Shared and Distinct Genetic Sources of Variability in Visual Aesthetic Value

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Abstract

An open question is how individual sensory experiences acquire different subjective aesthetic values. Variability in visual aesthetic value is known to be formed and shaped over a lifetime, with individual experiences playing a crucial role. However, whether the formation of visual aesthetic value is solely influenced by environmental exposure is still a matter of debate. Here, we considered differences in aesthetic value emerging across three visual domains; abstract images, scenes and faces. We examined variability in two major dimensions of ordinary aesthetic experiences: similarity between each individual's preferences and the group's average (taste-typicality) and the overall aesthetic value evoked by visual images (evaluation-bias). We build on a discovery sample from the Australian Twin Registry originally analysed by Germine et al. ¹, and validate our findings in a partially overlapping sample analysed by Sutherland et al. ², where respectively 1547 and 1243 monozygotic and dizygotic twins rated visual images belonging to the three domains. First, we revealed that the three visual domains evoked different degrees of individual variability in preferences. We then showed that genetic influences could explain 25% to 41% of the variance in taste-typicality and evaluation-bias. Multivariate analyses showed that genetic effects were partially shared across visual domains. Results indicate that major dimensions of aesthetic evaluations are comparably heritable to other complex human traits. The exception was taste-typicality for abstract images for which we found only shared and unique environmental influences. Our study reveals that diverse sources of variation, both genetic and environmental, influence the formation of aesthetic value across distinct visual domains.

Introduction

Both the long history of aesthetics^{3,4} and the recently renewed interest in this field^{5–11} have led to substantial discoveries in how humans evaluate sensory experiences. These discoveries revealed organisational principles which guide the formation of visual aesthetic value, from the value assigned to ordinary sensory experiences to visual art^{12–15}, corresponding neural correlates^{16–22} (see²³ for a review), and informed recent computational models of how aesthetic value comes to be^{24–26}. One such emerging principle indicates that inter-individual differences in aesthetic evaluations are the norm rather than the exception²⁷. People tend to display different aesthetic sensitivity towards features of the stimuli being evaluated^{28,29}, and differ in the extent to which they are open to, and derive pleasure from, aesthetically rewarding experiences^{30–32}. Further, people show a great degree of variation in individual taste^{13,15,33} even for stimuli for which aesthetic evaluations are mostly agreed upon, such as faces^{1,13,34}.

Although extensive research has investigated such inter-individual differences, with recent discoveries starting to shed light on major underlying dimensions of such variability¹⁵, one question remains overlooked: what are the sources of differences in aesthetic evaluations? Many studies suggest that aesthetic value is formed and shaped by prior experiences in individuals, groups, and societies^{14,33,35–39}. However, complementary evidence challenges the idea that the environment alone is the only source of variation in aesthetic value. For example, evidence from behavioural genetic studies shows that genetic predispositions make substantial contributions to variation in attitudes, interests, and engagement toward music and arts^{40–43}, proneness to instances of aesthetic experiences⁴⁴, and even major dimensions of cultural taste and participation⁴⁵.

Yet, little is known about the extent to which genetic variation contributes to what makes subjective aesthetic evaluations differ between individuals. There exist only a few studies that have systematically tested whether the formation of aesthetic value is caused by environmental exposure alone, or if variation in aesthetic evaluations is also constrained by genetic predispositions^{1,2,46–48}. These studies employed the Classical Twin Method (CTM^{49,50}), a widely used approach to quantify genetic and environmental contributions to variation. The CTM compares monozygotic (MZ) twin pairs, who share the same fertilised egg and are roughly genetically identical, to dizygotic (DZ) twin pairs, who are derived from two fertilised eggs and are on average 50% genetically identical (with respect to allelic variation). Based on the extent to which MZ co-twins are more similar to each other than DZ co-twins are on a given trait, it is possible to quantify the amount of variability that correlates with genetic factors, also known as heritability (h^2).

Using the CTM, two studies^{47,48} examined the extent to which idiosyncrasies in aesthetic judgments were in line with the opinions of experts for images of paintings and drawings. The authors found contradictory results, with h^2 estimates for aesthetic judgements ranging from 0%⁴⁸ to 67%⁴⁷, a broad spread that is likely related to small sample sizes making it difficult to draw reliable conclusions (59 and 57 Italian and North American same-sex twin pairs in the first and 61 Italian same-sex twin pairs in the second, respectively)⁵¹. Three other studies, from Zietsch et al.⁴⁶, Germine et al.¹ and Sutherland et al.², investigated larger twin samples focusing on facial aesthetic

preferences. Heritability estimates were 33% for specific preferences for dimorphic male traits (i.e., the masculinity of the face being evaluated)⁴⁶, and 22% and 30% for more general individual preferences for faces (2160 Finnish female twins and siblings, 796 Australian same-sex twin pairs, and 1264 Australian same-sex twins, respectively)^{1,2}. Nevertheless, a description of the extent to which genetic or environmental influences impact the formation of variation in aesthetic evaluations beyond individual preferences of faces is still lacking.

Here we extend previous work by investigating the etiology of foundational metrics of aesthetic evaluations of three image domains, namely abstract images, scenes and faces, with a complementary re-analysis for the latter domain. We also go beyond a pure description of univariate etiological sources of variation on aesthetic evaluations by examining possible shared genetic and environmental etiological sources that exert their influences across different visual domains.

First, we revealed that aesthetic evaluations for abstract images, scenes and faces consistently elicited a diversified range of reliable individual preferences. Individuals expressed the most dissimilar (idiosyncratic) preferences for abstract images, intermediate similarity for faces and most similar (shared) preferences for scenes. We then quantified the extent to which genetic and environmental factors influence inter-individual variation in aesthetic evaluations. We compared the extent to which pairs of individuals, including pairs of twins, differed in their preferences. This allowed us to answer whether familial genetic relatedness relates to variability in aesthetic preferences. We then analysed the causes of variation in the primary dimensions of inter-individual differences in aesthetic value⁴⁶. Specifically, we examined how typical individuals' aesthetic evaluations were compared to the group average (taste-typicality¹⁵), which has been recently claimed to be the primary dimension along which inter-individual differences in aesthetic values vary¹⁵. We complemented our analyses by describing the causes of variation in the overall aesthetic value expressed by individuals, which we refer to as evaluation-bias, a largely neglected metric in many contemporary studies assessing aesthetic evaluations^{1,15,34}. Finally, based on evidence suggesting that aesthetic value is represented in both a domain-general and a domain-specific manner²⁰, we explored the degree to which etiological influences are shared across the three image domains. While doing so, we distinguished genetic and environmental influences on the observed covariation between taste-typicality or evaluation-bias across visual domains from the amount of genetic and environmental correlations (see⁵² for details and methods). All measures and analyses were tested for robustness and confounders using a genetically informative partially overlapping validation sample with additional data on aesthetic evaluations².

