or individually in the breeding room.

Of the 77 subjects from the first wave, 30, including 23 parent-reared and 7 hand-reared subjects, were housed in a family group (n = 13) or with same-sex peers (n = 17). The remaining 47 subjects, including 33 that were parent-reared, 13 that were hand-reared, and 1 with an unknown rearing history, were single-housed. Of the 24 subjects from the second wave, 22 subjects, including 18 that were parent-reared, 3 that were hand-reared subjects, and 1 with an unknown rearing history, were housed in a family group (n = 7), with an opposite sex marmoset for breeding (n = 2), or with same-sex peers (n = 13). The remaining 2 subjects from the second wave were parent-reared and single-housed. Of the 27 subjects from the third wave, 25 parent-reared subjects and 1 hand-reared subject were housed in a family group (n = 1), with an opposite-sex marmoset for breeding (n = 4), or with same-sex peers (n = 19). The remaining subject was parent-reared and single-housed.

Ratings

Questionnaires

Personality. Ratings were made using the Hominoid Personality Questionnaire (HPQ). The HPQ consists of 54 items, each consisting of a trait adjective paired with one to three sentences that set the adjective in the context of primate behavior. For example, the trait adjective "**FEARFUL**" (boldface and capitals in the original) is paired with the descriptor sentences "Subject reacts excessively to real or imagined threats by displaying behaviors such

as screaming, grimacing, running away or other signs of anxiety or distress." The HPQ's instructions ask raters to assign a rating of 1 ("Displays either total absence or negligible amounts of the trait.") to 7 ("Displays extremely large amounts of the trait.") to each item. The HPQ's instructions also request that raters do not discuss their ratings.

A detailed description of the HPQ's development can be found in Weiss (46). We summarize it here. The HPQ grew out the 48-item Orangutan Personality Questionnaire (40), which grew out of the 43-item Chimpanzee Personality Questionnaire (28). Forty-one of the HPQ's 54 items were sampled from Goldberg's (47) trait terms of the five major domains of human personality (28). The remaining 13 items were adapted from items (48) or facets (49) from other human personality inventories, or were created for by the authors of these instruments (28, 29, 40).

We used a Japanese translation of the HPQ. A study of chimpanzees revealed that the translation did not adversely affect the HPQ's psychometric properties (29).

Subjective Well-Being. Ratings were made on a four-item scale that was based on a questionnaire used to measure subjective well-being in captive chimpanzees (38). Each item was devised so as to assess a different concept of subjective well-being that have been described in the human literature (38, 50-54). The first item (moods) concerned the extent to which an individual experienced positive versus negative affect. The second item (social) concerned whether the individual experienced pleasure from social interactions. The third item (goals) concerned whether the individual was able to achieve its goals, bearing in mind that different individuals may have different, personal goals. The fourth item (be marmoset) asked raters how "happy" they would be if they were that marmoset for a week and was therefore intended to measure global well-being or happiness. The subjective well-being scale's instructions ask raters to assign a rating of 1 ("Displays either total absence or

negligible amounts of the trait or state.") to 7 ("Displays extremely large amounts of the trait.") to each item. The instructions also request that raters do not discuss their ratings.

We used the Japanese version of the subjective well-being questionnaire. A previous study of chimpanzees revealed that the translation did not adversely affect this instrument's psychometric properties (29).

Raters and Ratings

The same three keepers (two men and one woman) who had completed the questionnaires in the first wave of data collection (see 34 for details) completed the questionnaires for the second and third wave of data collection.

The keepers had known the subjects they rated for 1.1 to 9.8 years (mean = 3.7 years, SD = 2.2). Two of the keepers (one man and one woman) rated all 128 subjects on all of the HPQ and the subjective well-being questionnaire items. The third keeper rated 81 subjects. This resulted in a total of 337 ratings or an average of 2.63 ratings per subject.

Genotyping

A buccal swab was taken from each subject and kept in a 90% ethanol solution until DNA extraction. DNA was extracted by DNeasy Blood and Tissue kit (Qiagen, CA, USA). PCR amplification was conducted in a 10 μl (the total volume) reaction mixture containing 10ng of DNA template, 0.4μM of each primer (forward: 5'-tggattcccttcctccgaaa-3', reverse: 5'-aggtgttgattccctagggt-3'), 0.5U of LA Taq DNA polymerase, 400 μM of dNTPs, and GC buffer I (TaKaRa, Shiga, Japan). After denaturing DNA samples at 95°C for 1 min, we set up 40 cycles of 95°C for 30 seconds, 60°C for 30 seconds, 74°C for 1 minute, and a final extension at 74°C for 10 minutes. A total of 1,473 base pair fragments including whole single exon region were amplified. We then sequenced the polymerase chain reaction products, both forwards and backwards, using 3130xl Genetic Analyzer (Applied Biosystems, CA, USA). The internal primer 5'-tcatgctggttctctatggg-3' was also used for sequencing. Primers were

designed based on the NCBI Reference Sequence NC_013897. In the end, we identified three novel SNPs (G840C, G841A, and T901A) in the third intracellular region of the receptor (see Figures 1 and 2). G840C was a synonymous SNP coding alanine at the 280th amino acid sequence, G841A was a nonsynonymous SNP that caused a methionine substitution at the 281st amino acid sequence, and T901A was a nonsynonymous SNP that caused a serine to threonine substitution at the 301st amino acid sequence.

Analyses

Analyses were conducted using version 3.6.3 of R (55). Unless otherwise stated, the functions used were from the version 1.9.12 of the psych package (56) and version 1.0.7 of the EFA.MRFA package (57).

Item Interrater Reliabilities

We used a custom function in R to compute interrater reliabilities the HPQ and subjective well-being questionnaire items. This function computed two types of intraclass correlations (*ICC*s) that were described by Shrout and Fleiss (35). The first, *ICC*(3,1), indicated the reliability of individual ratings, that is, it was an estimate of the reliability of the rating from a single rater. The second, *ICC*(3,*k*), indicated the reliability of the mean rating coming from *k* raters, which was equal to 2.63 in the present study. We excluded items that had reliabilities that were not greater than zero (see 46 for a discussion).

Exploratory Factor Analyses

Personality. Analyses were based on the aggregate (mean) of personality ratings for the 128 subjects. Simulation studies have variously revealed that the number of subjects required for satisfactory factor recovery is a function of the item communalities, the item loadings, the ratio of items to factors (58-60). These same simulations indicated that the subject-to-item ratio is irrelevant. Previous rating-based studies of common marmoset personality (22, 23, 34) have found that between 72% and 97% of questionnaire items were

reliable, between three and five factors, median salient loadings of around .6 or .7, and communalities that were between wide and high (see ref 59 for definitions of these types of communalities). As such, we have a large enough sample size to conduct factor analyses on these data.

