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Individual differences in aesthetic engagement are reflected in resting-state fMRI connectivity: Implications for stress resilience

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ABSTRACT

Objective: Individual differences in aesthetic engagement—the propensity to be moved by art, nature, and beauty—are associated with positive health outcomes, as well as stress resilience. The purpose of the current study was to identify potential neural substrate mechanisms underlying individual differences in aesthetic engagement and reported proneness to aesthetic chill.

Methods: Data from the Human Connectome Project (HCP) 1200 Subjects Release were utilized. Resting-state fMRI connectivity was extracted for 361 regions in the brain including cortical, subcortical and cerebellar regions for each participant, using participant-specific segmentation and parcellation of subcortical gray matter nuclei and a network-based statistics analytical approach. The Aesthetic Interests subcluster of the Openness to Experience scale (NEO-Five Factor Inventory; NEO-FFI) was used to characterize individual differences in aesthetic engagement and chill.

Results: Participants reporting higher aesthetic engagement, particularly proneness to aesthetic chill responses, exhibited significantly higher connectivity between the default network and sensory and motor cortices, higher connectivity between the ventral default and salience networks, and decreased connectivity between the cerebellum and somatomotor cortex.

Conclusions: Current findings suggest that greater integration of the default mode network, involving processing of internal narrative, with neural representations of sensory perception and salience detection may be a mechanism underlying individual differences in aesthetic engagement. Thus, these individual differences may reflect general integration of environmental perception with internal emotional experience, which in turn may facilitate comfort with novelty, self-regulation, and positive adaptation to potentially stressful experiences.

Introduction

Aesthetic engagement involves being moved by art and beauty and absorbed in music and nature. For some individuals, aesthetic stimuli with particular qualities evoke a peak emotional experience often labeled “awe” which can be accompanied by “aesthetic chill” – sympathetic nervous system activation resulting in goosebumps or hair standing on end (piloerection). These peak emotional responses to aesthetic stimuli appear to be universal, in that they are experienced across cultures; however, they are probably not “basic emotions”—approximately half the population deny experiencing aesthetic chill (McCrae, 2007). Thus, there are clear individual differences in propensity to aesthetic engagement and related emotional and physiological responses, at least by self-report. The personality factor thought to underlie such propensity is Openness to Experience, described as “the breadth, depth, and permeability of consciousness, and … the recurrent need to enlarge and examine experience” (McCrae and Costa, 1997, p. 826) and is broadly characterized as comfort with novelty and motivation for cognitive exploration (DeYoung, 2014). Consequently, individual differences in proneness to aesthetic engagement and chill may reflect positive response to novelty in aesthetic stimuli (e.g., music, film, nature, art, poetry).

Abbreviations: RSFC, resting state functional connectivity; HCP, Human Connectome Project; NEO-FFI, NEO Five Factor Inventory; DMN, Default Mode Network.

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There is a growing interest in aesthetic chill and related peak emotional experiences, as well as the emerging fields of "neuro-aesthetics" (Pearce et al., 2016) and the neuroscience of personality (DeYoung, 2010). Aesthetic sensitivity is associated with pro-social engagement (Milfont and Sibley, 2012), as well as pro-environmental attitudes (Markowitz et al., 2012), emissions-reducing behavior to address climate change (Brick and Lewis, 2016), belief in human behavior driven climate change (Milfont et al., 2015), and a sense of connection to humanity and nature (Lee et al., 2015). There is also reason to believe individual differences in aesthetic engagement confer health benefits. In addition to studies linking Openness to positive health outcomes (e.g., Turiano et al., 2012), the Aesthetics facet is associated with decreased cardiac death risk among patients with cardiac disease (Jonassaint et al., 2007) lower systemic inflammation (Jonassaint et al., 2010; see also Stellar et al., 2015 for associations with awe), and healthy eating habits (Brummett et al., 2008). In addition, very low scores on the Aesthetics facet of Openness appear to mark incipient cognitive decline in older adults (Williams et al., 2013). Importantly, individuals higher in aesthetic engagement evidence less cardiovascular reactivity and greater physiological and affective "positive engagement" in talking about recent stressful experiences compared to individuals reporting low aesthetic interest (Williams et al., 2009). Collectively, prior research suggests that gaining a better understanding of individual differences in such peak emotional experiences is an important research endeavor.

The mechanisms underlying proneness to aesthetic engagement and positive outcomes have not been well articulated. Peak emotional responses to aesthetic stimuli appear to reflect integration of perceptions of the external environment with internal physiological changes, resulting in very positive, occasionally transcendent, emotional experiences (though see Panksepp, 1995, 2003 for evidence of sadness-related aesthetic chill). Such integration in the context of novel experience may translate to better stress regulation and should be evident in the brain network architecture of individuals high in this propensity. The current study examined the neural substrates underlying individual differences in reported aesthetic engagement and aesthetic chill using resting state functional connectivity (RSFC) data from Human Connectome Project (HCP) database (Van Essen et al., 2013).

The nature of aesthetic chill and related emotions

Aesthetic chill, sometimes accompanied by "goose bumps" (or emotional piloerection) (Benedek and Kaernbach, 2011) has been proposed to be a marker of Openness to Experience. Evidence for this supposition comes, in part, from examination of the factor loadings of the item focused on aesthetic chill in the NEO Personality Inventory-Revised (NEO PI-R; Costa and McCrae, 1992) across languages and cultures (McCrae, 2007). Aesthetic chill is hypothesized to correspond to the experience of awe, which has been described as resulting from the perception of "vastness" (i.e., larger than the self's frame of reference) and the "accommodation" (adjustment of mental structures) to that perception (Keltner and Haidt, 2003). Indeed, aesthetic chill response to music is a reliable indicator of peak emotional experience (Grewe et al., 2009). Study of chills in response to music indicates that they often correspond to dramatic shifts in musical features (e.g., crescendo, disharmonies) (Grewe et al., 2007; Sloboda, 1991)—in other words, novel events or features that may run counter to expectation. Although the physiological experience of chills, generally, may be connected to a variety of experiences (Maruskin et al., 2012), *aesthetic* chill appears to be unique in demonstrating reliable individual differences in Openness to Experience (Silvia and Nusbaum, 2011).