Results

Visual domain-specific inter-individual differences in aesthetic evaluations.

We re-analysed data originally obtained by Germine et al.¹, publicly available at <https://osf.io/c3hz6/>, comprising a discovery sample of 1,115 MZ and 432 DZ twins, mean age 45 y (sd = 13 y, ranging from 21 to 68 y). To test the validity and replicability of our results, we also re-analysed data from a validation sample collected by Sutherland et al.², publicly available at

https://osf.io/35zf8/?view_only=e76c6755dcea4be2adc5b075cae896e8, comprising 825 MZ and 418 DZ twins, mean age 47 y (sd = 15 y, ranging from 16 to 80 y, see Table 1). The twins had originally rated 65 abstract images in the discovery sample, including a subset of 15 repeated images. They had also rated 65 and 74 images of scenes (including 15 and 24 repeats), and 260 and 150 images of faces (60 and 50 repeats) in the discovery and validation samples, respectively (see Figure 1a and Methods for details). Before analysis, we estimated intra-individual reliability (*intra_r*) by calculating the Pearson correlation between repeated ratings for the same images within individuals, and excluded participants for whom this reliability was less than .5 (following ^{13,15}). We also excluded participants who showed no variation in ratings within domains, following Germine et al. ¹. (Table 1 gives the final sample, also see Supplementary S1.) Variance Partition Components (VPC^{2,53}) extracted from multilevel models fitted to ratings of only one twin per pair (to avoid confounding familial resemblances, see Methods see Supplementary S2) confirmed that images elicited a remarkably diversified range of stable inter-individual differences in aesthetic evaluations, with individual-level VPCs capturing between 18% to 34% of the total variance within visual domains (Figure 1b). VPCs capturing the effect of image repetition (i.e., exposure) indicated small systematic effects (1% to 3%) on the overall variance in aesthetic ratings (but see Supplementary S2 for a detailed discussion). Thus, for subsequent analyses we used the average ratings of the repeated images within participants to increase the signal-to-noise ratio of the ratings.

Table 1: *Samples of monozygotic (MZ) and dizygotic (DZ) twin pairs per visual domain.*

	MZ male	MZ female	DZ male	DZ female
All	133 (133)	425 (424)	54 (54)	162 (162)
All (val.)	126 (94)	350 (245)	37 (23)	219 (137)
Abstracts	130 (103)	420 (360)	54 (41)	161 (145)
Abstracts (val.)	- (-)	- (-)	- (-)	- (-)
Scenes	133 (123)	425 (419)	54 (51)	162 (159)
Scenes (val.)	126 (91)	350 (245)	37 (22)	219 (137)
Faces	133 (122)	425 (407)	54 (51)	162 (158)
Faces (val.)	125 (89)	340 (232)	37 (21)	216 (128)

Top two rows show original samples ^{1,2} before exclusion. Remaining rows show the final numbers of twin pairs after applying exclusion criteria for each visual domain. The number of complete pairs is shown between parentheses. Val. Validation sample (i.e., Sutherland et al. ² sample.)

Measures of inter-individual differences in aesthetic evaluation.

To quantify individual aspects of aesthetic value, we computed pair- and individual-level metrics (Figure 1c). The pairwise aesthetic agreement was calculated as the inter-individual correlation (*inter_r*) of the ratings per domain within each MZ, DZ, and matched unrelated pair (UR) classes (adapted from ³³). UR comprised two same-sex, familial unrelated individuals selected from the twin sample and matched to minimise their age differences (see Methods). How typical individuals' aesthetic evaluations were compared to the group average, which we refer to as taste-typicality, were quantified by computing the mean minus two (*mm2*; adapted from ¹³). The *mm2*

was calculated by correlating all the ratings given by one twin per domain with the average ratings of every other individual, excluding the individual's twin (see Methods and Supplementary S3 for a detailed discussion on taste-typicality and how it relates to previous metrics used in the literature). The overall aesthetic value evoked by each domain in each participant, which we refer to as evaluation-bias, was computed as the intra-individual average of each participant's ratings (Figure 1c). To avoid violating assumptions of statistical tests carried out later on taste-typicality and evaluation-bias data, we additionally excluded seven pairs (3 UR and 4 MZ pairs) and six pairs (3 UR, 2 DZ, and 1 MZ pair) from the discovery and the validation sample with extreme pairwise ratings. We also excluded two additional individuals with extreme outlying taste-typicality scores (one for faces, one for scenes) from the discovery sample and three individuals with extreme outlying taste-typicality scores for faces in the validation sample. Distributions and descriptive statistics for pairwise aesthetic agreement, taste-typicality, and evaluation-bias scores are given in the Supplementary material.

To confirm that these individual-level metrics captured a substantial proportion of inter-individual variability in aesthetic evaluation, we computed a Principal Component Analysis (PCA) of the individual ratings for each domain. PCA was run only on the first members of each pair to avoid familial confounding. We identified two major axes of variability in the aesthetic evaluation of images, which jointly explained 43%, 41%, and 45% of the variance in ratings for abstract images and images of scenes and faces, respectively. Pearson correlations between the individual scores extracted from the first PC and the evaluation-bias measure were all $r > .99$ in the discovery sample. Correlations between the individual scores extracted from the second component and taste-typicality Fisher z transformed values (see Methods) were $r(699) = -.66$, 95% CI $[-.70, -.62]$, for abstract images, $r(758) = .71$, 95% CI $[.68, .74]$, for scenes, and $r(751) = .72$, 95% CI $[.68, .75]$, for faces (all $p < .001$). Results were replicated in the validation sample, with correlations between the first PC and evaluation-bias scores being all $r > .99$, and correlations between the second PC and taste-typicality equal to $r(584) = .66$, 95% CI $[.61, .71]$, for scenes, and $r(560) = .62$, 95% CI $[.57, .67]$ for faces (all $p < .001$). Correlations were similar for second twin members (see supplementary S4 for details). These findings indicate that taste-typicality and evaluation-bias scores relate to the major dimensions of inter-individual differences in aesthetic value.