We used the fa function from Revelle's psych package to conduct maximum likelihood exploratory factor analyses. Before conducting our factor analyses, however, we used four methods to determine how many factors to extract. First, we inspected the scree plot. Second, we used Revelle's psych package's fa.parallel function to conduct a parallel analysis (61) in which we compared eigenvalues from a principal components analysis of our data to the distribution of 1000 eigenvalues generated from principal components analysis of resampled and randomly generated data. Our decision to use principal components analysis for our parallel analysis was based on the findings of a recent study that showed that the number of dimensions identified in this manner is more accurate (62). Third, we used the VSS function from Revelle's psych package to determine, for solutions that included one to eight factors, which had the lowest Bayesian Information Criterion (BIC; 63). Fourth, we used the hullEFA function from Navarro-Gonzalez and Lorenzo-Seva's EFA.MRFA package to determine the number of factors via the Hull method (64), which performs well with personality data (65). We also inspected the factors to ensure that they were interpretable.

After extracting the factors, we applied an oblique (promax) and an orthogonal (varimax) rotation. If the promax rotation yielded factors that were strongly correlated and/or a different structure, we retained and interpreted those factors. Otherwise, we retained and interpreted the varimax-rotated factors. In interpreting the factors, we specified that salient loadings were those equal to or greater than |0.4|. We then labeled each factor based on our interpretation of it and attempted to find suitable labels from previous findings in nonhuman

primates, and humans. If we could not find a label that was a good description of the factor, we devised our own.

In addition to conducting this first-order factor analysis, we found evidence (results to be discussed) suggesting that there may be second-order personality factors underlying these data. We thus conducted an exploratory factor analyses of the factor correlation (Phi) matrix obtained from the promax-rotated factors. For the same reason, we conducted an additional item-level factor analysis as a robustness check.

Subjective Well-Being. Analyses were based on the aggregate (mean) of the subjective well-being ratings for the 128 subjects. Previous work in 77 of these subjects revealed that a single factor loaded on all four subjective well-being items (34). We therefore used the fa function from Revelle's psych package to conduct a maximum likelihood exploratory factor analysis in which we extracted a single factor from these data.

Unit-Weighted Factor Scores

For the remaining analyses, we used a custom R function to compute unit-weighted factor scores for the personality and subjective well-being data. This involved, for each item, finding the largest salient loading. If that loading was positive, we assigned it a weight of +1. If that loading was negative, we assigned it a weight of -1. In all other cases, we assigned a weight of zero. We then weighted and summed the item ratings.

Factor Reliabilities

For the first- and second-order personality factors, and for subjective well-being, we again used the custom function in R that we used to compute Shrout and Fleiss's *ICC*(3,1) and *ICC*(3,*k*) for the items to compute these *ICC*s. As with the item-level analyses, *k* was equal to 2.63. In addition, we used Revelle's psych package to compute Cronbach's alpha (α), a measure of the internal consistency reliability of a scale and to compute McDonald's

omega hierarchical (ω_h), a measure of the degree to which a general factor saturates a scale's items.

Personality Factor Comparisons

To compare the first- and second-order factors to factors found in three previous studies of common marmoset personality (22, 23, 34), we first generated unit-weighted factor scores based on the personality structures described in these studies. In generating these scores, because there was not a total overlap of questionnaire items across these studies, it was sometimes necessary to substitute items that were similar in meaning or in the constructs that they purportedly assessed. Details about how these unit-weighted scores were created can be found in Table S1.

After computing these unit-weighted factor scores, we obtained correlations between the scores based on the factor loadings from the present study and the scores based on component and factor loadings from previous studies. We compared the absolute magnitude and highlighted the highest correlation or, in the case where the confidence intervals of two or more correlations overlapped, highest correlations.

Personality-Subjective Well-Being Associations

We used Pearson correlation coefficients to examine the associations between the first- and second-order personality factors and, both, the subjective well-being items and the total score.

Genetic Associations

To examine the genotype-personality associations, for each first- and second-order personality factor, we fit a linear model using the lm function. The personality factor scores in these analyses were standardized (mean = 0, SD = 1). The variables in the models included sex (male = 1, female = 0), age in years, and a categorical variable that indicated genotype. Because there were problems with genotyping four subjects, these individuals were excluded

from the analyses. In addition, the G840C genotypes for two subjects and T901A genotype for one subject were unclear, and so these individuals were not included in tests of associations between personality and the G840C and T901A genotype, respectively. Finally, only one subject had the AA version of G841A and only nine subjects had the GA version of this genotype. We therefore decided to not examine associations between this genotype and personality.

Although the subjects were related to one another, we did not test for these effects within the context of an animal model (cf. 34). Moreover, because we conducted multiple, sometimes non-independent, tests, we applied a Bonferroni correction to the results.

Ethics

Data were collected at the RIKEN Center for Biosystems Dynamics Research. This study complied with the current laws of Japan, including the Act on Welfare and Management of Animals. All experimental and husbandry procedures were performed in accordance with RIKEN's Guidelines for Conducting Animal Experiments, and in accordance with the ARRIVE (Animal Research: Reporting of In Vivo Experiments) guidelines. All procedures were approved by the Animal Care and Use Committee of the Kobe Institute of RIKEN (MA2009-10-16).

Results

Interrater Reliabilities of Items

Personality

The interrater reliabilities of the 54 items from the Hominoid Personality Questionnaire are presented in Table 1. The reliabilities of individual ratings and of mean ratings for the items anxious, persistent, quitting, and unperceptive were negative, and so we excluded these items from further analyses. The reliabilities of individual ratings for the items

innovative and decisive were less than 0.01 and the reliability of mean ratings for these items were equal to 0.01, and so we decided to also exclude these items from further analyses.

Of the remaining 48 items, the interrater reliabilities of individual ratings ranged from 0.02 (inventive) to 0.45 (dominant). The mean and standard deviation for these estimates were 0.21 and 0.11, respectively. The interrater reliabilities of mean ratings for the remaining items ranged from 0.06 (inventive) to 0.68 (dominant). The mean and standard deviation for these estimates were 0.40 and 0.16, respectively.

Subjective Well-Being

The interrater reliabilities of individual ratings were 0.16, 0.10, 0.15, and 0.15 for the item about positive versus negative moods, the pleasure derived from social interactions, the ability to achieve goals, and how happy a rater would be if they were that marmoset. The corresponding reliabilities of mean ratings were 0.33, 0.23, 0.32, and 0.30.