In general, cognitive science and imaging research suggests that aesthetic experiences are a function of the interaction between top-down processing (e.g., orienting of attention, prior experiences) and bottom-up perception and sensation (Cupchik et al., 2009; Shimamura, 2012). Evoked aesthetic chill in prior PET scan research is associated with reward circuitry (e.g., ventral striatum, midbrain, amygdala, ventral medial prefrontal cortex, orbitofrontal prefrontal cortex) (Blood and Zatorre, 2001). There is also initial evidence that individual differences in chill response to music, specifically, are reflected in white matter connectivity (Sachs et al., 2016). Given that patterns of RSFC predict task-related activation (Kelly et al., 2008; Mennes et al., 2010), prior research suggests that examination of RSFC among individuals reporting varying degrees of aesthetic engagement would be meaningful.

Resting state functional connectivity in Openness

Whereas task-related brain activation patterns in response to aesthetic stimuli have been examined, RSFC characterizing individual differences in propensity to aesthetic engagement and proneness to aesthetic chill, specifically, have not been investigated. Several studies have examined RSFC in relation to the broader personality factor, Openness to Experience, however. Adelstein et al. (2011) found that Openness (full scale NEO PI-R) was associated with greater functional connectivity in the midline default mode network (DMN) and dorsolateral prefrontal cortex, based on seed regions in the anterior cingulate and precuneus ($n = 39$). Openness (Italian translation of the NEO PI-R) was related to greater connectivity between the substantia nigra/ventral tegmental area and dorsolateral prefrontal cortex in 46 healthy adults (Passamonti et al., 2015) consistent with Openness reflecting dopaminergic networks (DeYoung, 2013). Beaty et al. (2016) differentiated Openness and Intellect in examining RSFC of the DMN, using graph metrics to examine "efficiency." Although it was concluded that Openness is reliably associated with default network "functioning," facet-level examination of the Big Five Structure Inventory in a German sample ($n = 86$) indicated that Aesthetics was not significantly associated with DMN efficiency. Finally, Openness/Intellect (Portuguese adaptation of the NEO-FFI) was associated with increased activity of the right inferior parietal and decreased bilateral superior parietal and precuneus in a sample of 49 healthy adults (Sampaio et al., 2014). The authors suggest that these findings are consistent with sensitivity to external "contextual" stimuli and prior findings of Openness associations with parietal functioning (Behrmann et al., 2004; DeYoung et al., 2010).

Previous studies of neuroanatomical correlates of Openness are also relevant to current study hypotheses. In particular, examination of surface-based morphometry indices in the HCP database indicate that Openness is related to thinner cortex in PFC regions, but greater surface area in parietal, temporal, and occipital regions, as well as greater folding in orbitofrontal, parahippocampal, posterior cingulate, and temporal areas ($n = 507$; Riccelli et al., 2017). These findings support the supposition that variations in attention and salience networks may underlie individual differences in Openness. The pattern of cortical thinness and increased surface area and gyrification is consistent with greater cognitive maturation and may be reflected, potentially, in greater functional connectivity (Hogstrom et al., 2013).

Although these previous studies provide initial evidence of Openness-specific brain architecture, there has been limited investigation of the aesthetic engagement component, specifically. Tentatively, based on RSFC and brain structure research on Openness, as well as the known characteristics of the Aesthetics facet, it is hypothesized that network-level examination of RSFC would reveal greater connectivity between brain networks central to monitoring the external environment ("salience" network; sensory cortices) and self-referential processing (DMN). Given the focus on HCP participants, the regions of Openness association with surface area and gyrification reported by Riccelli et al. (2017) may suggest refined predictions within the broader networks (e.g., parahippocampal region of the DMN).

The current study

The current research utilized the publicly available Human Connectome Project (HCP) database, providing neuroimaging, behavioral, and cognitive data of unprecedented scope and quality (Van Essen et al., 2013). Resting-state functional connectivity was examined in relation to individual differences in reported aesthetic engagement and proneness to aesthetic chill, derived from the NEO-FFI (Costa and McCrae, 1992).

Methods

Participants

We analyzed data from 1000 participants from the Human Connectome Project 1200 Subjects Release. Multiband BOLD resting state data from this release consisted of FIX ICA cleaned BOLD resting state data (Griffanti et al., 2014). Of the 1206 participants in the complete dataset, 1003 had 4 complete runs of resting state data (60 min per subject). Three additional participants were excluded who did not have complete values for the NEO-FFI (Costa and McCrae, 1992) yielding 1000 subjects in the analysis cohort. The HCP sample is relatively young (mean age = 28.7 years; SD = 3.7; age range 22–37) and healthy. Demographic and basic health information on the participants for the current study are shown in Table 1.

Brain parcellation

Resting functional MRI data were analyzed using brain parcellations at 2 levels of granularity. Average time series were extracted from each of 17 distributed brain networks associated with the cortical parcellation of Yeo et al. (2011). Each network was treated as a single region of interest, and BOLD time series was averaged across all voxels for each of the 17 networks for each of the 1180 vol in each of the 4 runs for each subject after excluding the first 20 vol of each run.

A finer parcellation consisted of 333 regions in the cerebral cortex (Gordon et al., 2016). Fourteen participant-specific subcortical regions were added using Freesurfer-derived segmentation (Fischl et al., 2002) of bilateral thalamus, caudate, putamen, amygdala, hippocampus, pallidum, and nucleus accumbens, segmented independently for each participant. 14 cerebellar regions were also added (Buckner et al., 2011) comprising left- and right-hemispheric representations of a 7-network parcellation. This combined parcellation scheme covering cortex, subcortical structures, and the cerebellum comprised a total of 361 regions (Ferguson et al., 2017). Average BOLD time series were extracted for each volume in each run for each subject.