Figure 1. *Inter-individual differences in aesthetic evaluations.* **a.** Stimuli used by Germine et al. 2015 and Sutherland et al. 2020. The authors originally investigated the etiology of individual preferences for faces (dashed box) but also collected data on abstract images and scenes. **b.** Multilevel modelling for twins' (one per pair only) ratings of abstract images and images of scenes and faces (results for all twins are shown in Supplementary S2). The variance components quantify the amount of variance in ratings due to the image (hence shared among individuals), individual features (therefore unique to the individual), the exposure of the images (hence due to the repetition), and their interactions. **c.** The pair-level and individual-level metrics used to quantify the three aesthetic phenotypes: pairwise-agreement, taste-typicality, and evaluation-bias. Pairwise-agreement reflects the agreement within a MZ (yellow), DZ (turquoise), or unrelated pseudo-randomised (UR) pair; Taste-typicality reflects how similar an individual set of ratings is in comparison to the average ratings of everyone else but their twin. Evaluation-bias reflects the overall aesthetic value evoked by a domain of visual images. **d.** Results from the PCA over the individual ratings for abstract images. PC1 and PC2 individual scores are plotted in the bottom panel. Colour represents the taste-typicality (left) and evaluation-bias (right) scores.

Monozygotic twins show higher pairwise aesthetic agreement than dizygotic twins and unrelated pairs.

To investigate genetic contributions, we used the discovery sample and assessed the extent to which pairwise aesthetic agreement differed across MZ, DZ, and UR pairs. An ANOVA (type III 3X3; domain X pair class) carried out on Fisher z-transformed $inter_z$ values (see Methods), revealed a significant, albeit small, effect of pair class on pairwise aesthetic agreement, $F(2, 4242) = 101.883, p < .001$ ($\eta_p^2 = 0.05$; 95% CI [0.03, 0.06]; results were robust to inclusion of outliers, see Supplementary S5). Marginal pairwise agreement averaged across visual domains was highest for MZ, followed by DZ and UR pairs, $inter_r = .64$, 95% CI [.63,.65]; $inter_r = .60$, 95% CI [.58,.61], and $inter_r = .54$, 95% CI [.53,.55] (all $p < .001$, Bonferroni corrected).

Additional posthoc comparisons revealed that pairwise agreement differences were significant for all pair classes (i.e., pairwise agreement MZ > DZ > UR within each domain, all $p < .05$), except for differences between MZ and DZ for faces, for which the difference was not significant ($p = .09$, all p -values Bonferroni corrected). Effect sizes and CI were all above 0, ranging from $d = .21$, 95% CI [.05, .37], for the observed MZ > DZ pair classes difference for faces, to $d = .86$, 95% CI [.74,.98], for the MZ > UR pair classes difference for abstract images. Analysis of the validation sample revealed similar results (Figure 2d), consistent with the directionality of all the

effects reported in the discovery sample. The only exception was the MZ and DZ pairwise agreement for faces, for which the difference was significant ($p < .001$; $d = .43$, 95% CI [.23, .63]). Thus, under the assumptions of the CTM, results indicated that genetic factors play a significant, albeit small, role in preferences for visual images. Moreover, results indicated that unrelated familial individuals are less similar in their aesthetic preferences than related ones.

Univariate CTM estimate genetic effects for all dimensions of aesthetic value except taste-typicality for abstract images.

To quantify and describe genetic and environmental sources of variation in aesthetic evaluations, we compared similarities across MZ and DZ twins' taste-typicality and evaluation-bias for abstract images and images of scenes and faces. The phenotypic variance in taste-typicality and evaluation-bias was partitioned into genetic (additive, A) and environmental (shared or common [C] or unique environmental [E]) variance components by performing univariate Structural Equation Modelling (SEM) of the twin data ⁵⁴, using the direct symmetric approach ⁵⁵ (see Methods). Exclusion criteria matched those reported above for PCA. Means, phenotypic and twin correlations, and 95% CI, were extracted from the saturated model, which included sex and age as covariates. Homogeneity of means and variance across twin order and zygosity were met, as tested by comparing the saturated model and the most parsimonious models with equated mean and variances ⁵⁶ (reported in the Supplementary File 1). Based on the pattern of twin correlations and 95% CI between DZ and MZ twins ⁵⁷ (Figures 2c and 2e, see Supplementary Table S1 for details), it was expected that either AE or ACE models would account for variance in all traits for faces and scenes. For evaluation-bias for abstract images, either AE or ADE models were expected to best account for variance, while for taste-typicality for abstract images, a CE model was expected. None of the parsimonious ACE or ADE models were found to significantly decrease model fit when compared to the full saturated model (all differences in $\chi^2(\Delta df=6)$, $p > .05$).

Further model comparisons confirmed that AE models were the best fitting models for taste-typicality (scenes and faces ACE vs AE, $\chi^2(\Delta df=1)$, $p > .05$) and evaluation-bias data (all ACE vs AE, $\chi^2(\Delta df=1)$, $p > .05$), for all stimulus domains, except for taste-typicality of abstract images (ACE vs AE, $\chi^2(\Delta df=1) = 5.30$, $p = .02$). Genetic influences (A) explained 36% (h^2 95% CI [.29; .43]) of the variance in taste-typicality for images of scenes, and 32% (h^2 95% CI [.24; .40]) and 26% (h^2 95% CI [.18; .33]) of the variance in evaluation-bias for abstract images and scenes. Estimates were similar to those obtained for faces, except for variation in taste-typicality for abstract images, which was entirely explained by environmental influences, with 29% (95% CI [.22; .36]) for shared environmental factors (C). Consistent results were observed in the validation sample (Table 2, a comprehensive summary is reported in Supplementary File 2).

To frame our results within the estimated magnitude of h^2 for other complex human traits, we stratified our estimates within h^2 obtained from the largest meta-analysis of twin studies to date ⁵⁴ (see Figure 2g). Averaged h^2 estimates for the major dimensions of aesthetic value for all visual domains, except taste-typicality for abstract images, ranked amongst the 30th percentile for the magnitude of h^2 . Taste-typicality for abstract images was the exception, ranking at the bottom for h^2 estimates, with only shared environmental but no genetic influences over its variability.