Maximum Likelihood Exploratory Factor Analyses

Personality

First-Order Analysis. Parallel analysis and inspection of the scree plot indicated that there were five factors (see Figure S1). The Hull method (see Figure S2) also indicated that there were five factors and the lowest BIC (see Table S2) was achieved when extracting five factors. We therefore extracted five factors. A promax rotation of these factors yielded two interfactor correlations that were large (rs $\geq |0.5|$) and two that were medium-sized (rs $\geq |0.3|$). The mean and standard deviation of the absolute interfactor correlations were 0.26 and 0.20, respectively. Comparison of the varimax- and promax-rotated factors revealed that the congruence coefficients for two factors fell below 0.95 (see Table S3) and an inspection of the factor loadings indicated that the promax-rotated factors differed some from their varimax-rotated counterparts. Given these results, we interpreted the promax-rotated factors

(see Table 2), which explained 63% of the variance (the varimax-rotated factors are presented in Table S4).

The first factor loaded on items related to high Extraversion and high Agreeableness in humans (e.g., 47). Compared to other studies of common marmosets, this factor somewhat resembled the Sociability factor in one study (34) and the Agreeableness factor from two other studies (22, 23).

The second factor loaded on items related to high Extraversion and low Agreeableness in humans (e.g., 47). Compared to other studies of common marmosets, it is best described as a narrow version of factors labeled Dominance (34), Extraversion (22), and Assertiveness (23). To be consistent with a prior study of a subset of these animals (34), we labeled this factor Dominance.

The third factor had positive loadings on items related to high Neuroticism and low Conscientiousness in humans, and also negative loadings on items related to low Neuroticism and high Conscientiousness (e.g., 47). In a previous study of a subsample of these animals (34), the Dominance and Neuroticism factor loaded on some of these items. Compared to other studies of common marmosets, it resembled most closely factors labeled Conscientiousness and Patience in one study (23) and the Conscientiousness factor in another (22). Humans that are high in Neuroticism and low in Conscientiousness are described as exhibiting an undercontrolled style of impulse control (66). We thus labeled this factor Impulsiveness.

With the sole exception of a negative loading on the item cautious, the fourth factor primarily loaded on items related to high Openness in humans (e.g., 47). Previous studies of common marmosets have labeled factor such as these Openness (22) and Inquisitiveness (23). We therefore labeled this factor Openness.

The fifth factor loaded on items related to low Extraversion and high Neuroticism in humans (e.g., 47). In the previous study of a subset of these animals (34), Neuroticism had a positive loading on many of these items. In all three previous studies of this species, factors such as Dominance, Assertiveness, and Conscientiousness had negative loadings on these items (22, 23, 34). Given that this factor combined aspects of high Neuroticism and low degrees of Assertiveness or social prowess, we labeled it Negative Affect.

Second-Order Analysis. Because there were several non-negligible correlations between the factors, we factor analyzed the factor intercorrelation (Phi) matrix. This enabled us to test whether there were any second-order factors.

Parallel analysis and inspection of the scree plot (see Figure S3) indicated that there were two factors. We also tried to extract a single 'general' factor, but this solution exhibited poor fit (root mean square of the residuals = 0.14) and the factor did not load on Openness or Negative Affect. A promax rotation of the two-factor solution indicated that they were close to being orthogonal, and the loadings of the varimax-rotated factors were nearly identical to the promax-rotated factors (see Table 3). We therefore interpreted the varimax-rotated factors. After reflecting (multiplying its loadings by -1) the first factor, it had a positive loading on Sociability and a negative loading on both Dominance and Impulsiveness. We thus labeled this factor Pro-sociality. The second factor had a positive loading on Openness and a negative loading on Negative Affect. We thus labeled this factor Boldness.

Robustness Checks. Previous studies of common marmosets did not find higher-order factors; the interfactor correlations were modest (22, 23, 34). We therefore conducted two robustness checks.

The first check was to test whether the higher-order factors reflected the structuring of data collection. Specifically, because different subjects were rated in each of three waves, this may have led raters to rate the subjects belonging to each wave as more similar to one

another than to those in other waves. To test this, we residualized the 48 reliable items on a categorical variable that represented whether the subject was rated in the first, second, or third wave. We then factor analyzed the residualized item scores.

Inspection of the scree plot suggested that there were five factors and parallel analysis indicated that there were four factors (see Figure S4). The Hull test indicated that there were two factors (see Figure S5). The BIC was lowest for a five-factor solution (see Table S2). We therefore examined promax-rotations after extracting two, four, and then five factors.

For the two-factor solution (see Table S5), the first factor loaded predominantly on items that belonged to the three factors—Sociability, Dominance, and Impulsiveness—that loaded on Pro-Sociality. The second factor loaded predominantly on items that belonged to Openness and Negative Affect, that is, the factors that loaded on Boldness. For the four-factor solution (see Table S6), the first, third, and fourth factors resembled the Sociability, Negative Affect, and Openness. The second factor loaded predominantly on items related to high Dominance and high Impulsiveness. The five-factor solution (see Table S7) yielded five factors that were similar to the five factors found earlier.

The similarity, as indicated by Tucker's congruence coefficients, between the five factors obtained before and after item scores were residualized were equal to or greater than 0.98, suggesting that these were the same factors (see Table S8). Factor analysis of the residualized item scores, then, revealed either the same structure (the five-factor solution) or structures in which there were stronger associations between factors (the two- and four-factor solutions). These results are not consistent with the possibility that the higher-order factors are due to how the data were gathered.

The second check was to test whether the second-order factors are general evaluative factors used by raters (see ref 67 for a discussion and demonstration). To do so, we factor

analyzed ratings from each of the three raters separately. We also factor analyzed a weighted correlation matrix from which removed possible effects of raters

$$\mathbf{P}_w = \frac{1}{N}\sum_{i=1}^{k}\mathbf{P}_i n_i$$

where $\mathbf{P}_w$, the weighted correlation matrix, is the sum of the products of the correlation matrices of each of k (3 in the present case) raters, $\mathbf{P}_i$, and the subjects, n_i rated by that individual rater, divided by the total number of subjects, N.

For ratings from one keeper who rated all of the subjects, the scree plot and parallel analysis (see Figure S6), BIC (see Table S2), and Hull method (see Figure S7) indicated that there were five factors. We thus extracted five factors and subjected them to a promax rotation (see Table S9). The factors resembled those obtained in the initial factor analysis and the interfactor correlations were similar in magnitude. We then conducted a second-order factor analysis in which we forced a two-factor solution. Although one second-order factor just missed our criterion for a salient loading on a first-order factor, these factors resembled Pro-sociality (reversed) and Boldness (see Table S10).

