Genetic underpinnings of chills from art and music

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Abstract

Art can evoke strong emotional responses in humans. Here, we examine genetic contributions to chills, a marker of such responses. We gather self-reports from a genotyped sample of thousands of partly related individuals from the Netherlands (N = 15,642). Using genomic relationships based on common single-nucleotide polymorphism (SNP) data for more than 100 million pairs of individuals, we find that up to 30% of the variation in proneness to aesthetic (visual art and poetry) and music chills can be explained by familial relatedness effects, one-fourth of which is attributed to SNP variation. Furthermore, we reveal a moderate genetic correlation of .55 between aesthetic and music chills, pointing to shared genetic variation affecting susceptibility to strong emotional responses across different art forms. Finally, we find that a polygenic index capturing genetic propensities towards art (N = 234,880) is associated with susceptibilities both to aesthetic and music chills. Our results show that additive genetic variation, but also familial relatedness beyond shared common SNPs, contributes to proneness to chills from artistic, poetic, and musical expressions. These results open up a promising path towards studying the human attitude towards art, via both state-of-the-art genomics and intergenerational models of transmission.

Introduction

Darwin experienced them while hearing the anthem in King's College Chapel, which gave him "intense pleasure so that [his] backbone would sometimes shiver"[1]. Nabokov elevated them as "the telltale tingle" needed to bask in the book of genius[2]. When people encounter art, they may experience intense physiological responses that coincide with peak subjective pleasure and emotions, described as "chills"[3]. Since chills are clear, measurable events[4] that link subjective responses with physiological manifestations[4–7], they serve as a model for studying responses to art[3,6–11]. Investigations of chills have revealed that the pleasure evoked by music and poetry recruits neural systems similar to those involved in the evaluation of other biologically relevant non-abstract stimuli[3,7], and have linked stable subjective differences to inter-individual variability at both physiological and neurobiological levels[8,10,12].

Here, we investigate the genetics behind individual differences in proneness to chills, which we suggest can offer an additional approach for empirically studying how humans respond to art. As with many other complex human traits[13], proneness to chills is partly heritable[14]. For example, across diverse cultures, proneness to chills from visual art and poetry (referred to as aesthetic chills) has moderate heritability (h^2), with genetic effects suggested to explain 36% to 43% of the variance in studies of large twin-based samples, including more than 10,000 individuals from the Netherlands[14], and thousands from Germany, Denmark, North America, Australia, and Japan[15]. However, key questions about the genetics of inter-individual differences in proneness to chills remain unanswered. First, to date, h^2 estimates have been derived from family studies only, mainly from those relying on the Classical Twin Design (CTD). As such, it is unclear whether previous results reflect molecular genetic effects or biases introduced by unmet assumptions inherent to the CTD. Second, there is a complete lack of evidence regarding whether genetic effects on aesthetic chills may extend to other artistic domains, such as music, since the only estimates derived so far are specific to chills from visual art and poetry. This gap raises additional questions of whether sensitivity to different art forms is shaped by entirely different processes or is tied to similar underlying biological mechanisms. Finally, it is still unclear whether the genetics of proneness to chills is indeed an index of broader predispositions towards art, or if it reflects an independent phenomenon.

To resolve these uncertainties, we used a large sample of more than fifteen thousand genotyped individuals from Lifelines, a large multi-generational cohort study of individuals living in the North of the Netherlands[16], from whom we gathered self-reports on their proneness to aesthetic and music chills. We applied a molecular approach to quantify h^2 that contrasts patterns of measured genotypic resemblance with phenotypic resemblance in unrelated and related individuals[17,18]. The strength of this approach relies on the possibility of partitioning family-based (also called pedigree-based) estimates for h^2 (h_{ped}^2) into two types of h^2. The first, obtained from unrelated individuals and referred to as the Single-Nucleotide Polymorphism heritability (h_{SNP}^2), estimates the additive effect of genetic variants common in the population under study, captured using DNA genotyping chips. The second type of heritability, obtained instead from related individuals, assesses h_{ped}^2 biases due to, for instance, non-additive genetic and environmental effects shared between members of families[19,20] and is sometimes referred to as the (still) missing heritability (i.e. the difference between h_{SNP}^2 and h_{ped}^2)[21]. Moreover, by collecting information on people's proneness to chills evoked by different art modalities, we could investigate similarities and differences between responses to diverse forms of artistic, poetic and musical expression. We accomplished this by estimating genetic correlations (r_g) between aesthetic and music chills. Finally, we investigated the degree to which proneness to chills might reflect a broader genetic predisposition towards art. To do so, we leveraged the largest genome-wide association study (GWAS) on personality to date[22] to construct polygenic indices (PGIs) related to artistic interests and active imagination, testing their association with proneness to chills in our target sample.