Table 2: *Univariate modelling of genetic and environmental contributions to inter-individual differences in aesthetic evaluation*

Images	Model	-2LL, AIC	df, χ^2	A	C D	E
Taste typicality						
Abstract Images ¹	CE	349.52, 359.52	1409, 0.04	0	0.29 [0.22; 0.36]	0.71 [0.64; 0.78]
Scenes ¹	AE	373.23, 383.23	1518, 0.03	0.36 [0.29; 0.43]	0	0.64 [0.57; 0.71]
Scenes ²	AE	276.70, 286.50	1204, 1.76	0.30 [0.19; 0.39]	0	0.70 [0.61; 0.81]
Faces ¹	AE	-804.66, -795.66	1505, 0.05	0.33 [0.25; 0.40]	0	0.67 [0.62; 0.76]
Faces ² †	AE	-439.82 -429.82	1161, 0.84	0.31 [0.21; 0.41]	0	0.69 [0.59; 0.79]
Evaluation-bias						
Abstract Images ¹ †	AE	3523.48, 3533.48	1410, 1.17	0.32 [0.24; 0.40]	0	0.68 [0.60; 0.76]
Scenes ¹	AE	3110.07, 3120.07	1520, 0.18	0.26 [0.18; 0.33]	0	0.74 [0.67; 0.82]
Scenes ²	AE	2855.31, 2865.31	1203, 0.21	0.31 [0.21; 0.40]	0	0.69 [0.60; 0.79]
Faces ¹	AE	3062.91, 3072.91	1507, 0.07	0.41 [0.33; 0.47]	0	0.59 [0.53; 0.66]
Faces ²	AE	3164.23, 3174.23	1165, 0.05	0.32 [0.21; 0.41]	0	0.68 [0.59; 0.79]

Note: -2LL (- 2 Log likelihood); AIC (Akaike Information Criteria); df (Degrees of freedom); A (Additive genetic); C|D (Common environmental or Dominance genetic); E (Unique environmental and error). 1 = discovery sample ¹; 2 = validation sample ²; † models compared to full ADE. Sex and age are included as covariates in every model. Significance and comparative statistics for the reduced models (AE, CE|DE, and E) are obtained by comparison with the respective full ACE|ADE model. (All ACE|ADE models fit were considered good compared to the respective full saturated models).

Figure 2 Classical Twin Method reveals etiological influences on inter-individual differences in aesthetic evaluations. Panels **a** and **b** show the average pairwise agreement across different visual domains and pair classes for the discovery (left) and the validation (right) sample. Panels **c** to **f** show the pattern of twin correlations extracted by the respective saturated models grouped by zygosity. In yellow are correlations between MZ twin pairs; in turquoise, correlations are between DZ twin pairs. Bars represent 95% confidence intervals (CI). **g**. Framing of etiological estimates for inter-individual differences in aesthetic evaluations within the etiology of other human complex traits. Bar plot with etiological environmental (E, C) and genetic (A) estimates accounting for variation of other human traits (adapted from http://match.ctglab.nl/#/multiple/reported_ace.) Etiological estimates were extracted from the large twin meta-analysis by Polderman et al.⁵⁴, obtained on same-sex twins only, with the averaged h^2 estimates for taste-typicality for scenes and faces and evaluation-bias for all domains. Taste-typicality for abstract images is shown separately, given that a different CTM model captures its etiology better (i.e., CE). UR = unrelated; DZ = dizygotic; MZ = monozygotic; A = additive genetic; C = common environment; E = unique environment and unsystematic effect (e.g., measurement error). † Taste-typicality for faces and scenes. * Taste-typicality for abstract images.

Fitting of multivariate CTM models shows shared and distinct genetic influences on inter-individual differences in aesthetic value across visual domains.

We went on to investigate the associations between taste-typicality and evaluation-bias across the different visual domains. Correlations between taste-typicality and evaluation-bias twins scores are shown in Figure 3. On the one hand, perhaps unsurprisingly, correlations between taste-typicality and evaluation-bias were not significant (all $p > .05$, Bonferroni corrected for 15 comparisons), except for taste-typicality for scenes and evaluation-bias for faces ($r(695) = .11$, $p = .048$, Bonferroni corrected), which, however, did not replicate for other twin members ($r(702) = .08$, $p = .43$, Bonferroni corrected, see Figure 3). This was expected, given that the two metrics strongly correlate with the two major orthogonal axes of covariation (see PCA results

above). On the other hand, correlations for taste-typicality and evaluation-bias across domains were significant, ranging from small to moderate, with the exception of taste-typicality for abstract images and scenes, which was not significant in either sample, $r(687) = .05$, $p > .99$ and $r(696) = .09$, $p = .34$. Thus, individuals with taste-typicality and evaluation-bias scores in one domain tend to have similar scores in others.

Figure 3. Phenotypic correlations for taste-typicality and evaluation-bias across visual domains. Pearson phenotypic correlations (r) for the taste-typicality and evaluation-bias were obtained separately from pairs' members to avoid familial confounding effects. **a.** Discovery and **b.** validation samples, respectively. Light grey segments adjacent to the axis ticks indicate taste typicality, while black segments indicate evaluation-bias. Crosses represent the non-significant Pearson correlations ($p < .05$; Bonferroni corrected).

To partition covariation across visual domains into genetic and environmental sources, we applied the multivariate CTM (see Methods). This method exploits MZ and DZ cross-trait cross-twin correlations (e.g., the evaluation-bias for abstract images of twin 1 with the evaluation-bias for scenes of twin 2) to partition phenotypic covariance between traits into genetic and environmental covariance components. Further, the multivariate CTM makes it possible to quantify genetic and environmental correlations, which estimate the overlaps in variance components across traits. Multivariate models were specified following univariate results. There was a good fit for the multivariate model for taste-typicality data, which included A components for scenes and faces only, and a C component for abstract images (Figure 4a; Saturated vs full ACE $\chi^2(\Delta df=33) = 42.84$, $p = .12$, ACE vs Specified model, $\chi^2(\Delta df=6) = 2.77$, $p = .84$, see Methods). The final model indicated that shared genetic effects accounted for more than half of the covariation between taste-typicality across visual domains (bivariate $h^2 = .69$, 95% CI [.50, .87]) and that overlapping genetic effects jointly explained variation in taste-typicality for images of scenes and faces (genetic correlation (ρ_A) = .53, 95% CI [.38, .64]). This pattern was in contrast with overlapping unique environmental effects on inter-individual differences for taste-typicality, which were small across all visual domains (Figure 4b). Similarly, the AE multivariate model fit for evaluation-bias data was good (Saturated vs full ACE $\chi^2(\Delta df=33) = 32.74$, $p = .48$, ACE vs. Specified model, $\chi^2(\Delta df=8) = 5.11$, $p = .75$). Bivariate heritability estimates spanned from bivariate $h^2_{\text{abstract-scenes}} = .31$, 95% CI [.19, .42], to bivariate $h^2_{\text{faces-abstract}} = .44$, 95% CI [.31, .56]. Genetic correlations were moderate, ranging from $\rho_{A_{\text{faces-scenes}}} = .46$, 95% CI [.30, .60], to bivariate $\rho_{A_{\text{scenes-abstract}}} = .56$, 95% CI [.40, .69]. Unlike for taste-typicality, we also found environmental correlations to be substantial (Figure 4b).