Table 1
Participant Demographic, Behavioral, and Health Information (N = 1000 participants, 532 females, 468 males).

Variable	*n*	*M*	SD
Age (years)	1000	28.72	3.71
Education (years)	999	14.96	1.77
Height (cm)	999	67.50	3.91
Weight (lb)	999	171.79	38.91
Body mass index	999	26.40	5.08
Blood pressure (systolic, mmHg)	988	123.43	13.78
Blood pressure (diastolic, mmHg)	988	76.37	10.56
Number of childhood conduct problems	999	0.54	0.77
Number of panic disorder symptoms	999	0.07	0.26
Number of depressive symptoms	970	1.27	2.56
Number of cigarettes per week	982	6.58	21.77
Number of drinks per week	982	4.90	7.08
Race (%)			
American Indian, Alaskan	2 (0.2%)		
Asian, Hawaiian, Other Pacific Island	61 (6.1%)		
Black or African American	139 (13.9%)		
White	757 (75.7%)		
More than one	24 (2.4%)		
Unknown or not reported	17 (1.7%)		
Missing data	0 (0.0%)		
Ethnicity (%)			
Hispanic/Latino	90 (9.0%)		
Not Hispanic/Latino	897 (89.7%)		
Unknown or not reported	13 (1.3)		
Missing data	0 (0%)		
Handedness (%)			
Right handed	909 (90.9%)		
Left handed	88 (8.8%)		
Mixed	3 (0.3%)		
Missing data	0 (0.0%)		

n = subsample size. *M* = mean. SD = standard deviation.

Data postprocessing

BOLD time series, both for the 17 network parcellation and for the 361 ROI parcellation, had already been subject to FIX ICA cleaning procedure (Griffanti et al., 2014). We additionally performed a linear regression analysis on each network's and each ROI's time series in which 12 detrended head motion time series, obtained from the minimally preprocessed data release for the same participants, were used as regressors in a general linear model. The residuals were then linearly detrended, and volumes before and after mean head motion greater than 0.2 mm were censored from the data with remaining time series concatenated (Power et al., 2012). Correlation coefficients were estimated between each pair of networks or ROIs. These values were Fisher transformed to improve normality, and a matrix consisting of correlation coefficients representing functional connectivity for 17×17 networks or 361×361 ROIs was averaged for each subject across the four runs for that subject.

Personality metrics

For each participant, subclusters of the Openness to Experience factor (Chapman, 2007; Saucier, 1998) in the NEO-Five Factor Inventory (NEO-FFI) (Costa and McCrae, 1992) were extracted by scoring *Intellect*, items 48 (reversed), 53, and 58 (Cronbach's alpha = .71); *Aesthetic Interests*, items 13, 23 (reversed), and 43 (Cronbach's alpha = .77); as well as the full Openness factor score (Cronbach's alpha = .76). Given the specific focus on aesthetic engagement and prior research on the item as a "universal marker" of Openness (McCrae, 2007) the NEO-FFI aesthetic chills item (item 43: *Sometimes when I am reading poetry or looking at a work of art, I feel a chill or wave of excitement*) was also examined separately. Note that prior factor analytic studies also identified a third subcluster of the NEO-FFI Openness scale—*Unconventionality*; however, the internal reliability in the current sample was modest (Cronbach's alpha = .43), so it was not further examined. The other four NEO-FFI factors (Neuroticism, Extraversion, Agreeableness, Conscientiousness) were also examined to determine the specificity of Openness, subcluster scales, and aesthetic chill associations. Descriptive statistics are shown in Table 2.

Personality vs. connectivity associations

For each pair of networks or ROIs, functional connectivity was compared to Openness, Intellect, Aesthetics, and chills by measuring p-value and t-statistic of a general linear model including functional connectivity, age, sex, mean head motion, and the respective personality metric. For 17×17 network comparisons, significant values were established using false discovery rate $q < 0.05$ across network pairs. No FDR-corrected functional connectivity ROI pairs were significant in the 361×361 ROI dataset for any of the 4 personality metrics.

Network-based statistic

To assess for broader patterns within the set of 361×361 ROIs for the chills metric, we performed a network-based statistic approach (Zalesky et al., 2010). The 361×361 was thresholded at $p < 0.01$, uncorrected, and a graph was constructed from 361 nodes, with edges placed between nodes for which the p-value was less than 0.01 for a relationship between functional connectivity and the participant's reported sensitivity to chills. From this graph, a maximal connected component consisted of 328 ROIs.

Table 2
NEO- five factor inventory (NEO-FFI) descriptive statistics.

Variable	*n*	*M*	SD	Range		Cronbach's α
				Minimum	Maximum	
Neuroticism	1000	16.46	7.35	0	43	0.84
Extraversion	1000	30.72	5.96	10	47	0.78
Openness to Experience	1000	28.46	6.22	10	47	0.76
Agreeableness	1000	32.01	4.95	13	45	0.76
Conscientiousness	1000	34.47	5.89	11	48	0.82

n = subsample size. M = mean. SD = standard deviation.

To assess significance of this component, Monte Carlo simulations were performed in which 5000 random variables were substituted for the chills scores, each of which was entered into the general linear model with the functional connectivity, age, sex, and head motion, and a maximal connected component size was estimated for the $p < 0.01$ thresholded graph for each of the 5000 random variables. The maximal connected component size for chills sensitivity was greater than 95.9% of the maximal connected component for the other random variables. This analysis was repeated for a threshold of $p < 0.001$, and the chills sensitivity graph produced a maximal connected component including 162 ROIs, greater than the maximal component for 96.3% of the graphs produced by random variables.