For ratings from the second keeper who rated all of the subjects, the scree plot indicated that there were four or five factors and parallel analysis indicated that there were four factors (see Figure S8). BIC (see Table S2) and the Hull method (see Figure S9) also indicated that there were four factors. We thus extracted four factors and subjected them to a promax rotation (see Table S11). This solution included what appeared to be an Agreeableness factor (the first factor), the third factor was a Gregariousness factor (a narrow facet of Extraversion), and the remaining two factors that were difficult to interpret. The interfactor correlations were not consistent with there being a second-order factor.

For ratings from the keeper who rated 81 subjects, the scree plot and parallel analysis (see Figure S10), BIC (see Table S2), and Hull method (see Figure S11) indicated that there

were three factors. We thus extracted three factors and subjected them to a promax rotation (see Table S12). These factors included a broad variant of Dominance, a factor that encompassed activity and low levels of negative affect, and a narrow variant of Impulsiveness.

For the weighted correlation matrix, the scree plot indicated that there were five factors and parallel analysis indicated that there were three factors (see Figure S12). The BIC indicated that there were three factors (see Table S2). We thus extracted three factors and subjected them to a promax rotation (see Table S13). The first and third factors loaded on many of the traits that belonged to the factors that made up the second-order Pro-sociality and Boldness domains, respectively. The second factor was similar to Impulsiveness. The correlation between the first and third factors was low, but the correlation between Impulsiveness and Pro-Sociality was between medium and large, and therefore was consistent with the definitions of these factors. We then conducted an analysis in which we extracted five factors and subjected them to a promax-rotation. The five factors resembled those from our initial factor analyses as did the interfactor correlations (see Table S14). The second-order factor analysis of these correlations revealed a (reversed) Pro-Sociality factor and a Boldness factor (see Table S15).

Subjective Well-Being

Parallel analysis and an examination of the scree plot indicated that there was a single factor (see Figure S13). This factor explained 67% of the variance and had salient loadings on all four items (see Table 4).

Reliabilities of Factors

Personality

The interrater reliabilities of the individual ratings for Sociability, Dominance, Impulsiveness, Openness, and Negative Affect were 0.52, 0.39, 0.28, 0.25, and 0.26,

respectively. The interrater reliabilities of mean ratings for these factors were 0.74, 0.63, 0.50, 0.46, and 0.48, respectively. For Pro-Sociality and Boldness, respectively, the interrater reliabilities of individual ratings were 0.45 and 0.30, and the interrater reliabilities of mean ratings for these second-order factors were 0.69 and 0.53.

The internal consistency reliability (Cronbach's α) for Sociability, Dominance, Impulsiveness, Openness, and Negative Affect were 0.95, 0.95, 0.88, 0.85, and 0.81, respectively. The degree to which a general factor saturated (McDonald's ω_h) Sociability, Dominance, Impulsiveness, Openness, and Negative Affect was 0.81, 0.85, 0.75, 0.80, and 0.68, respectively.

Subjective Well-Being

For the total subjective well-being score, the interrater reliability of individual ratings was 0.21 and the interrater reliability of the mean of ratings 0.41. Cronbach's α for this scale was 0.87.

Personality Factor Comparisons

Iwanicki and Lehmann (22) found four factors, which they labeled Extraversion, Agreeableness, Conscientiousness, and Openness. Compared to our first-order factors, their Extraversion factor was most similar to Dominance, their Agreeableness factor was equally similar to the Sociability and (low) Dominance, their Conscientiousness factor was most similar to Sociability, and their Openness was most similar to the same-named factor that we found (see Table 5). Compared to our second-order factors, Iwanicki and Lehman's Extraversion was equally similar to (low) Pro-sociality and high Boldness; their Agreeableness and Conscientiousness factors were most similar to Pro-sociality; and their Openness factor was most similar to Boldness (see Table 6).

Koski, Buchanan-Smith (23) found five factors, which they labeled Conscientiousness, Agreeableness, Assertiveness, Patience, and Inquisitiveness. Compared to

our first-order factors, their Conscientiousness factor was equally similar to (low) Dominance and (low) Impulsiveness; their Agreeableness factor was most similar to Sociability; their Assertiveness factor was similar to (low) Sociability, Dominance, and (low) Negative Affect; their Patience was most similar to Sociability; and their Inquisitiveness was most similar to Openness (see Table 5). Compared to our second-order factors, their Conscientiousness, Agreeableness, and Patience factors were all most similar to Pro-sociality; their Assertiveness factor was equally similar to Boldness and (low) Pro-sociality; and their Inquisitiveness factor was most similar to Boldness (see Table 6).

Inoue-Murayama, Yokoyama (34) found three factors, which they named Dominance, Sociability, and Neuroticism. Compared to our first-order factors, their Dominance factor was most similar to Dominance; their Sociability factor was most similar to Sociability; and their Neuroticism factor was most similar to Negative Affect (see Table 5). Compared to our second-order factors, their Dominance and Sociability factors were most similar to low and high Pro-sociality, respectively; their Neuroticism factor was most similar to (low) Boldness (see Table 6).

Personality and Subjective Well-Being Associations

The correlations between the four subjective well-being items and the personality factors are presented in Table 7. Sociability was significantly associated with higher scores on all four of the scale items and subjective well-being. Dominance was not significantly related to any of the scale's items or the factor. Impulsiveness was significantly related to lower and Openness was significantly related to higher balance of positive versus negative moods, how happy raters thought they would be if they were the marmoset, and subjective well-being. Negative Affect was negatively related to how happy raters would be how happy raters thought they would be if they were the marmoset. The second-order factor Pro-sociality was significantly associated with being rated as higher on all four items and higher subjective

well-being. The second-order factor Boldness was not significantly associated with the pleasure subjects derived from social interactions, but it was significantly related to being higher in the other three items and in subjective well-being.

Personality-Genotype Associations

G840C Genotypes

Twenty-seven subjects had the GG genotype, 23 had the CC genotype, and 72 were heterozygous. In the first set of analyses, we compared subjects with the GC genotype and subjects with the GG type to those with the CC genotype. Compared to subjects with the CC genotype, subjects with the GC or GG genotypes were significantly higher in Dominance; these effects, however, did not prevail correction for multiple tests (see Table S16). In a second set of analyses, we compared the 95 subjects who were carriers of the C allele (CC or GC genotype) to the 27 subjects with the GG genotype. None of the comparisons were statistically significant (see Table S17). In a third set of analyses, we compared the 99 subjects who were carriers of the G allele (GG or GC genotype) to the 23 subjects with the CC genotype. Carriers were significantly higher in Dominance, but again, this effect did not prevail correction for multiple tests (see Table S17).