Findings from the validation sample (Figure 4c) were consistent with the results from the discovery sample reported above. In particular, the multivariate AE model for the taste-typicality data for scenes and faces, specified in the discovery sample,

resulted in a good fit for the data in the validation sample (Saturated vs full ACE $\chi^2(\Delta df=17) = 26.38$, $p = .07$, ACE vs Specified model, $\chi^2(\Delta df=3) = 0.86$, $p = .83$). Similarly, an AE multivariate model was a good fit for the evaluation-bias data in the validation sample (Saturated vs full ACE $\chi^2(\Delta df=17) = 13.25$, $p = .72$, ACE vs Specified model, $\chi^2(\Delta df=3) = 0.22$, $p = .97$).

Figure 4 Multivariate biometric modelling results. **a**. Simplified path diagrams for the specified multivariate SEM CTM models fit on MZ and DZ twin discovery sample data. On the top is the multivariate SEM for the taste-typicality data. For clarity, we report specified parameters on the SEM diagram and estimated parameter results. For example, the variance for the additive genetic component for the taste-typicality score for scenes and faces is denoted by σ^2_{Asce} , while the additive genetic covariance between taste-typicality for scenes and faces is denoted by $\sigma_{AsceAfac}$; on the bottom is the multivariate SEM for the evaluation-bias data. **b**. Multivariate CTM results, from left to right: Bivariate heritability, h^2_b (e.g., $h^2_{b_scef} = \sigma_{AsceAfac} / (\sigma_{AsceAfac} + \sigma_{EsceEfac})$), i.e., the amount of covariance between two traits accounted for by additive genetic variance (the amount accounted for by environmental components are simply $1 - h^2_b$); and the genetic and environmental correlations matrices, (e.g., $\rho_{A_scef} = \sigma_{AsceAfac} / \sqrt{(\sigma_{Asce}^2 + \sigma_{Afac}^2)}$, $\rho_{E_scef} = \sigma_{EsceEfac} / \sqrt{(\sigma_{Esce}^2 + \sigma_{Efac}^2)}$). **c**. Matrices obtained from the validation sample ². NA represent covariance components that were not modelled.

Sensitivity analyses discount contributions of potential confounding effects.

In order to account for possible confounds, we used non-aesthetic ratings obtained in the validation sample on a control task (see Methods) using the same face stimuli ². We calculated control-typicality and control-bias scores as the *mm2* and the within-individual rating average of the control task. Control-typicality reflected the tendency to display typical scores on a non-aesthetic image rating task. Control-bias reflected the general tendency to give high or low ratings on average on a non-aesthetic task. Taste-typicality and control-typicality, and evaluation-bias and control-bias scores were positively correlated (Supplementary Figure S6), indicating possible confounding effects. To assess whether such effects biased our etiological estimates, we regressed taste-typicality and evaluation-bias on the control-typicality and control-bias scores (in addition to sex and age) and re-ran both univariate and multivariate CTM on the residuals. The correlations between MZ and DZ with residualised taste-typicality and evaluation-bias were similar to those extracted by the model fitted without accounting for possible confounders (Supplementary Table S2). Crucially, univariate and multivariate CTM modelling indicated that the same models specified for uncontrolled scores accounted for residual scores, with estimates for the genetic components being nearly identical to those obtained without controlling for

confounders (Taste-Typicality Saturated vs full ACE $\chi^2(\Delta df=17) = 24.43$, $p = .11$, ACE vs Specified model, $\chi^2(\Delta df=3) = 1.18$, $p = .76$; Evaluation-Bias Saturated vs full ACE $\chi^2(\Delta df=17) = 14.24$, $p = .65$, ACE vs Specified model, $\chi^2(\Delta df=3) = 0.33$, $p = .95$; Supplementary Figure S8 and Table S3). Therefore, sources of variability in major dimensions of aesthetic value, as found in this study, are not confounded by individuals' general typicality or overall biases in rating scale uses.

Discussion

Building on previous work by Germine et al.¹ and Sutherland et al.², we confirmed that the environment shapes inter-individual differences in the aesthetic evaluations of visual images, yet revealed that genetics too play an important role. On the one hand, we found that genetic influences have small effects on which visual images people prefer, as genetically related individuals tend to display only slightly more similar ratings of images than unrelated individuals, regardless of the evaluated visual domain. These results strengthen earlier claims that environmental influences are a source of variation in aesthetic preferences for faces^{1,2}, and extend such claims to previously not investigated visual domains such as abstract images and scenes. On the other hand, we show that variability in taste-typicality (how similar individuals' preferences are to the group preferences) and evaluation-bias (the overall aesthetic value evoked by visual images), which are foundational metrics of aesthetic value relating to major axes of inter-individual differences, are substantially influenced by genetic effects across two well-powered datasets. These latter results challenge the traditional view that environmental experiences alone shape inter-individual differences in the formation of aesthetic value.

We also found that the genetic effects contributing to the major dimensions of aesthetic value extend across visual domains. There were substantial genetic overlaps for taste-typicality and evaluation-bias for abstract images, scenes, and faces. This was indexed by the amount of covariance explained by genetic factors (bivariate heritability estimates) between taste-typicality for scenes and faces and evaluation-bias for all visual domains, and by the shared genetic effects on the variation of such traits across visual domains (genetic correlations). The first finding indicates that genetic influences partially account for the observed relationship across domains for both taste-typicality and evaluation-bias. The second finding shows that the genetic effects on such aesthetic dimensions overlap across domains, suggesting that shared genetic factors underlie variation in major dimensions of visual aesthetic value. Nonetheless, genetic correlation estimates across domains were far below 1, indicating that different genetic effects also play a role.

Despite sufficient power to detect genetic effects of similar magnitude to those detected among the other visual domains, we found no evidence of genetic influences on variation in taste-typicality for abstract images. These findings bear on the important question of how aesthetic processes may differ for biological (natural) versus artefactual (non-natural) categories of objects (see^{13,58}). As previously suggested by the literature and confirmed in this study, individuals tend to show a high degree of aesthetic agreement for images of faces and natural landscapes, both of which are natural kinds, but much less for abstract images^{13,33,59,60}. However, until now, there was no empirical evidence to show that different genetic and environmental sources of variation, could influence the formation of aesthetic value for these distinct visual

categories. Our rare finding of a behavioural trait in which individual differences appear to be purely influenced by environmental factors (i.e., taste-typicality for abstract images) raises the question of whether aesthetic processes underlying the evaluation of other human-made artefactual objects, such as visual art and music, are free from genetic predispositions.