Characterization of maximal connected component

To evaluate the maximal connected component of the graph associated with functional connectivity values that were correlated with sensitivity to chills (using the $p < 0.01$ threshold), we clustered ROIs that showed similar t-statistics between chills and functional connectivity. In the 361 × 361 matrix of t-statistics between functional connectivity and chills, a correlation coefficient was computed between each pair of rows. This similarity matrix was clustered using the infomap algorithm (Rosvall and Bergstrom, 2008) using software at *mapequation.org* (version 0.19.11). The clusters were subsampled to include only nodes present in the maximal connected component, and 8 nontrivial clusters (comprising at least 5 nodes) were present. Brain images showing each of these 8 clusters were obtained, and the matrix of t-statistics between functional connectivity and chills were displayed, grouped into these 8 clusters.

Results

For 1000 participants from the Human Connectome Project dataset (Table 1), we estimated functional MRI connectivity between 17 networks of the Yeo et al. (2011) parcellation of the cerebral cortex. Synchrony between the time series for each pair of networks was measured for each subject, averaged across four 15-min resting state fMRI acquisitions per subject. Functional connectivity was compared to the Openness to Experience scale from the NEO-FFI as well as to subcluster scales of Intellect and Aesthetics, and to the single aesthetic chills item. Age, sex, and mean head motion were included as subject level covariates in the analysis. Results are shown in Fig. 1 for each of the four personality metrics.

A single connection between network 8 (including regions of the anterior insula and anterior cingulate) and network 15 (including bilateral parahippocampal region and ventral nodes of the default network) showed a significant association with Openness (corrected for multiple comparisons using false discovery rate $q < 0.05$). No network pairs showed significant relationship between functional connectivity and the Intellect subcluster. Four network pairs showed a relationship between functional connectivity and Aesthetics, all involving regions of the default network to networks comprised of cinguloinsular and superior temporal cortex. Six network pairs showed a significant relationship between functional connectivity and sensitivity to chills, including the same network pairs as for Aesthetics as well as connections between the default network, posterior cinguloinsular cortex, and anterior visual cortex. Functional connectivity comparisons were performed separately for Openness, Intellect, Aesthetics, and chills because these factors were highly correlated across subjects and no results were significant in partial correlation analyses including all factors jointly.

To further evaluate the robustness of these results, we divided the sample into two 500-participant cohorts by alternating subject ID numbers between the two cohorts. In both samples, a similar distribution of network pairs showed correlation between chills and functional connectivity ($p < 0.05$), including 5 of the 6 network pairs identified in the full sample, shown in Fig. 1, bottom row.

For the 5 network pairs showing significant correlation between functional connectivity and chills, including replication in both participant subsamples, we performed multivariate models evaluating whether the correlation was specific to chills in the context of the other four NEO-FFI personality factors. Results are shown in Fig. 2, left, with all of the 5 network pairs showing specificity of partial correlations between functional connectivity and chills when including Agreeableness, Conscientiousness, Neuroticism, and Extraversion in the model in addition to age, sex, and mean head motion (bivariate correlations among predictor variables in Table 3; partial correlations and p-values in Table 4). Of note, we used corrected scoring of the Agreeableness factor rather than the initial data supplied with the 1200 subjects release of the Human Connectome Project dataset (Gray, 2017). Similarly, because the Human Connectome Project sample includes 120 pairs of monozygotic twins and 64 pairs of dizygotic twins in addition to non-twin siblings, we performed a multivariate model demonstrating that correlations between functional connectivity and chills were not driven by any of these twin or sibling cohorts (Fig. 2, right).

A finer parcellation of the cerebral cortex, subcortical gray nuclei, and cerebellum comprised of 361 ROIs did not show multiple comparison corrected significant results for any of the four Openness personality metrics at the level of individual ROI pair connections. Using a graph-theoretic network-based statistic approach, the relationship between functional connectivity and sensitivity to chills was thresholded for all ROI pairs and a graph was constructed with nodes at each ROI and edges for chills vs. functional connectivity relationship exhibiting $p < 0.01$. The maximal connected component of this graph consisted of 328 ROIs, shown in Fig. 3. ROIs are grouped for visualization by functional network from Gordon et al. (2016) with network assignments as reported in Lopez-Larson et al. (2017).

We additionally evaluated correlations between functional connectivity and chills separately in both male and female cohorts given a prior report of sex differences in resting-state neural correlates of Openness (Sutin et al., 2009). The distribution of correlations across brain networks between functional connectivity and chills were similar to that observed in the maximally connected cluster for both male and female participants ($p < 0.05$, uncorrected; Fig. 3, mid and lower panel).

The maximally connected component for connectivity covariation with chills was significantly larger than expected based on Monte Carlo simulations of 5000 random variables compared to functional connectivity (also with age, sex, and mean head motion as covariates), and was larger than 96% of maximal components derived from random variables. Thus, whereas this component may be considered significant, individual