T901A genotypes

Twelve subjects had the TT genotype, 35 had the AA genotype, and 76 were heterozygous. Because of this imbalance in the number of subjects, we only compared the 88 subjects who carried the T allele to the 35 subjects with the AA genotype. None of the comparisons were statistically significant (see Table S18).

Discussion

We found five common marmoset personality domains. We labeled these domains Sociability, Dominance, Impulsiveness, Openness, and Negative Affect. The correlations between these domains suggested the presence of second-order factors. Further analyses

revealed two second-order factors, one that we labeled Pro-sociality, which had a positive loading on Sociability and negative loadings on Dominance and Impulsiveness, and another that we labeled Boldness, which had a positive loading on Openness and a negative loading on Negative Affect. The interrater reliabilities of unit-weighted factor scores that represented the first- and second-order domains indicated that, even at the lower end, the degree to which variance in these scores were comprised of true-score variance was comparable to what has been found in studies of other primate species (68), including humans (e.g., 69). The interrater reliability estimate for subjective well-being was, however, markedly lower than what has been found in other species, for example, chimpanzees (29, 38). The personality factors were related to subjective well-being and its constituent items in ways consistent with the meaning of the factors. There was no strong evidence that they were associated with polymorphisms of the serotonin 1a receptor gene.

The personality domains found in our study showed considerable overlap with those found in prior studies of this species. Openness resembled eponymous domains, or domains labeled Inquisitiveness, that had been identified in studies in which common marmoset personality (12, 14, 22, 23). Although we did not find a clear match to the domain labeled Conscientiousness in Iwanicki and Lehmann (22) and Koski, Buchanan-Smith (23), Impulsiveness and Pro-sociality showed considerable overlap with that construct. Specifically, in addition to being related to behavioral consistency and reliability, Conscientiousness in these past studies had loadings prosocial behavior, tolerance, and low levels of aggression (22, 23) whereas Impulsiveness was also related to emotionality and reactivity. Finally, Dominance, Sociability, and Negative Affect resembled domains that had been found in at least one of these earlier studies. On the other hand, the Patience domain identified by Koski, Buchanan-Smith (23) and possibly by Iwanicki and Lehmann (22) was not clearly represented among the domains; the best match was Pro-sociality.

One major difference between this study and comparable rating-based studies (22, 23, 34) was our identification of two second-order factors. Our follow-on analyses suggested that these factors may partly reflect a tendency for some raters to see some traits as more correlated than others, but these analyses could not exclude the possibility that Pro-Sociality and Boldness belong to a higher-level of personality organization, perhaps reflecting group personalities in this species (12).

There have been reports of higher-order factors of human personality (70, 71), including a general factor of personality (e.g., 72, 73). However, these and other, similar reports have been criticized on numerous grounds (see, e.g., 74, 75, 76). Moreover, studies including of nonhuman primates, which are not beset by the problems noted by these critics tend not to find evidence for higher-order personality factors or correlations among lower-order factors (67, 76-82).

The problems in human studies identified by these critics are also absent in the present study: each animal was rated by two or three keepers, the correlations among the latent variables were considerable, and statistically adjusting for rater effects increased rather than decreased some correlations among factors. Still, these second-order factors were not identified in similar studies, including the previous study of this group of common marmosets (22, 23, 34). As such, replication and an examination of this phenomenon using more flexible modeling techniques (e.g., ref 11) are needed before we can conclude that these second-order factors represent a higher-level of personality organization and identify whether they are caused by social processes in common marmosets (cf. 12).

Together with findings from prior studies, the findings in this study are consistent with the possibility that common marmosets evolved a personality structure that includes domains that are more commonly associated with species, such as brown capuchin monkeys (32), chimpanzees (28), and humans (83). As these species only share distant common

ancestors with common marmosets and have very different socioecologies, these traits are not likely to be homologous. Instead, these traits likely reflect convergent evolution, and evolved to deal with the demands that come with cooperative breeding. Likewise, the differences between common marmoset personality and that of the other species may also be attributable to their being cooperative breeders or other unique features of their socioecology that we have yet to discover. In any event, studies that examine the role that Conscientiousness and/or Patience play in infant rearing, and especially by helpers, among common marmosets and other cooperative breeders are needed to test this hypothesis.

As in our study of a subsample of these subjects (34), we found a pattern of personality-subjective well-being correlations that were consistent with those found in studies of humans (36, 37) and nonhuman primates (29, 38-42). Similar associations have also been reported for felids (84, 85). These findings, and those in humans and great apes that indicate that a common genetic background underlies these traits (86-91), are consistent with the possibility that these relationships are ancestral.

Our failure to find an association between SNPs related to the serotonin 1a receptor gene is not consistent with previous findings of an association between this genotype and personality in chimpanzees (45). It is possible that our failure to find an association resulted from the personality measure that we used. However, the associations between personality and serotonin-related genes in humans appear to be false positives (92). As such, without additional evidence from well-powered studies to the contrary, we are led to conclude that we did not find significant associations between these SNPs and personality domains because there were none.

This study had three shortcomings. First, nearly 40% of the subjects were single-housed. Behaviors related to some of the traits might therefore have been rare or absent. Second, the factor structure was compared to those from studies that used different, although

partly overlapping, instruments. It is unclear to what degree this would have obscured similarities or blurred differences between the structures in these studies. This limitation also prevented us from using other statistical methods to compare these structures. Third, as we alluded to earlier, to identify genetic effects, considerably larger sample sizes. Still, we judged that it was worth reporting the genetic associations so that they may contribute to future meta-analyses.

To use a cliché, this study yields more questions than answers about common marmoset personality. Nevertheless, it highlights the promise that large collaborative studies of this species may hold for understanding the proximate and ultimate origins of their personality and ours.