Regarding taste-typicality for faces, perhaps unsurprisingly, our results are broadly in line with the claims of Germine et al. ¹ and Sutherland et al. ². Taste-typicality is highly similar to the original metric employed by the authors. As such, the resulting heritability for taste-typicality for faces should not be considered entirely novel, despite some notable differences in analytic procedure. However, our finding partially contrasts the previous authors' conclusion by challenging the extent to which the original metric employed by the authors can be used to infer individual preferences for, or impressions of, faces. For those studies, comparisons between MZ and DZ twin individual preference scores were used to quantify the extent to which genetic or environmental factors contribute to variation in individual preferences or impressions. Yet, we found that pairwise preference and taste-typicality are not equivalent measures for individual preferences (discussed extensively in Supplementary material). Our work indicates that metrics that quantify how typical individual's aesthetic evaluations are compared to the group average hold only a small amount of information about the etiology of actual preferences ² within a pair, for any domain. For example, a pair of twins can have extremely diverging aesthetic preferences yet have an identical taste-typicality score (see Supplementary). As such, we believe that comparison between MZ and DZ twin taste-typicality scores can only be used to obtain descriptions of the etiology of how typical individuals' aesthetic evaluations are, such as described by Chen et al. ¹⁵, and are not particularly suited for pairwise preferences. Our stance is strengthened by the presence of inferred genetic effects (albeit small) on pairwise preferences for abstract images (higher pairwise agreement for MZ versus DZ twins), but the absence of heritability for taste-typicality for the same visual domain.

Another interesting point pertains to evaluation-bias as a measure employed to quantify inter-individual variability in aesthetic evaluations. We found that evaluation-bias was strongly correlated with the first axis of inter-individual differences in aesthetic value, while taste-typicality strongly correlated with the second axis. This contrasts a recent study which found taste-typicality rather correlated with the first and not the second axis ¹⁵. These results indicate that evaluation-bias, not taste-typicality, systematically captures the majority of variance in aesthetic valuations of different visual domains. This finding, strengthened by the moderate estimates for heritability and genetic correlations across visual domains, even after accounting for scale biases, suggests evaluation-bias is a meaningful foundational metric of inter-individual differences in the way visual sensory stimuli acquire aesthetic value.

We note that our study has some limitations. In re-analysing existing datasets to shed light on new questions, we were necessarily confined to the image domains and measurement techniques used in the original studies. For example, the sets of scenes contained images such as photographs of construction sites or classrooms, which diminish the extent to which we could interpret our results in light of a natural versus artefactual kind distinction. Further, ratings collected were slightly different between the two samples, with participants in one study being asked about the *attractiveness* (*visual pleasantness*) of images of scenes and abstract images,

while participants in the other study were asked only about *attractiveness*. There were also differences in the numerical extremes of the possible answers (e.g., from 1 to 7¹ to 1 to 9²). Moreover, we assumed that residual differences between the repeated ratings were a type of measurement error, an implicit assumption that does not align with findings from the empirical aesthetics literature on the effect of repeated exposures (e.g., systematic effects of "mere exposure"¹⁴ or habituation⁶¹).

Despite these limitations, the results from the multilevel modelling demonstrated that different domains captured a sufficiently diversified amount of idiosyncrasies, consistent with growing evidence indicating that common aesthetic preferences emerge from shared representations of sensory experiences^{13,33}. They also revealed highly replicable variance component estimates across the samples, suggesting that slight differences in the wording of questions did not substantially affect the level of inter-individual differences in response. Moreover, these results revealed a minimal systematic effect of two image repetitions on overall variance in aesthetic ratings, suggesting that repeated exposure impacted ratings negligibly, justifying our assumption that, in these samples, any such variation is largely measurement noise.

Conclusions

We found monozygotic (MZ) twins to be more similar than dizygotic (DZ) twins in their aesthetic evaluations of abstract images and scenes, and of images of faces. Differences were small, suggesting weak genetic effects on visual aesthetic preferences. Nonetheless, we found that genetic factors accounted for about one-third of the variance in how similar individuals' preferences are to the group's preferences (taste-typicality) and in the overall aesthetic value evoked by visual images (evaluation-bias), two major dimensions underlying inter-individual differences in aesthetic valuation. Findings were robust to replication and confound. Compared with other complex human traits, these estimates frame variation in aesthetic evaluations within the 30th percentile for the amount of variance explained by genetic factors. Yet, we also found for inter-individual differences in taste-typicality for abstract images the presence of shared and unique environmental effects only. These particular results align with the view that, for some traits, environmental exposure alone influences the formation of aesthetic value, albeit only for one dimension of aesthetic value (taste-typicality) and one visual domain (abstract images), raising interesting questions about the formation of aesthetic value for other human-made artefactual objects. Finally, genetic effects explained a substantial part of the association between taste-typicality for images of scenes and faces, and evaluation-bias for all visual images in both samples investigated in this study. Genetic correlations suggest a partial overlap between such genetic sources of variation, indicating both shared and distinct genetic contributions to variation in aesthetic value, especially between taste-typicality for images of scenes and faces.

In sum, our analyses show that, while the environment is indeed the leading cause of differences in visual aesthetic evaluations, it is not the only influence. Although aesthetic evaluation of visual images represents a fundamental, inherently subjective, and pervasive aspect of internal representations of the external sensory world, they are also partially influenced by the genetic variants that people carry.

Methods

Stimuli

The set of stimuli used by Germine et al. ¹ were originally divided by the authors into three groups: abstract images, scenes, and faces. A total of 50 abstract images and 50 scenes were collected from two previous studies ^{33,62}. Abstract images were composed of six sub-domains: "1) abstract shapes created using Maya 3D rendering software, 2) kaleidoscopic images constructed by reflecting a sliver of a real-world image about a number of symmetry axes, 3) pseudo-coloured electron microscope images obtained from the Centre for Microscopy and Microanalysis at The University of Queensland, 4) fractal images created with publicly available interactive programs, 5) satellite imagery courtesy of the US Geological Survey, and 6) the other category of images collected from public Internet sources" ^{33, p.4}. Images of sceneries were originally selected by Vessel et al. ³³. For faces, 200 images of faces were selected from four different resources. Respectively, 1) 50 from the MIT database, 2) 50 from the Glasgow Unfamiliar Face Database, 3) 50 from the GenHead software, and 4) 50 as a collection of various sources (Facial Recognition Technology Database, the NimStim Set of Facial Expressions, and the Karolinska Directed Emotional Faces; see Germine et al., ¹ for details). The final sets of images were divided into six blocks: one block for abstract images (50 images + 15 repeated images), one block for scenes (50 images + 15 repeated images), and four blocks for images of faces (50 images + 15 repeated images per block). Participants were not made aware of such subdivisions by the original authors. Repeated images were added to each block by Germine et al. ¹ to assess the intra-individual reliability ($intra_r$) of the ratings. Participants were asked to rate how "attractive ("visually pleasing")" images were using a 1 to 7 rating scale.