Results

Working with Lifelines[16], we gathered self-report data on proneness to chills in response to diverse art forms from 35,114 adults (21,249 women). Some 15,642 of these individuals (9,922 women) had genotype data available, and their ages covered the entire adult lifespan, ranging from 18 to 96 years old. Proneness to aesthetic and music chills was assessed using the self-reported items "Sometimes when I am reading poetry or looking at a work of art, I feel a chill or wave of excitement"[23] and "I sometimes feel chills when I hear a melody that I like"[24], respectively. Participants were asked to report how much they agreed with these statements by choosing one out of five response options ranging from "strongly disagree" to "strongly agree". Within-trait descriptive statistics and between-trait phenotypic similarities and differences are reported in the Supplementary File.

To assess the extent to which genetic influences account for variation in proneness to aesthetic and music chills, we applied a linear mixed model with a Genome-based Restricted Maximum Likelihood (GREML) estimator[18]. This method estimates the amount of the observed phenotypic variance that can be explained by genomic relatedness between individuals, as indexed by SNP-derived Genetic Relatedness Matrices (GRMs). Taking advantage of the family relatedness structure of the participants included in the Lifelines cohort, we constructed two complementary SNP-derived GRMs, one representative of the pairwise genomic relatedness (π) across all individuals and another for which π below a set threshold was adjusted to zero[17]. Using this approach, known as threshold GREML[25], we could partition h_{ped}^2 into h_{SNP}^2 and $h_{\pi\geq.02}^2$, the latter assessing effects beyond common SNP variation. As shown in Figure 1, GREML-based analysis of adjusted two-stage rank normalised and residualised data for age, sex, genotyping array, and ten genomic principal components indicates significant h_{SNP}^2 for aesthetic ($\chi^2(1) = 9.66$, $p = 9.42 \times 10^{-4}$) and music ($\chi^2(1) = 11.16$, $p = 4.17 \times 10^{-4}$) chills, with h_{ped}^2 explaining up to 30% of the total variance in proneness to chills (see Table 1). These findings indicate that the proneness to chills from art, poetry and music is influenced by genetic variation. Results obtained from raw and transformed data did not differ (see Supplementary Table S1).

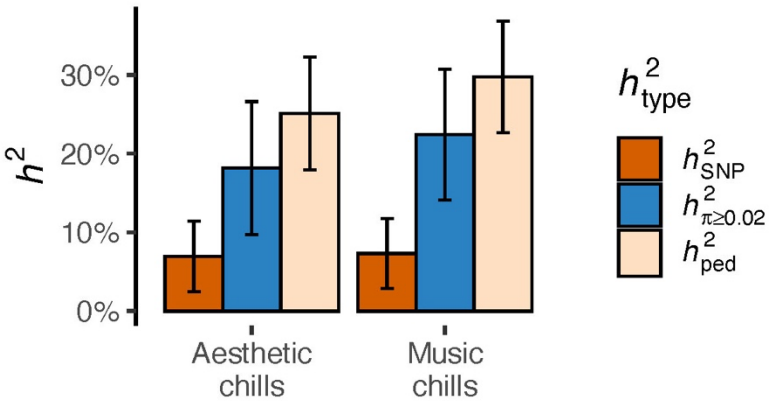

Figure 1. *Genetic influences on proneness to chills.* Heritability (h^2) estimates from GREML analysis reveal genetic influences on proneness to chills from visual art and poetry (i.e., aesthetic chills) and music. Left to right: In warm orange, SNP-based heritability (h_{SNP}^2); in azure blue, the excess heritability in related individuals ($h_{\pi\geq.02}^2$); in light peach, pedigree-based heritability (h_{ped}^2). Error bars represent the approximate 95% Confidence Intervals (CI) derived from the Standard Errors (i.e. 95% CI = estimate ± 1.96*SE).