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Table 1

Interrater Reliabilities of Items from the Hominoid Personality Questionnaire

Item	*ICC*(3,1)	*ICC*(3,*k*)
Sociable	0.45	0.68
Sympathetic	0.43	0.66
Solitary	0.43	0.67
Protective	0.42	0.66
Helpful	0.38	0.62
Friendly	0.36	0.60
Aggressive	0.34	0.57
Gentle	0.34	0.58
Irritable	0.33	0.57
Affectionate	0.32	0.55
Stingy/greedy	0.29	0.51
Dominant	0.28	0.50
Individualistic	0.28	0.51
Submissive	0.28	0.51
Imitative	0.28	0.51
Independent	0.27	0.50
Excitable	0.26	0.48
Conventional	0.26	0.48
Bullying	0.23	0.44
Impulsive	0.23	0.44
Dependent/follower	0.23	0.44
Defiant	0.23	0.45
Stable	0.21	0.41
Jealous	0.21	0.41
Cautious	0.19	0.39
Active	0.19	0.38
Fearful	0.18	0.37
Autistic	0.18	0.36
Thoughtless	0.17	0.36
Erratic	0.17	0.35
Playful	0.16	0.33
Intelligent	0.16	0.33
Reckless	0.15	0.32
Curious	0.14	0.30
Sensitive	0.14	0.30
Inquisitive	0.13	0.28
Cool	0.13	0.29
Predictable	0.13	0.28
Lazy	0.11	0.25
Timid	0.10	0.22
Clumsy	0.09	0.21

Disorganized	0.09	0.20
Vulnerable	0.07	0.16
Unemotional	0.06	0.15
Distractible	0.05	0.13
Manipulative	0.05	0.12
Depressed	0.04	0.09
Inventive	0.02	0.06
Innovative	0.00	0.01
Decisive	0.00	0.01
Anxious	-0.03	-0.08
Persistent	-0.06	-0.19
Quitting	-0.08	-0.24
Unperceptive	-0.12	-0.39

Table 2

Pattern Matrix from the First-Order Factor Analysis of the Hominoid Personality Questionnaire

Item	Factor Loadings					h^2
	Soc	Dom	Imp	Opn	Neg	
Helpful	**0.89**	0.10	-0.05	0.09	-0.08	0.79
Sympathetic	**0.83**	-0.01	-0.07	0.07	0.08	0.76
Protective	**0.80**	0.01	0.02	0.02	-0.15	0.66
Individualistic	**-0.78**	0.09	-0.05	0.13	0.25	0.71
Dependent/follower	**0.77**	0.06	-0.05	0.23	0.39	0.69
Independent	**-0.73**	0.27	-0.31	0.10	0.08	0.62
Imitative	**0.71**	0.04	0.07	0.20	0.18	0.49
Solitary	**-0.71**	0.05	-0.04	-0.17	0.34	0.74
Affectionate	**0.64**	-0.09	-0.16	0.21	0.12	0.65
Sensitive	**0.64**	-0.08	-0.17	-0.02	0.04	0.61
Sociable	**0.62**	-0.27	-0.16	0.16	-0.15	0.85
Conventional	**0.60**	0.11	-0.33	-0.13	0.19	0.62
Intelligent	**0.59**	0.26	-0.18	0.00	-0.19	0.39
Gentle	**0.50**	-0.35	-0.24	0.15	0.09	0.83
Reckless	**-0.50**	-0.16	0.39	0.38	-0.03	0.62
Friendly	**0.49**	**-0.46**	-0.15	0.13	0.02	0.86
Jealous	0.02	**0.92**	-0.04	0.21	0.15	0.83
Stingy/greedy	-0.08	**0.87**	-0.06	0.28	0.15	0.86
Bullying	-0.04	**0.85**	0.00	0.11	0.07	0.77
Dominant	-0.09	**0.79**	0.06	0.01	-0.07	0.80
Manipulative	0.21	**0.72**	-0.10	0.04	-0.33	0.57
Aggressive	-0.12	**0.69**	0.15	-0.05	-0.17	0.80
Defiant	-0.09	**0.65**	0.20	-0.01	-0.20	0.78
Irritable	0.00	**0.50**	**0.48**	-0.18	-0.11	0.74
Excitable	-0.02	0.16	**0.78**	-0.08	-0.06	0.78
Unemotional	-0.10	0.14	**-0.77**	0.00	0.26	0.52
Impulsive	-0.10	0.06	**0.75**	0.13	0.13	0.76
Cool	0.18	-0.05	**-0.66**	-0.06	0.01	0.65
Fearful	0.23	-0.10	**0.62**	**-0.42**	0.28	0.51
Distractible	-0.11	-0.05	**0.53**	0.23	0.10	0.40
Disorganized	-0.10	0.15	**0.52**	0.18	0.12	0.51
Stable	0.21	-0.19	**-0.46**	0.07	-0.38	0.64
Thoughtless	-0.22	-0.03	**0.41**	0.38	0.02	0.45
Predictable	0.12	-0.08	**-0.40**	0.04	0.02	0.27
Erratic	-0.20	0.32	0.35	-0.06	0.20	0.55
Curious	0.14	0.13	0.08	**0.73**	0.02	0.61
Inquisitive	0.17	0.11	0.06	**0.72**	0.09	0.55
Inventive	0.27	0.18	-0.05	**0.68**	0.11	0.51

Playful	0.23	-0.12	0.32	**0.65**	-0.04	0.60
Cautious	**0.47**	0.08	0.24	**-0.59**	0.22	0.53
Active	0.28	0.18	**0.41**	**0.52**	-0.12	0.69
Autistic	0.04	-0.13	0.10	0.19	**0.68**	0.44
Timid	0.14	0.00	0.34	-0.18	**0.65**	0.58
Depressed	-0.17	0.07	-0.27	-0.04	**0.64**	0.51
Clumsy	-0.04	0.17	-0.06	0.00	**0.58**	0.33
Vulnerable	-0.03	-0.19	-0.02	0.04	**0.57**	0.39
Lazy	-0.23	-0.05	**-0.45**	-0.17	**0.49**	0.59
Submissive	0.33	-0.20	-0.19	0.00	**0.49**	0.62
Proportion of variance	0.20	0.14	0.13	0.08	0.08	

	Factor Correlations				
Factor	Soc	Dom	Imp	Opn	Neg
Soc	1.00				
Dom	-0.53	1.00			
Imp	-0.45	0.57	1.00		
Opn	0.06	0.15	0.18	1.00	
Neg	-0.06	-0.18	-0.04	-0.38	1.00

Note. *N* = 128. Soc = Sociability, Dom = Dominance, Imp = Impulsiveness, Opn = Openness, Neg = Negative Affect, h^2 = communalities. Factors extracted using a maximum likelihood estimation and rotated using the promax procedure. Factor loadings greater than or equal to |0.4| are in bold.

Table 3

Pattern Matrix from the Second-Order Factor Analysis of Personality Factors

	Promax Rotation		Varimax Rotation		
First-Order Factor	Pro-Sociality	Boldness	Pro-Sociality	Boldness	h^2
Dominance	**-0.79**	0.15	**-0.80**	0.21	0.68
Sociability	**0.72**	0.21	**0.70**	0.15	0.51
Impulsiveness	**-0.67**	0.08	**-0.68**	0.13	0.48
Openness	-0.01	**0.62**	-0.06	**0.62**	0.38
Negative Affect	-0.01	**-0.61**	0.04	**-0.61**	0.37
Proportion of variance	0.32	0.17	0.32	0.17	

Note. N = 128. h^2 = communalities. Factors extracted from the factor correlation matrix from Table 2 using a maximum likelihood estimation and rotated using the promax and varimax procedures. The Pro-Social factor for both structures were reflected, that is, the loadings were multiplied by -1. The promax-rotated factors correlated -0.15. Factor loadings greater than or equal to |0.4| are in bold.