The set of stimuli used by Sutherland et al. ² was originally divided into two groups, sceneries, here refer as scenes, and faces. For scenes, 50 images of sceneries were selected following the same criteria used by Germine et al. from the same resource. For faces, 150 images of faces were selected from the MIT database, which was chosen as the only resource to maximize the ecological validity of the stimuli. The final images were divided into two blocks: one block for scenes (50 images + 24 repeated images) and one for faces (150 images + 50 repeated images per block, see ² for details). Participants were asked to rate images using a 1 to 9 rating scale.

Exclusion criteria

Similarly to Germine et al. ¹ and Sutherland et al. ², we excluded participants with ratings $sd = 0$, within each visual domain. Additionally, similarly to Vessel et al. ¹³ and Chen et al. ¹⁵, we excluded $intra_r < .5$ individuals within each visual domain, indicating poor test-retest reliability in ratings. $Intra_r$ was computed within each participant as the Pearson correlation of their rating for the repeated images per visual domain. Additionally, given the sensitivity to extreme outliers in many of the statistical tests we conducted later, we excluded pairs and individuals with metrics with values above 3 times the Inter Quartile Range (IQR) in any metrics per visual domain from further respective analyses.

Pairwise aesthetic agreement

The pairwise aesthetic agreement was quantified as the inter-individual Pearson correlation ($inter_r$) of pairs' ratings. To create a familial unrelated reference for the pairwise aesthetic agreement, we additionally computationally created unrelated pairs (UR) with pseudo-random pairing by matching every second twin member of a pair with a first member from another pair. UR pairs were matched for sex and did not differ in age within each domain (see Supplementary S5). To conduct statistical analysis on the pairwise aesthetic agreement scores, we transformed $inter_r$ to $inter_z$ following Fisher's z transformation. Similar to Vessel et al. ¹³, we reported r values transformed back from the z values to aid the interpretability of the results.

Taste-typicality and Evaluation-bias

The mean minus 2 ($mm2$), adapted from the mean minus one ($mm1$; Vessel et al.¹³) to account for familial resemblances, was computed to quantify taste-typicality scores ¹⁵. Taste-typicality reflects the similarity between each individual's set of aesthetic ratings per visual domain and the group average ratings. The $mm2$ is simply the Pearson correlation between the ratings given by one participant with the average ratings of every other participant, excluding the participant's twin (hence mean minus two), and is calculated independently for each visual domain. We used Fisher z transformation to transform the $mm2$ values to further carry computations on taste-typicality scores ($mm2$ values reported in the result section were z-to-r transformed to aid interpretability, as in Vessel et al. ¹³). It is important to note that our taste-typicality score is almost equivalent to the individual preferences score of Germine et al. (except for accounting for familial resemblances and not being regressed on other aesthetic ratings ¹) and to the taste-typicality score of Chen et al. (except for accounting for familial resemblances and being calculated from unstandardized data ¹⁵). Evaluation-bias was measured as the individual average of aesthetic ratings per visual domain, reflecting the magnitude of the overall pleasantness experienced by individuals when evaluating visual images.

Variance Partition Components

To calculate the amount of variance in visual aesthetic value shared and unique across individuals, we carried out Variance Component Analysis (VCA ⁵³) through random intercept-only multilevel models ^{2,63}. Multilevel models were independently fitted on each of the three visual domains using the following formula:

$$Lme4::lmer(Rating \sim 1 + ((1|Individual) + (1|Image) + (1| Individual:Image) + (1|Exposure) + (1|Exposure:Individual) + (1|Exposure:Image)))$$

Similarly to Sutherland et al., the random effects of the models included the image and the observer intercepts and the interaction between the two. Additionally, as in Martinez et al. ⁵³, our model included the exposure effect for images rated more than once, and its interaction with the image and the observer effects. This enabled us to partition the percentage of variance in visual aesthetic evaluations explained by the image (shared across observers), the observer, and the interaction between the two (unique to the observers). This was important as it allowed us to quantify idiosyncrasies within a domain: the interaction between the subject evaluating and the

stimulus evaluated, from the overall evaluation within a domain. For example, two participants might interact with abstract images very similarly (e.g., give ratings of 1, 2, 3, and 5, 6, 7 to the same three images, respectively), but express a very different overall rating for images in general (e.g., 2 and 6 respectively). Further, it allowed us to estimate the amount of systematic variance explained by the interaction between the observer and the image with the exposure (see Supplementary S2 for details). This further allowed us to justify the averaging procedure within participants' repeated ratings to increase the signal-to-noise ratio. To avoid familial confounding effects, we ran two multilevel models per domain, one for each twin of a pair. Results are shown for the first pair's members alone (see Supplementary S2 for models fitted on the second twin members). Variance Partition Components (VPC) were computed as the amount of variance explained by one effect (e.g., ind) over the total variance, e.g.:

$$VPC_{ind} = \frac{\sigma_{ind}^2}{\sigma_{img}^2 + \sigma_{ind}^2 + \sigma_{img*ind}^2 + \sigma_{exp}^2 + \sigma_{ind*exp}^2 + \sigma_{img*exp}^2 + \sigma_{res}^2}$$

Where σ^2 is the variance of the individual (ind), image (img), exposure (exp), terms and their interaction and the residual (res) one.

Principal Component Analysis

To reduce the dimensionality of the aesthetic rating data, we conducted Principal Component Analysis (PCA) independently per each visual domain, where each axis represents an image, each coordinate an individual rating for that image, and each individual occupies a specific point in space. PCA is a data dimensionality unsupervised learning procedure, which geometrically projects data to the sequentially orthogonal axis (PC; principal components) for which the projected data have their variance maximised⁶⁴. PCs were obtained through Singular Value Decomposition of the unscaled and centred data matrix, using the base R function `prcomp()`. To compare the extent to which taste-typicality and evaluation-bias related to the major axes of variation in ratings, we computed Pearson correlations between the individual evaluation-bias and the taste-typicality scores and the first and second PC scores, respectively. The correlations between taste-typicality and the second PC scores were conducted after Fisher's z transformation of the taste-typicality values⁶⁵.