Since both aesthetic and music chills displayed significant h_{SNP}^2, we assessed evidence for shared genetic contributions to variability in the two traits. First, we estimated the phenotypic correlation between proneness to aesthetic and music chills within the broader Lifelines sample of 35,114 individuals. Proneness to aesthetic and music chills correlated modestly, with a r of .43 (95% Confidence Interval (CI) [.42,.44]). Then, we applied a bivariate extension of GREML to estimate the genetic correlation between the proneness to aesthetic and music chills in the genotyped sample of 15,642 individuals. We found a moderate genetic correlation, with a r_g of .55 (95% CI [.20,.90], $\chi^2(1) = 5.10$, $p = .012$; which was significantly lower than 1, $\chi^2(1) = 6.04$, $p = .007$). These results suggest that a substantial proportion of the genetic variation associated with proneness to aesthetic chills is also associated with music chills. Yet, they also reveal some degree of specificity in genetic contributions to the different traits.

Finally, we assessed whether genetic proneness to chills could in part be reflected by broader genetic predispositions towards art. We derived individual PGIs from the largest genome-wide association study of openness to experience, which was previously conducted in a fully independent sample of 234,880 individuals[22]. To construct the PGIs, we used SNP associations with openness to experience, assessing, in particular, artistic interests and active imagination (see Methods). In a subsample of 11,678 Lifelines participants who were unrelated to each other ($\pi \geq .125$) we found that PGIs were significantly associated with proneness to aesthetic ($\beta = .06$, $p = 4.34 \times 10^{-9}$) and music chills ($\beta = .03$, $p = 5.43 \times 10^{-5}$) at the group level, explaining 0.3% (incremental r_{PGI}^2 95% CI [.01%,0.5%]) and 0.1% (incremental r_{PGI}^2 95% CI [0.03%,0.3%]) of the overall variance, respectively. Thus, genetic variation associated with individual differences in art interest contributes to proneness to chills across art domains. Table 1 provides a comprehensive overview of the results of these different investigations.

Table 1. *Overview of estimates.*

Component of interest	Parameter	Trait	Estimate	95% CI
Trait variance explained by common DNA variation (with additive effect)	h_{SNP}^2	Aesthetic chills	.07	[.02, .11]
		Music chills	.07	[.03, .12]
Gap between effects of common DNA variation and familial relatedness	$h_{\pi \geq .02}^2$	Aesthetic chills	.18	[.10, .27]
		Music chills	.22	[.14, .31]
Trait variance explained by overall effects of familial relatedness	h_{ped}^2	Aesthetic chills	.25	[.18, .32]
		Music chills	.30	[.23, .37]
Phenotypic correlation	r	Aesthetic-music chills	.43	[.42, .44]
Genetic correlation	r_g	Aesthetic-music chills	.55	[.20, .90]
Incremental percentage of variance explained by PGIs for openness to experience	r_{PGI}^2	Aesthetic chills	0.3%	[0.1%, 0.5%]
		Music chills	0.1%	[0.0%, 0.3%]
Partner phenotypic correlation	r_{AM}	Aesthetic chills	.09	[.05, .12]
		Music chills	.09	[.06, .13]
Cross-trait partner phenotypic correlation	r_{xAM}	Aesthetic-music chills	.01	[-.03,.04]

Note. h_{SNP}^2: GREML-SNP-based heritability; $h_{\pi \geq .02}^2$: GREML-based excess heritability in related individuals; h_{ped}^2: GREML pedigree-based heritability; r: Pearson-correlation; r_G GREML-SNP-based additive genetic correlation; r_{PGI}^2: $\Delta(r_{PGI+COVARIATES}^2 - r_{COVARIATES}^2)$; r_{AM} within-trait Pearson-correlation between partners; r_{xAM} cross-trait Pearson-correlation between partners. All results shown here were obtained from fully adjusted two-stage rank normalisation procedure (rank transformed) on the phenotype data[26], with exception of r_{PGI}^2, which used raw scores. Rank transformed and raw score derived estimates did not differ.

We note that assortative and cross-assortative mating can lead to bias when estimating h_{SNP}^2 and r_G. Assortative and cross-assortative mating refer to phenomena where two individuals are more likely to mate when they resemble each other in one or more (e.g., cross) traits. These phenomena have been shown to confound h_{SNP}^2 and r_g by upwardly biasing estimates[27,28]. To provide evidence of minimal upward bias on h_{SNP}^2, and help solidify the interpretation of r_g as an estimate for widespread pleiotropy unconfounded by both types of assortment, we estimated trait and cross-trait partner correlations in proneness to chills. To do so, we studied 3,424 partners for whom phenotypic data were available. We observed small yet significant partner correlations for aesthetic chills, r = .09 (95% CI [.05,.12]), and music chills, r = .09 (95% CI [.06,.13]). There was very little evidence of cross-trait partner correlation, with a non-significant correlation of only .01 (95% CI [-.03,.04]). These findings indicate that assortative and cross-assortative mating do not upwardly bias our estimates for h_{SNP}^2 and r_G (for details, see Supplementary File and reference[27]).