Table 4

Results from Factor Analysis of the Subjective Well-Being Scale

Item	Loading	h^2
Be marmoset	0.98	0.97
Balance of moods	0.86	0.73
Ability to achieve goals	0.82	0.67
Pleasure from social interactions	0.55	0.30

Note. N = 128. h^2 = communalities.

Table 5

Correlations Between Unit-Weighted Factor Scores Based on Factor Loadings in the Present Study and Factor Loadings from Three Previous Studies of Common Marmoset Personality

		95% Confidence Interval	
	r	Lower Bound	Upper Bound
Iwanicki and Lehman (2015)			
Extraversion			
Sociability	-0.50	-0.62	-0.36
Dominance	**0.82**	**0.75**	**0.87**
Impulsiveness	0.50	0.36	0.62
Openness	0.54	0.40	0.65
Negative affect	-0.70	-0.78	-0.60
Agreeableness			
Sociability	**0.86**	**0.81**	**0.90**
Dominance	**-0.84**	**-0.88**	**-0.77**
Impulsiveness	-0.76	-0.82	-0.67
Openness	-0.07	-0.24	0.11
Negative affect	0.25	0.08	0.41
Conscientiousness			
Sociability	**0.83**	**0.77**	**0.88**
Dominance	-0.47	-0.59	-0.32
Impulsiveness	-0.63	-0.73	-0.51
Openness	0.00	-0.17	0.18
Negative affect	0.05	-0.13	0.22
Openness			
Sociability	0.11	-0.07	0.28
Dominance	0.34	0.18	0.49
Impulsiveness	0.27	0.10	0.42
Openness	**0.96**	**0.94**	**0.97**
Negative affect	-0.40	-0.53	-0.24
Koski et al. (2017)			
Conscientiousness			
Sociability	0.62	0.51	0.72
Dominance	**-0.89**	**-0.92**	**-0.84**
Impulsiveness	**-0.84**	**-0.89**	**-0.79**
Openness	-0.39	-0.53	-0.23
Negative affect	0.18	0.01	0.35
Agreeableness			
Sociability	**0.95**	**0.92**	**0.96**
Dominance	-0.68	-0.77	-0.58
Impulsiveness	-0.72	-0.79	-0.62

Openness	0.03	-0.14	0.20
Negative affect	0.13	-0.05	0.29
Assertiveness			
Sociability	**-0.67**	**-0.76**	**-0.57**
Dominance	**0.67**	**0.57**	**0.76**
Impulsiveness	0.33	0.16	0.47
Openness	0.32	0.15	0.47
Negative affect	**-0.64**	**-0.73**	**-0.53**
Patience			
Sociability	**0.74**	**0.65**	**0.81**
Dominance	-0.37	-0.51	-0.21
Impulsiveness	-0.59	-0.69	-0.47
Openness	0.21	0.04	0.37
Negative affect	-0.03	-0.21	0.14
Inquisitiveness			
Sociability	0.34	0.18	0.48
Dominance	0.21	0.04	0.37
Impulsiveness	0.17	-0.01	0.33
Openness	**0.82**	**0.76**	**0.87**
Negative affect	-0.56	-0.67	-0.43
Inoue-Murayama et al. (2018)			
Dominance			
Sociability	-0.71	-0.79	-0.62
Dominance	**0.94**	**0.91**	**0.96**
Impulsiveness	0.83	0.77	0.88
Openness	0.34	0.18	0.49
Negative affect	-0.38	-0.52	-0.22
Sociability			
Sociability	**0.93**	**0.90**	**0.95**
Dominance	-0.40	-0.54	-0.25
Impulsiveness	-0.39	-0.52	-0.23
Openness	0.40	0.24	0.54
Negative affect	-0.12	-0.29	0.05
Neuroticism			
Sociability	-0.30	-0.45	-0.14
Dominance	-0.03	-0.20	0.14
Impulsiveness	0.35	0.19	0.49
Openness	-0.34	-0.49	-0.18
Negative affect	**0.82**	**0.75**	**0.87**

Note. *N* = 128. The highest correlation between the five factors found in this study and each factor found in a previous study are highlighted in bold. In cases where the confidence

intervals of two or more of the highest correlations overlapped, we highlighted both correlations.

Table 6

Correlations Between Unit-Weighted Factor Scores Based on Loadings from the Second-Order Factor Analysis in the Present Study and Factor Loadings from Three Previous Studies of Common Marmoset Personality

		95% Confidence Interval	
	r	Lower Bound	Upper Bound
Iwanicki and Lehman (2015)			
Extraversion			
Pro-sociality	**-0.72**	**-0.80**	**-0.63**
Boldness	**0.73**	**0.64**	**0.80**
Agreeableness			
Pro-sociality	**0.95**	**0.93**	**0.97**
Boldness	-0.18	-0.35	-0.01
Conscientiousness			
Pro-sociality	**0.73**	**0.64**	**0.81**
Boldness	-0.02	-0.20	0.15
Openness			
Pro-sociality	-0.20	-0.36	-0.03
Boldness	**0.83**	**0.76**	**0.87**
Koski et al. (2017)			
Conscientiousness			
Pro-sociality	**0.91**	**0.88**	**0.94**
Boldness	-0.35	-0.49	-0.19
Agreeableness			
Pro-sociality	**0.90**	**0.87**	**0.93**
Boldness	-0.05	-0.22	0.12
Assertiveness			
Pro-sociality	**-0.67**	**-0.76**	**-0.56**
Boldness	**0.56**	**0.43**	**0.67**
Patience			
Pro-sociality	**0.64**	**0.53**	**0.73**
Boldness	0.15	-0.02	0.32
Inquisitiveness			
Pro-sociality	-0.02	-0.19	0.16
Boldness	**0.84**	**0.78**	**0.88**
Inoue-Murayama et al. (2018)			
Dominance			
Pro-sociality	**-0.97**	**-0.98**	**-0.95**
Boldness	0.43	0.27	0.56
Sociability			
Pro-sociality	**0.66**	**0.55**	**0.75**
Boldness	0.32	0.16	0.47
Neuroticism			

Pro-sociality	-0.21	-0.37	-0.04
Boldness	**-0.68**	**-0.76**	**-0.57**

Note. N = 128. The highest correlation between the five factors found in this study and each factor found in a previous study are highlighted in bold. In cases where the confidence intervals of two or more of the highest correlations overlapped, we highlighted both correlations.