Pairwise aesthetic agreement analysis

We conducted statistical analysis on the z-transformed value ($inter_z$) of the pairwise agreement, quantified as a pair's inter-individual correlation ($inter_r$), following Fisher's z transformation for distribution of r values⁶⁵. Means were calculated from the z distribution. Similar to Vessel et al.¹³, to aid the interpretability of the results, we reported r values transformed back from the z values. We extended our analysis beyond taste-typicality scores^{1,2,15}, as an individual with similar individual preferences (see supplementary S3 for details) can have very different aesthetic ratings, opting instead for $inter_r$ as a proxy for pairwise agreement, with the additional step of averaging repeated image ratings before computing correlations to increase the signal to noise ratio of participants' ratings. To compare the differences in $inter_z$, a 3x3 type III ANOVA was performed using the ANOVA function as follows:

`ANOVA(lm(Interz ~ Pair * Domain, Data), contrasts=contrastList, type = 3)`

We performed pairwise comparisons on the estimated marginal means using the emmeans package ⁶⁶. Family-wise tests were Bonferroni corrected for multiple comparisons (i.e., 3 for pairwise domain contrasts, 3 for pairwise pair class contrast, and 9 for pairwise pair class | domain contrast). Graphic visualisation of the analysis can be found in Supplementary S5.

Univariate modelling

Variance can be partitioned into either genetic or environmental sources; whereas genetic sources of variation are considered to be either additive (additive, A) or non-additive (dominance, D), environmental sources of variation are considered to be shared (common, C) or unique to an individual (environment, E), with the latter also including measurement errors ⁵⁴. We performed model fitting using OpenMx version 2.20.3⁶⁷, in R-Studio, R version 4.1.2, on taste-typicality and evaluation-bias for abstracts, scenes and face images independently. Univariate models were adapted from Hermine Maes, available at <https://hermine-maes.squarespace.com/>. Assumptions (mean similarity and homogeneity of variance across twin order and zygosity) were tested in a saturated model. The goodness of the fit was evaluated by assessing Akaike's Information Criterion (AIC; lowest AIC meaning more parsimonious model) and by assessing the p-value associated with the χ^2 value (alpha=.05; p-values higher than .05 do not indicate significant deterioration of the model fit). The χ^2 test was performed by taking twice the difference between the Log-Likelihood of the full model with more parameters versus the Log-Likelihood of the more parsimonious model. Phenotypic twin correlations, means, and variances were extracted from the saturated model. Based on the pattern of phenotypic correlations between MZ and DZ twin pairs, we fitted either an ACE or an ADE biometric model from two groups (MZ and DZ same-sex), with sex and age as a covariate. Relative sub-models (i.e., AE, CE, E) were tested against the full ACE model after the latter was tested against the saturated model. The significance of the CTM informed models was evaluated similarly to that described above. We repeated the procedure as mentioned above for taste-typicality and evaluation-bias for each domain. Narrow-sense heritability (h^2) was calculated as the proportion of the variance explained by the A component relative to the total phenotypic variance:

$$h^2 = \frac{\sigma_A^2}{\sigma_A^2 + \sigma_C^2 + \sigma_E^2}$$

Likelihood-based 95% Confidence Intervals (CI) around the estimates were calculated using the mxCI OpenMx function (see <https://www.rdocumentation.org/packages/OpenMx/versions/2.18.1/topics/mxCI> for details.)

Multivariate modelling

Multivariate modelling exploits patterns of cross-trait cross-twin covariances to partition phenotypic covariance between any two traits into bivariate A, C, and E components. Within the multivariate model, it is also possible to compute genetic correlations (ρ_A), which test for overlapping genetic influences (e.g., pleiotropy) on variation in two traits. We first performed fitting for four saturated plus four full

multivariate models, one per aesthetic measure per sample. Two saturated plus two biometric models were fitted to the taste-typicality and the evaluation-bias data from the discovery sample after regressing out sex and age; Similarly, two saturated plus two biometric models were fitted to the taste-typicality and the evaluation-bias data from the validation sample after regressing out sex and age. Multivariate models were adapted from Hermine Mess's script, following Meike Bartel's Boulder International Behaviour Genetic Workshop tutorial, available at <https://ibg.colorado.edu/cdrom2020/maes/multivariateScripts/mulACEvc.R>. To reduce parameter bias estimation, variance-covariance components were estimated directly by the direct symmetric approach⁵⁵. Fit statistics were evaluated as described for the univariate models. We additionally tested whether the specified models provided a good fit to the data by comparing first the full multivariate ACE (21 parameters = 3 means, 9 variance components, 9 covariance components) with the full multivariate saturated model and then testing the nested multivariate sub-models against the full ACE. Genetic correlations were computed as:

$$\rho_A = \frac{\sigma_{A1A2}}{\sqrt{\sigma_{A1}^2 + \sigma_{A2}^2}}$$

With σ_{A1A2} being equal to the genetic covariance, and σ_{A1}^2 and σ_{A2}^2 representing the amount of variance in the traits 1 and 2 (e.g., scenes and faces) explained by additive genetic factors, respectively. CIs around the estimates were calculated as reported above.

Sensitivity analysis

We obtained typicality and bias scores in the validation sample as the *mm2* and the within-participant mean of a non-aesthetic task. In the non-aesthetic task, originally administered by Sutherland et al.² in the same individuals on the same images, twins rated the perceived dominance of faces. We named the typicality and the bias score obtained from such dominance ratings as the control-typicality and control-bias scores. We assume any relationship between taste-typicality and control-typicality and evaluation-bias and control-bias to be a confounder (i.e., the overall tendency to display typical judgments and the participant's tendency to give systematically higher or lower ratings regardless of the task). Accordingly, we regressed the taste-typicality and evaluation-bias scores, additionally to individuals' sex and age, on the Fisher z transformed control-typicality and the control-bias scores, and re-ran twin and phenotypic correlation analysis, and univariate and multivariate CTM on the residuals of such regressions. We avoided regressing potentially meaningful aesthetic relationships by regressing out control scores obtained from dominance ratings only. Regression was carried out in the statistical package umx⁶⁸.

Author contribution

GB and TJCP conceived the study; GB analysed the data; TJCP, EAV, and DJAS validated the work; TP and SEF conceptually validated the work; GB visualised the data; GB and MDT drafted the manuscript; SEF, MDT, TJCP, EAV, LFT, and DJAS revised the manuscript; TP and EAV supervised the research; All authors reviewed the last version of this manuscript.

Data and software availability

All data were made available by the original authors of the first two studies, Germine et al. and Sutherland et al.², and can be found at <https://osf.io/c3hz6/> and https://osf.io/35zf8/?view_only=e76c6755dcea4be2adc5b075cae896e8, respectively. After publication, all processed data and code used to generate the results reported in this paper will be made available by the authors.

Acknowledgements

We thank the Australian Twin Registry, Laura Germine et al., and Sutherland et al., for their original work and for making their data openly available. We further thank Laura Germine for their initial input on a previous version of the work. GB was supported by the German Federal Ministry of Education and Research (BMBF) and the Max Planck Society.

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