Discussion

Our results provide converging evidence for existence of a genetic predisposition to the ability to experience chills from cultural products, such as artistic, poetic, and musical expression. By investigating the similarity between genotypic and phenotypic resemblance in related and unrelated individuals, we find significant SNP-based heritability for aesthetic and music chills, aligning with the claim that proneness to chills may represent a “vector of biological variation”[29]. Furthermore, we reveal a substantial genetic correlation between the traits, which indicates that proneness to chills from different art modalities is partly tied to shared genetic variation. In line with these findings, we also find that genetic propensities for artistic interests are significantly associated with proneness to aesthetic and music chills. At the same time, genetic correlations between propensity to aesthetic and music chills are significantly lower than 1, indicating less than full overlap in the underlying genetic architecture for responses to different forms of artistic expression.

Notwithstanding the significant SNP-based heritability, this explained only around a fourth of the total pedigree heritability and a fifth of the previously reported twin-based heritability for aesthetic chills (obtained from another sample of the Dutch population[14]). While in line with well-established concepts of “missing heritability”[30], as SNP-based estimates tend to explain only one-third to one-half of family-based estimates of complex human traits[20,21,31], the gap observed here for proneness to chills seems relatively large. (Note, however, that this is still smaller than the gap observed for some other behavioural characteristics, for which h_{SNP}^2 is only about one-tenth of the h_{twin}^2; see reference[31] for an example). The observed gap between SNP- and family-based heritability estimates likely involves a complex mixture of factors, including non-additive genetic variants, rare variants, and common environmental effects shared across families[17], but also possible violations of CTD-specific assumptions, including the equal environment assumption, the absence of gene-by-shared environment interaction, or unmodelled high-order epistasis (gene-by-gene interaction at different genetic loci[32]). Future studies with different research paradigms will help to better understand this gap. In particular, more sophisticated twin-based approaches, such as extended family twin designs (in which parents, partners, and siblings of twins are included[33,34]), may be particularly suited to explain the gap observed in this study.

In addition, our study reveals the association between proneness to chills and polygenic indices for openness to experience—mainly assessed as individuals' interest towards the arts and self-reported active imagination (see below and Methods). We note that the percentage of variance in proneness to aesthetic and music chills explained by the PGI is less than 1%. However, the modest proportion of variance accounted for here is in line with theory-driven expectations on PGI-based predictions. In particular, it is known that the expected percentage of phenotypic variance that can be explained by a PGI is a function of the heritability of the target phenotype being predicted, the one from which the PGI is derived, and their genetic correlation, as well as the sample size of the original GWAS, along with the effective number of SNPs included[35,36]. Considering the observed heritability of proneness to chills and the previously reported heritability of openness to experience[22] (h_{SNP}^2 = .05), then the maximum expected percentage of variance that we could have explained is 1.10% and 1.14%, for aesthetic and music chills, respectively, even assuming an unlikely perfect genetic correlation of 1. These expectations of ~1% are not far from our observed incremental r^2, thus contextualising our estimates for the absolute percentage of variance explained by the PGI as being relatively close to theoretical expectations (see Supplementary File for details).

This study comes with a few limitations. First, our PGI analyses made use of summary statistics from meta-GWAS efforts conducted with self-reports that included art interest and other broader characteristics defining openness to experience[22]. As such, individual PGIs may assess more complex genetic predispositions than art interest alone. However, we note that the largest cohort included in the meta-analysis, including 220,015 individuals from the Million Veteran Program (comprising 94% of the combined samples), was conducted on the sum score of only two self-report items, one assessing art interests and the other evaluating active imagination. As such, we expect the genetic signal used to construct the PGI to reflect individual traits that revolve around art interest and imagination over other aspects of openness to experience. Second, the results in the present study were obtained from a population representative of the Netherlands and focused on individuals of European descent. Further studies should assess the generalisability of our findings beyond ancestries of European descent and culture. Indeed, the cross-cultural prevalence of experiencing chills[37] and proneness towards these[23], and the observation that such proneness may rely less on cultural bounds and influences from Western humanistic traditions than other traits[23,29], leads to intriguing questions for future research. In particular, it will be interesting to ask whether proneness to chills may be used to investigate the genetics of human attitudes towards art across cultures. Moderating effects introduced by cultural or generational differences in genetic influences could be an especially promising avenue of study[38]. Third, our results do not provide insights into how molecular associations with proneness to chills may extend to biological mechanisms underlying related physiological processes, such as piloerection (i.e., hairs standing on end). Previous research suggests that piloerection tends to co-occur with the experience of chills[39], although this is not always the case[40]. At the same time, the findings of genetic associations with proneness to chills may allow future research to better disambiguate between these two seemingly tied phenomena.