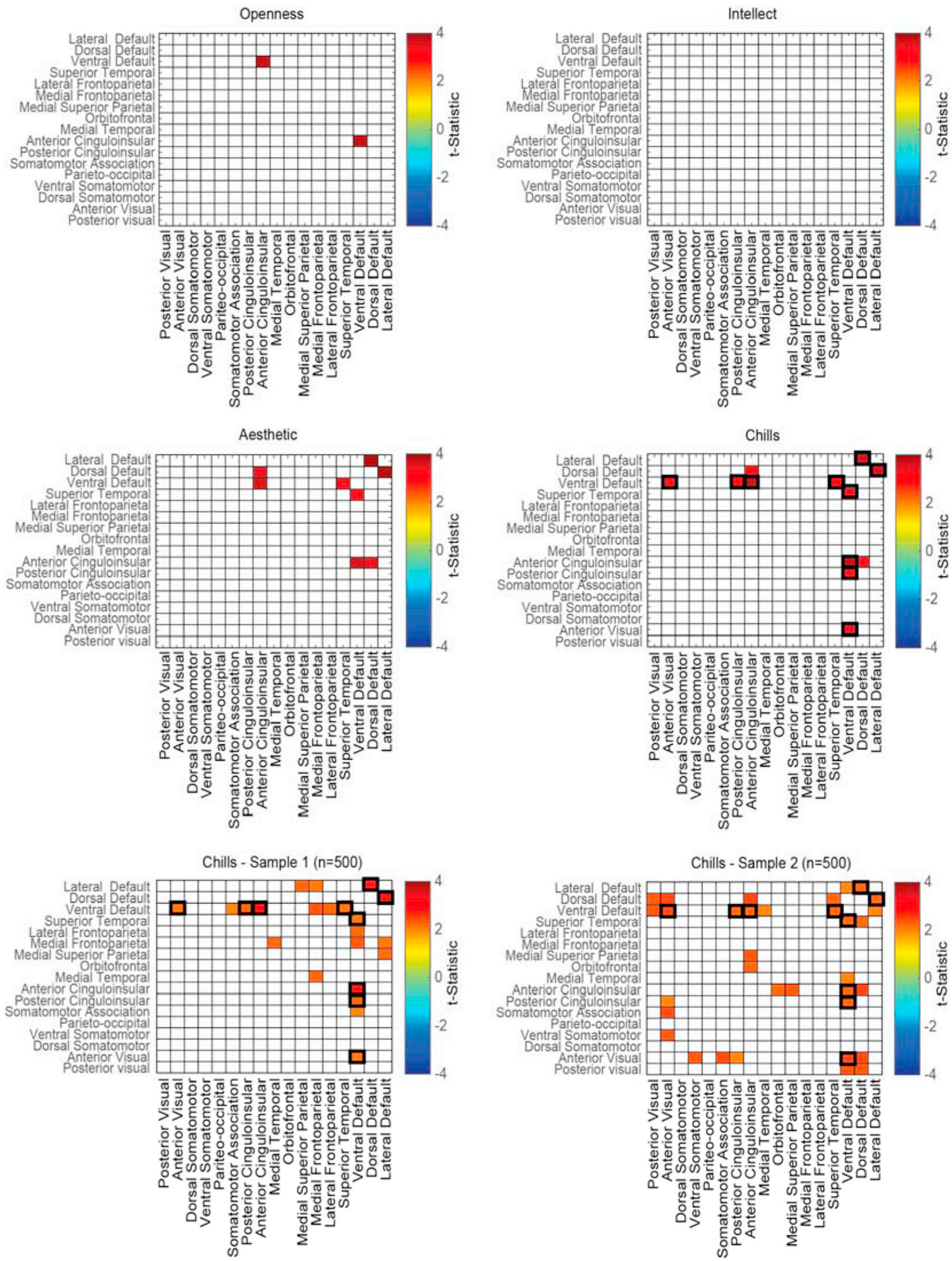

Fig. 1. Functional network connectivity between pairs of 17 brain networks and personality metrics. Color scale shows t-statistic, with significant network pairs showing $p < 0.05$, corrected, for full sample analyses and $p < 0.05$, uncorrected, for split sample analyses (bottom). Age, sex, and mean head motion were included as subject level covariates in all analyses. Black squares show connections in common across samples. Network names are descriptive based on functional regions present. The networks are listed in the same order as in Yeo et al. (2011).

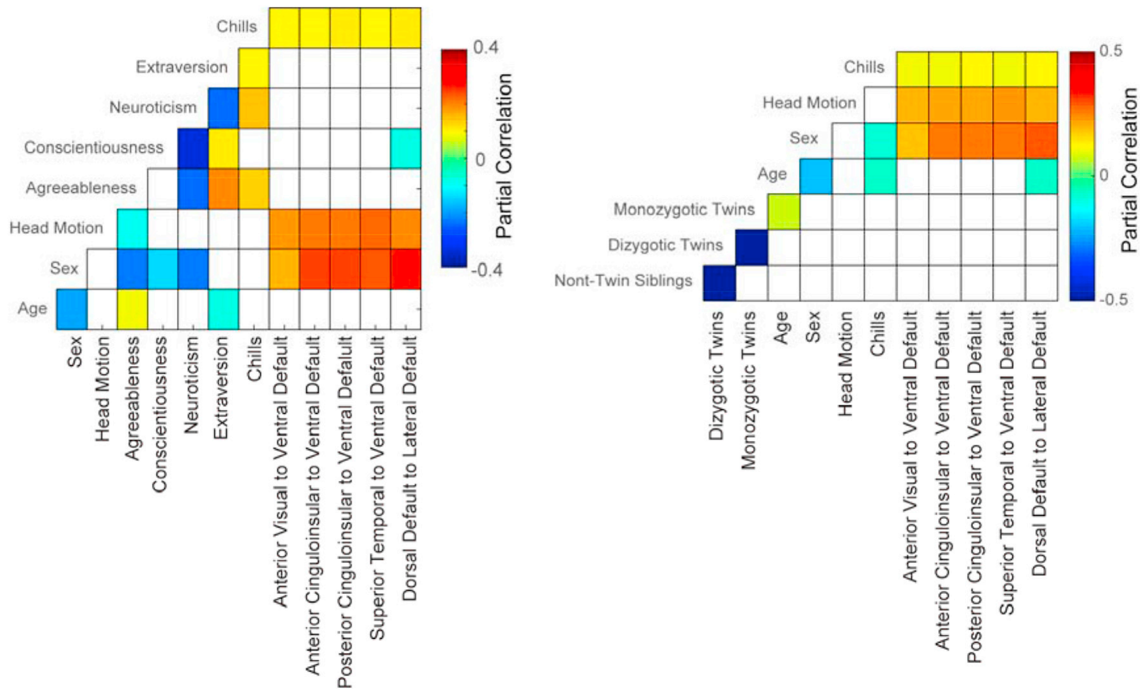

Fig. 2. Partial correlation of functional network connectivity between 5 pairs of networks, personality metrics, and twin status. Color scale shows partial correlation, with significant associations showing $p < 0.05$, corrected. Age, sex, and mean head motion were included as subject level covariates in all analyses and personality factors (left) and twin status (right) were additionally included. Functional connectivity results were included one at a time in a model with other factors because of similarity of functional connectivity results to each other across subjects.