Table 7

Correlations Between Subjective Well-Being Scale Items and Factor and Personality Factors

		95% Confidence Interval	
	r	Lower Bound	Upper Bound
Moods			
Sociability	**0.42**	**0.16**	**0.62**
Dominance	-0.18	-0.40	0.06
Impulsiveness	**-0.27**	**-0.50**	**-0.02**
Openness	**0.38**	**0.12**	**0.59**
Negative affect	-0.14	-0.34	0.08
Pro-sociality	**0.33**	**0.07**	**0.55**
Boldness	**0.32**	**0.05**	**0.54**
Social			
Sociability	**0.53**	**0.30**	**0.71**
Dominance	-0.22	-0.45	0.03
Impulsiveness	-0.24	-0.47	0.01
Openness	0.14	-0.08	0.35
Negative affect	-0.11	-0.30	0.09
Pro-sociality	**0.38**	**0.12**	**0.59**
Boldness	0.15	-0.08	0.36
Goals			
Sociability	**0.39**	**0.13**	**0.60**
Dominance	-0.08	-0.25	0.10
Impulsiveness	-0.22	-0.44	0.03
Openness	0.25	-0.01	0.47
Negative affect	-0.22	-0.44	0.03
Pro-sociality	**0.26**	**0.00**	**0.48**
Boldness	**0.28**	**0.02**	**0.51**
Be marmoset			
Sociability	**0.45**	**0.20**	**0.64**
Dominance	-0.18	-0.39	0.06
Impulsiveness	**-0.28**	**-0.50**	**-0.02**
Openness	**0.33**	**0.07**	**0.55**
Negative affect	**-0.27**	**-0.49**	**-0.01**
Pro-sociality	**0.34**	**0.08**	**0.56**
Boldness	**0.36**	**0.10**	**0.57**
Subjective well-being			
Sociability	**0.53**	**0.30**	**0.70**
Dominance	-0.19	-0.41	0.05
Impulsiveness	**-0.30**	**-0.52**	**-0.04**
Openness	**0.32**	**0.06**	**0.54**
Negative affect	-0.21	-0.43	0.03
Pro-sociality	**0.39**	**0.13**	**0.60**
Boldness	**0.32**	**0.06**	**0.54**

Note. $N = 128$. Estimates in bold are significant at $P < .05$.

Figure 1

The sequence is based on NC_013897. Primer sequences are underlined. Start and stop codon sequences are in boxes. The third intracellular region is enclosed in the parentheses. Nucleotide substitutions are shown in capital and bold letters; G840C (A280A), G841A (V281M), T901A (S301T).

tggattcccttcctccgaaacttccttggagactgggcggaagaccccaggggaaggggcgaaaggga
tcttcgctctgctttttcttccttcctctttcccgcgcggggctcacaggcatggatgtgctcagccc
tggtcagggcaacaataccacatcatccccgggtccctttgagaccgccagcaacactactggtatct
ccgacgtgaccttcggctaccaagtgatcacctctctgctgttgggcacgctcatcttctgtgcggtg
ctgggcaatgcctgcgtggtggctgccatcgccctggagcgctccctgcagaacgtggccaattatct
tattggctctttggcggtcaccgacctcatggtgtcggtgttggtgctgcccatggccgcgctgtatc
aggtgctcaacaagtggactctgggccaggtcacctgcgacctgttcatagccctcgacgtgctgtgc
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cgactacgtgaacaagaggacgccccggcgcgctgctgcgctcatctcgctcacttggcttattggct
tcctcatctccatcccgcccatgctgggctggcgcaccccggaagaccgctcggaccccgacgcatgc
accattagcaaggaccacggctacactatctactccaccttcggcgctttctacatcccgctgctgct
catgctggttctctatgggcgcatattccgagctgcgcgcttccgcattcgcaagacagtgaaaaagg
tggagaagaccggagcggacacccgccgtggagcatctccggccccgcagcccaagaagagcgtgaat
ggagaatcggggagcaggaactggagactgagcgtggagagcaagtcagagagtgctctgtgcgccaa
tggcgc**GG**tgaggcaaggtgacgacggcgccgccctggaggtgatcgaggtgcaccgggtgggcaac**T**
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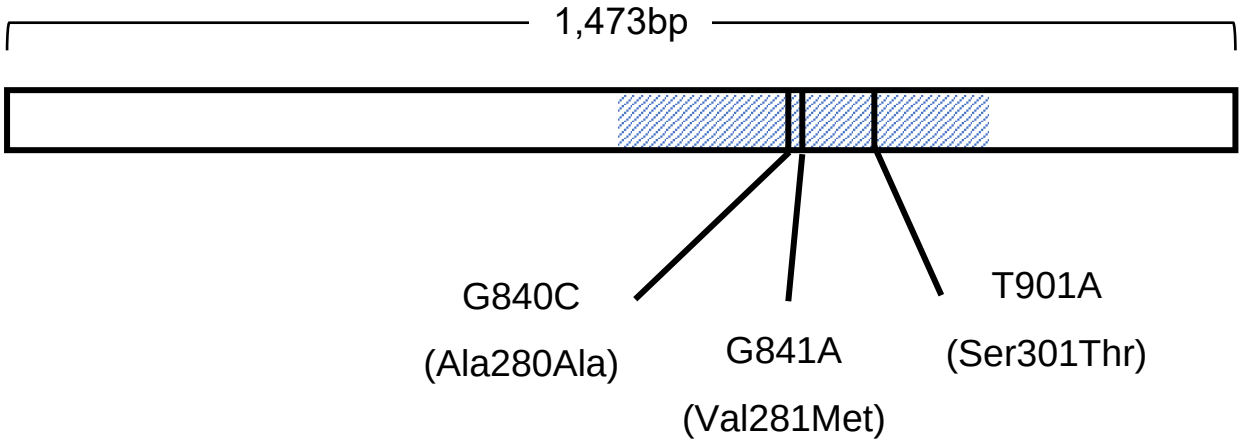
ctttaagtgtaagttctgccgccaatgatgatggaggagtagccggccagtgcgggggttacaggatc
cgccccattcactatgcttggaccaaccctagggaatcaacacct

Figure 2

Locations of the Single Nucleotide Polymorphisms on the Single Exon of the Common Marmoset Serotonin Receptor 1a Gene



Note. The shaded region corresponds to the third intracellular region