In conclusion, our research highlights shared molecular heritability for proneness to chills from art, poetry, and music. Furthermore, it reveals that proneness to chills is associated with genetic propensities towards art. Yet it also reveals larger estimates for genetic effects on proneness to chills in related individuals, hinting at deviations from pure additive genetic transmission of sensitivity to art and underscoring the need for extended intergenerational designs to relax classic modelling assumptions. We anticipate that large-scale genetic studies of proneness to chills, together with extended family designs, could further illuminate the origins and biological bases of affective responses elicited by art, and even clarify whether the aetiology of these subjective experiences differs from that of other sensory experiences[41].

Materials and Methods

Ethics

The general Lifelines protocol has been approved by the University Medical Center Groningen medical ethical committee (2007/152), and the "Speech, Language and Musicality" study was reviewed by the medical ethical committee of the Erasmus Medical Center (MEC-2022-0313). All participants gave informed consent prior to taking part in the survey.

Sample

Individuals included here participated in the Lifelines study "Speech, Language and Musicality". Lifelines is a multi-disciplinary prospective population-based cohort study examining in a unique three-generation design the health and health-related behaviours of 167,729 persons living in the North of the Netherlands. It employs a broad range of investigative procedures in assessing the biomedical, socio-demographic, behavioural, physical, and psychological factors which contribute to the health and disease of the general population, with a special focus on multi-morbidity and complex genetics[16].

Phenotyping

Aesthetic and music chills were measured using validated items in the revised NEO personality inventory (NEO PI-R[23]) and the Barcelona Music Reward Questionnaire (BMRQ[8]). The questionnaires were collected in Dutch. Of the 35,114 individuals from whom we collected data on proneness to aesthetic and music chills, a subset of 15,642 had available genotype data from across the genome.

Genotyping

Genotyping was carried out by the UMCG Genetics Lifelines Initiative (UGLI) using the Infinium Global Screening Array® for 9251 individuals (release 1) and the FinnGen Thermo Fisher Axiom® for 6391 individuals (release 2). Information about quality control of genotyped data and samples and genetic imputation can be found at https://wiki.lifelines.nl/doku.php?id=ugli. Further information can be found in Supplementary File.

Covariates

Following De Hoyos et al.[26], data were transformed before model fitting using a fully adjusted two-stage rank normalisation procedure[42]. Age, sex, genotyping array, and the first ten genomic principal components were the covariates of interest. Results from untransformed raw data are included in Supplementary Table S1.

Genome-based Restricted Maximum Likelihood

Estimates for h_{SNP}^2, $h_{\pi\geq.02}^2$**,** and h_{ped}^2 of aesthetic and music chills were obtained by using a threshold GREML approach[17,43] as implemented in the GCTA software (https://cnsgenomics.com/software/gcta/), version 1.93.2beta[18]. Similarly, a bivariate extension of GREML[44] was used to obtain estimates of the covariances between the variance components of the two phenotypes, which were then used to obtain estimates for r_G. To test whether h_{SNP}^2 and r_G estimates significantly differ from 0 and 1, GCTA applies a Likelihood Ratio Test comparing the model in which h_{SNP}^2 and r_G are freely estimated to a model in which h_{SNP}^2 and r_G are fixed to 0 and 1, respectively. To control for two comparisons, we used a more stringent α of .025. Schematic representations of the GREML approaches are given in Figure 2. The extended method section can be found in the Supplementary File. Robustness analysis with meta-analytic estimates obtained from subsamples corresponding to the two UGLI genotyping releases are provided in Supplementary Table S2. We note that, despite $h_{\pi\geq.02}^2$ being equal to h_{ped}^2 - h_{SNP}^2, $h_{\pi\geq.02}^2$ and h_{ped}^2 are sometimes used interchangeably in the literature to describe pedigree-based heritability[20,25]. The latter nomenclature is appropriate when $h_{\pi\geq.02}^2$ (or $h_{\pi\geq.05}^2$) and h_{SNP}^2 are not estimated simultaneously, as in reference[20].