Table 3
Partial correlations among reported aesthetic chill and covariate variables.

Variable	1	2	3	4	5	6	7
1. Chills							
2. Extraversion	.09**						
3. Neuroticism	.14***	-.24***					
4. Conscientiousness	-.05	.11***	-.34***				
5. Agreeableness	.13***	.19***	-.25***	.06*			
6. Head Motion	-.02	.05	-.02	.03	-.09**		
7. Sex	-.03	.01	-.23***	-.15***	-.24***	-.01	
8. Age	-.07*	-.08*	-.03	.01	.08*	.03	-.19***

Sex: 0 = Female, 1 = Male.
*p < .05, **p < .01, ***p < .001.

Table 4
Partial correlations of reported aesthetic chill and covariate variables with functional connectivity.

Variable	AV-VD	AC-VD	PC-VD	ST-VD	DD-LD
1. Chills[a]	.10**	.09**	.10***	.09**	.11***
2. Extraversion[b]	.05	.06	.03	.04	-.00
3. Neuroticism[b]	.01	.02	.04	-.00	-.00
4. Conscientiousness[b]	-.04	-.05	-.04	-.05	-.08*
5. Agreeableness[b]	-.03	-.03	-.02	-.03	.00
6. Head Motion	.19***	.21***	.20***	.22***	.20***
7. Sex	.16***	.24***	.25***	.23***	.27***
8. Age	-.01	-.01	-.02	-.00	-.06

AV = Anterior Visual, VD = Ventral Default, AC = Anterior Cinguloinsular, PC = Posterior Cinguloinsular, ST = Superior Temporal, DD = Dorsal Default, LD = Lateral Default.
Sex: 0 = Female, 1 = Male.
*p < .05, **p < .01, ***p < .001.
[a] Partial correlation controlling for the other four personality factors, sex, age, and head motion.
[b] Partial correlation controlling for sex, age, and head motion.

edges in the component are not necessarily significant.

To assess which brain regions contribute toward the component, ROIs were clustered so that regions showing similar patterns of functional connectivity vs. chills across the brain were placed in the same cluster using an infomap algorithm. T-Statistics for functional connectivity vs. chills are shown in Fig. 4, grouped by cluster. The largest cluster consists of primary sensory and motor regions (auditory, visual, somatosensory and somatomotor) as well as regions of the salience network (anterior insula, anterior cingulate). Other clusters include regions of the ventral attention network (clusters 2 and 3), cerebellum and right striatum (cluster 4), inferior temporal and posterior frontal cortex (cluster 5), regions of the default network (cluster 6), frontal pole and angular gyrus (cluster 6), and anterior temporal poles (cluster 8). Similar to the results in Fig. 1, connectivity patterns with respect to chills identify increased connectivity between sensory cortex, cinguloinsular, and default network regions. The maximal connected component also exhibits decreased connectivity between the cerebellum and areas of cluster 1 (sensorimotor cortex and salience network).

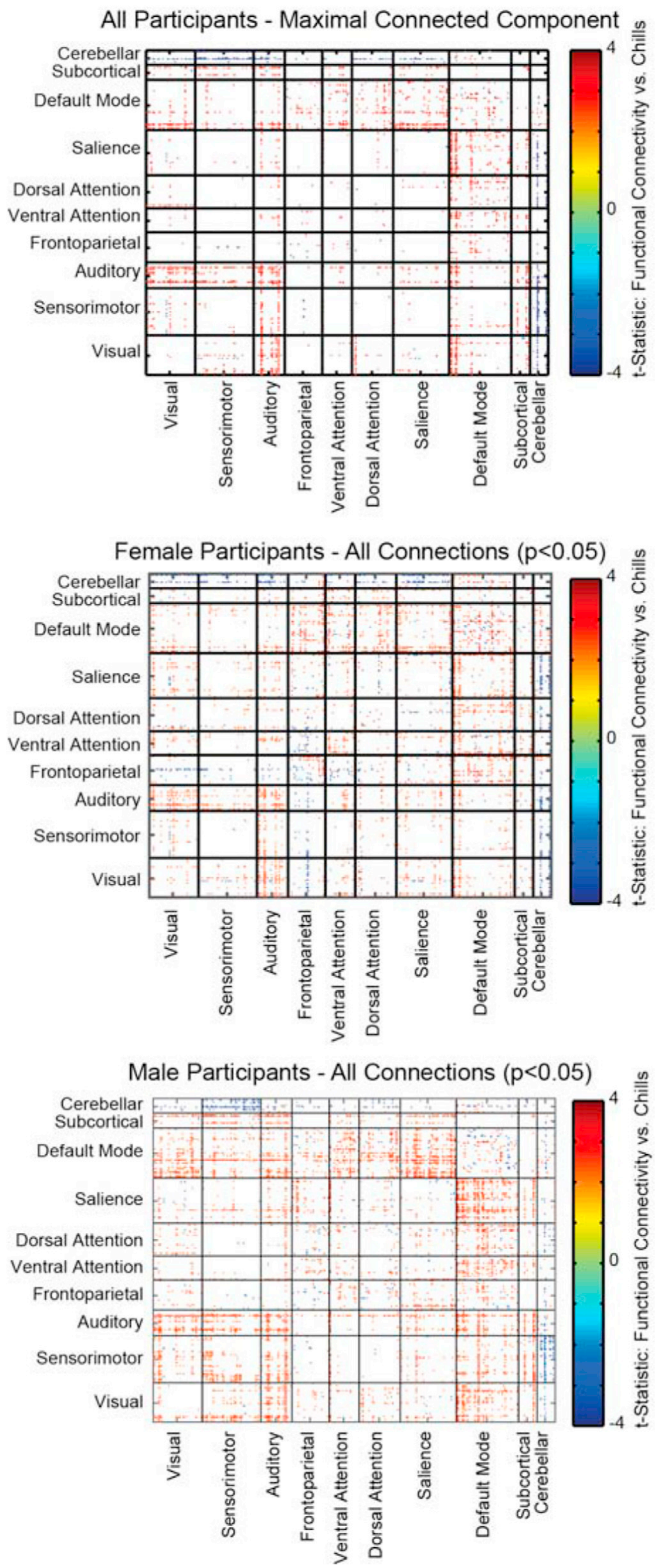

Fig. 3. Functional connectivity between pairs of 361 gray matter ROIs was compared to sensitivity to chills, with colored squares showing connections with $p < 0.01$. Only connections belonging to a maximal connected component are colored above, and all connections are shown with $p < 0.05$ for female and male cohorts below. Color scale represents t-statistic for functional connectivity vs. chills, with age and head motion as subject-level covariates.