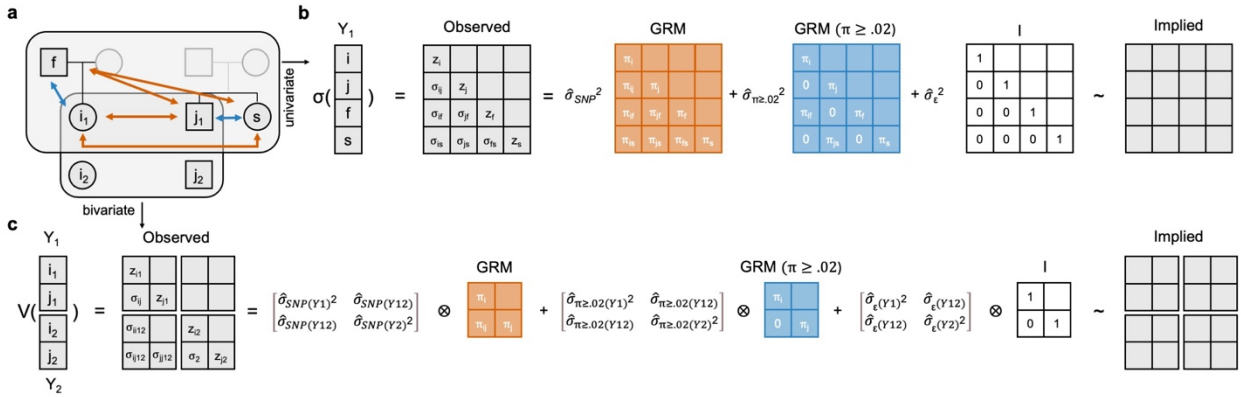

Figure 2. *Conceptual representation of the GREML approach*. **a** Illustration of the relatedness structure. Coloured arrows capture the pairwise genomic relationships (π) between unrelated (warm orange, e.g., *i* and *j*) and related (azure blue, e.g., *f* and *i*) individuals. When data are available for either one (Y_1) or two (Y_1 and Y_2) phenotypes, information about π can be used to estimate h^2 and r_G. **b** Univariate decomposition of the observed variance (σ^2) of Y_1 into different components (e.g., σ_{SNP}^2). Two Genomic Relatedness Matrices (GRMs), capturing all possible pairwise π between all and related (at $\pi \geq .02$) individuals, are used to obtain estimates for SNP contributions to phenotypic variation. Estimates are derived by maximising the likelihood of the observed data given the two GRMs. Intuitively, GREML finds estimates that make the observed and the implied matrix (in grey) as similar as possible. **c** Similar to the univariate case, bivariate GREML obtains estimates for the variance-covariance components by maximising the likelihood of the observed data given the two GRMs. GREML: Genome-based Restricted Maximum Likelihood Approach; π: pairwise genomic relationships; Y: phenotype; GRM: Genomic Relatedness Matrix; σ_Y^2: variance; σ_{Y12}: covariance; I: Identity matrix. Figure inspired by http://gusevlab.org/projects/hsq/.

Polygenic Index analyses

We computed individuals' Polygenic Index (PGI) for openness to experience using meta-analysis summary statistics from a GWAS meta-analysis that totaled 234,880 individuals. The largest GWAS cohort in this meta-analysis included 220,015 individuals, for which sum scores were derived from only two self-reports: "I see myself as someone who has few artistic interests" (reverse coded) and "I see myself as someone who has an active imagination" (five response options, "disagree strongly" to "agree strongly"). The remaining GWAS cohorts that contributed to the meta-analyses included summary statistics from OE scores derived from 12 to 48 items[45]. The Summary statistics were filtered, removing ambiguous, duplicated and rare (MAF < 0.01) SNPs. PGIs were calculated using PRS-CS (version Jan 4 2021)[46] in PLINK, using a European linkage disequilibrium panel from the 1000 Genomes. As in previous PGI-based analysis, we retained individuals potentially unrelated to the 3rd degree[47], corresponding approximately to π <.125[48]. After exclusion, genotyping data of 11,678 individuals with proneness to chills data remained for PGI analyses. We then regressed proneness to aesthetic or music chills raw scores on standardised PGIs, including the covariates used for GREML analyses (i.e., age, sex, genotyping arrays and ten genomic principal components). Incremental r^2 was obtained by subtracting the r^2 of a baseline model with only covariates. 95% Confidence Intervals (CI) were obtained by bootstrapping, resampling, with replacements, the incremental r^2 1000 times. Results from transformed data are included in the Supplementary Table S1.

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