Discussion

What underlies the propensity to be moved by art, nature, and beauty? And why would such propensity confer health benefits and, potentially, stress resilience? Using data obtained from 1000 participants of the Human Connectome Project (Van Essen et al., 2013), we find that individual differences in aesthetic engagement, and particularly proneness to aesthetic chills, are associated with functional connectivity in several brain networks. Individuals reporting higher aesthetic engagement and chill exhibited significantly higher connectivity between the default network and sensory and motor cortices, higher connectivity between the ventral default and salience networks, and decreased connectivity between the cerebellum and somatomotor cortex. The default network, which is thought to process internal narrative and cognition, may therefore be more integrated with neural representations of sensory perception and salience detection, suggesting a mechanism for aesthetic appreciation and peak emotional experiences to aesthetic stimuli.

Findings are consistent with the notion that aesthetic engagement and proneness to aesthetic chill may reflect a more general ability to integrate perception of environmental stimuli with internal emotional experience. Indeed, Openness to Experience, the overarching personality factor including these individual differences has been described as reflecting absorption in and motivation to "enlarge" sensory experiences (McCrae and Sutin, 2009). Current findings using a network-level analysis extend previous RSFC studies of Openness that have implicated the default and salience networks (Adelstein et al., 2011; Beaty et al., 2016; Passamonti et al., 2015) and demonstrate the specificity of the Aesthetics component (vs. Intellect) of Openness (Fayn et al., 2015). This specificity is perhaps not surprising, given the relatively high heritability estimates of the Aesthetics facet (McCrae et al., 2010). Findings are also consistent with the hypothesized association between Openness and the salience coding dopamine system (DeYoung, 2013), as well as research linking Openness to the temperament dimension "orienting sensitivity" (Evans and Rothbart, 2007). Although caution should be exercised in inferring mental states from neuroimaging findings (e.g., Poldrack, 2011), the greater connectivity of parahippocampal components of the DMN to the salience network could be interpreted to suggest that strong associations between aesthetic/sensory stimuli and emotion are encoded in memory and may contribute to the propensity to feel "moved" by such stimuli.

It is important to note that awe, the prototypical emotion associated with Openness and aesthetic engagement, is characterized as a unique combination of positive and negative affect (Keltner and Haidt, 2003). Moreover, aesthetic chill involves a sympathetic nervous system response, especially skin electrodermal responses (note that piloerection—hair standing up on the skin—is often seen in response to threat in animals [see Benedek and Kaernbach, 2011]) and pupil dilation (Laeng et al., 2016). Current findings, along with the prior literature, suggest that aesthetic engagement reflects a unique neural architecture that facilitates connecting physiology typically seen in a stress response to a combination of negative and positive affect, ultimately leading to expansive cognitive-emotional states. Prototypical stimuli known to evoke awe and aesthetic chill are characterized by "vastness" and a "need for accommodation" (Keltner and Haidt, 2003). In other words, these types of stimuli are novel to the point of being cognitively challenging. Having these experiences frequently may serve a "stress inoculation" function — repeat experience and comfort with mildly challenging stimuli that ultimately lead to enlarged cognition and peak emotions. The findings of the current study suggest that these individual differences are reflected in greater integration of sensory perception, environmental "salience," and self-referential processing.

Although previous network-level examination of RSFC in relation to aesthetic engagement has been limited, a number of other studies have reported similar patterns that may inform current findings. For example, increased DMN to other networks has been found after psilocybin use, interpreted as decreasing the distinction between externally-focused attention and introspection (Roseman et al., 2014). Notably, psilocybin

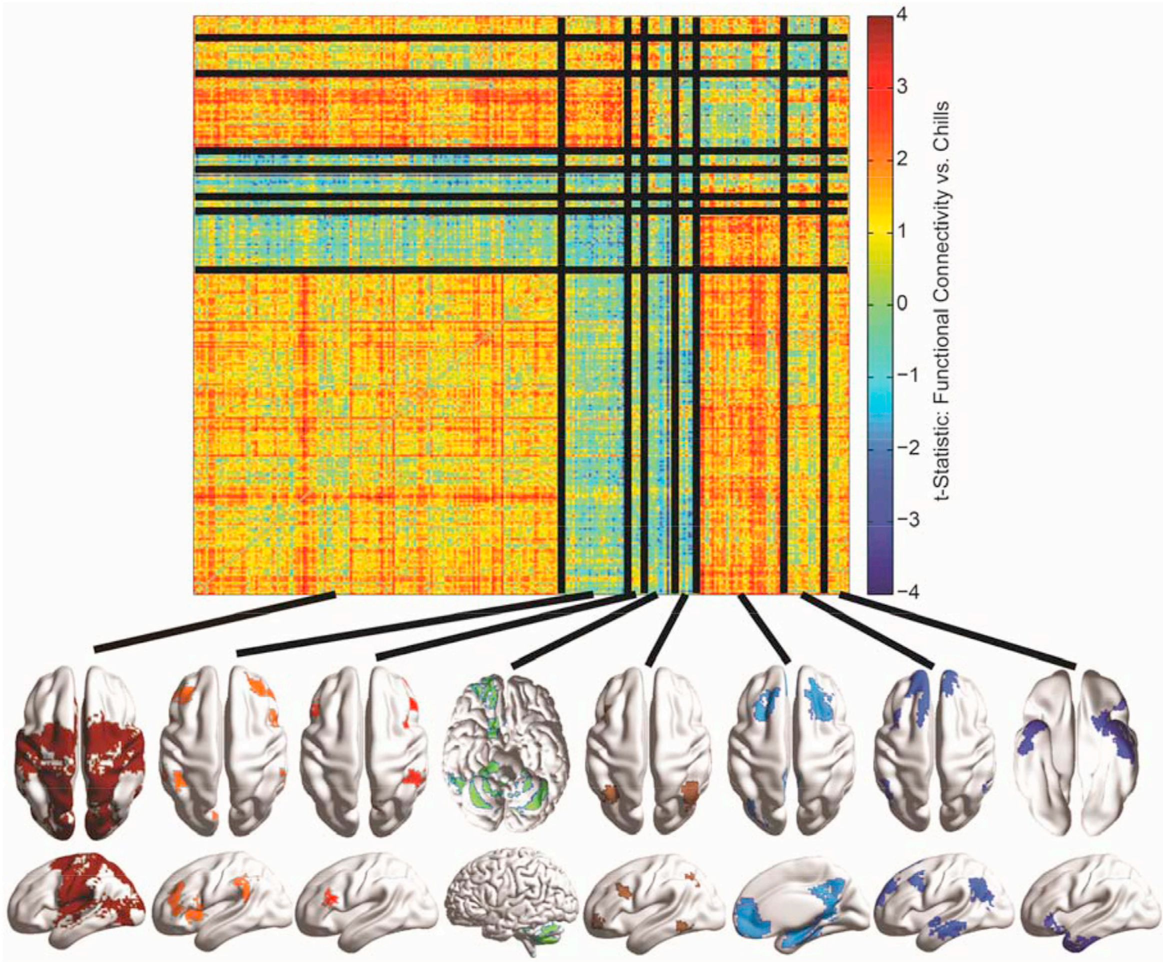

Fig. 4. Clustering of maximally connected component. For all ROIs included in the maximally connected component showing differences in connectivity with respect to aesthetic chills, a clustering was performed that grouped ROIs showing similar t-statistics of connectivity vs. chills with respect to the other ROIs. The brain regions comprising each of the 8 nontrivial components are shown in the images below, and t-statistic of functional connectivity vs. chills for each pair of ROIs is shown in the pseudocolor plot above, grouped by component.

exposure has been shown to increase Openness to Experience (MacLean et al., 2011). Increased functional connectivity between the DMN and sensory areas have also been found following mindfulness training (Kilpatrick et al., 2011). In addition, individual differences in the autonomous sensory meridian response—tingling on the scalp and neck in response to specific visual and auditory stimuli, accompanied by low-arousal positive emotions—have also been linked to increased RSFC between the DMN and visual resting state networks (Smith S.D. et al., 2017). Emotional awareness, the ability to understand and articulate emotions and a construct related to Openness (Lane et al., 1990), is associated with greater RSFC of the default mode and salience networks (Smith R. et al., 2017). Related, individual differences in creativity have been associated with greater RSFC across the default mode, salience, and executive networks (Beaty et al., 2018). In sum, individual differences in aesthetic engagement may demonstrate similar neural architecture to conceptually related characteristics, as well as the resultant changes from profound cognitive experiences and attentional training.

The weakened connection between the cerebellum and somatomotor cortex related to reported aesthetic engagement was not expected. It is possible that this pattern of connection contributes toward paroxysmal motor movements associated with chills, given a role for the cerebellum in motor control and coordination as well as sensory perception (Paulin, 1993). Research informing an interpretation of the reduced cerebellar-somatosensory connectivity is sparse; however, there is evidence supporting *increased* functional connectivity between these regions in populations with autism (Khan et al., 2015), ADHD (Kucyi et al., 2015), and schizophrenia (Shinn et al., 2015). Notably, such conditions are marked by defects in the interaction between attentional processes and internal or external environmental stimuli. Current findings, along with these prior studies, suggest that network-level cerebellar connections may play a role in individual differences in attention and processing of sensory information.

Strengths, limitations, and conclusions

The current study utilized the large-scale Human Connectome Project database, adding to the existing literature of smaller-sample studies of related individual differences. The network-level approach to examining RSFC offers the advantage of probing complex inter-regional brain dynamics that may identify network-level architecture of brain function (Zalesky et al., 2010). Although the effect sizes were modest, this was a very conservative test of the construct, given the use of the brief form of the NEO. Further, the use of the large, nationally representative HCP sample meant that the full continuum of personality individual differences was better captured compared to smaller studies, presumably providing a more accurate estimate of the association with neural architecture. Future research should examine aesthetic engagement more broadly and confirm propensity to aesthetic chill using laboratory-based methods. Indeed, the specificity of the connectivity patterns in the current study suggests that the findings may reflect a neural basis of chill responses to beauty uniquely, as opposed to Openness more generally. Future data collection in large scale imaging projects, such as the HCP, would also benefit from the use of full scale personality assessment, as well as informant reports of personality. Finally, the HCP sample is relatively young and healthy; generalization of findings to older adults should be made cautiously.

Examination of RSFC informs our understanding of potential neural architecture mechanisms underlying individual differences in aesthetic engagement and chill. Findings suggest that aesthetic engagement, an individual difference factor found previously to predict stress regulation and positive health outcomes, may derive from greater integration of sensory processes with self-reflection. An emerging question is whether increasing Openness in general, and aesthetic engagement in particular, may enhance stress-related restoration in the short term and/or improve stress resilience in the long term. Stress management approaches continue to focus primarily on reduction of negative events and responses to those events. There is reason to believe that exposure to aesthetic experiences may be a useful addition to traditional stress management strategies. Based on current findings, future research should examine whether such exposure results in neural architecture alterations that facilitate comfort with novelty, self-regulation, and positive adaptation to potentially stressful events.

Declarations of interest

None.

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