The neural determinants of abstract beauty

Samuel E. Rasche [1,*], Ahmad Beyh [1,*], Marco Paolini [2], Semir Zeki [1,†]

[1] *Laboratory of Neurobiology, Division of Cell & Developmental Biology, University College London, London, UK*
[2] *Department of Radiology, University Hospital, Ludwig-Maximilians-Universität, Munich, Germany*
* *Contributed equally to this work.*
† *Corresponding author.*

Abstract

Using functional magnetic resonance imaging (fMRI), we have enquired into the neural activity which correlates with the experience of beauty aroused by abstract paintings consisting of arbitrary assemblies of lines and colours. During the imaging experiments, 18 subjects viewed and rated 120 images of abstract paintings according to how beautiful they perceived them to be. There was a low agreement on the aesthetic classification of these paintings among participants. In contrast, a re-analysis of behavioural data from our previous study on face beauty revealed a much stronger inter-subject agreement for faces compared with abstract art. Representational similarity analysis (RSA) revealed that the experience of beauty when viewing abstract paintings correlated with the emergence of decodable patterns of activity in visual areas implicated in the processing of lines and colours (V1 through V4). Additionally, a parametric univariate analysis revealed higher activity in medial frontal cortex with higher aesthetic appeal. Both univariate and multivariate analyses of the imaging experiments gave broadly similar results to those obtained in previous studies on facial beauty. With abstract art, it was the involvement of visual areas implicated in the processing of lines and colours while with faces it was of visual areas implicated in the processing of faces. Both categories of aesthetic experience correlated with increased activity in medial frontal cortex. We conclude that, as with the experience of beauty in human faces, it is fundamentally the co-operative activity in these two geographically and functionally distant areas of the brain that is the basis for the experience of beauty. Further, this co-operation is enabled by "experience dependent" functional connections, in the sense that currently the existence and high specificity of these connections can only be demonstrated during certain aesthetic experiences. This does not exclude a role in aesthetic experiences for other areas which our imaging experiments have also revealed. We also conclude that the sensory areas of the visual brain have the additional role of participating in the selection of stimuli according to certain significant configurations which make them aesthetically appealing to the observer.

Keywords: neuroesthetics, beauty, abstract art, representational similarity analysis, experience-dependent brain connections

INTRODUCTION

What are the qualities in an object that arouse the sense of beauty, or what Clive Bell (1914) termed the "aesthetic emotion"? Yang et al. (2022) addressed this question by enquiring into the determinants of one of the most common sources of beauty, namely facial beauty. Features such as symmetry, proportion, and mathematically defined precise relationships between its constituent parts, have been posited by many, including leading artists such as Polykleitos and Leonardo Da Vinci, to be fundamental determinants of facial beauty, in the sense that without these biologically determined and inherited characteristics a face cannot be qualified as beautiful (Zeki, 2009; Zeki and Chén, 2020). But even though essential, these characteristics are not in themselves necessarily sufficient to render a face beautiful: there is, in addition, another, or other, unknown and mysterious characteristics that do so. What can they be? The Yang et al. (2022) study revealed that, when a face is perceived as beautiful and only then, a detectable neurobiological imprint in the form of particular decodable activity patterns emerges in sensory face-processing areas of the visual brain. The emergence of such decodable patterns correlates with the emergence of parallel decodable patterns in another part of the brain – the medial frontal cortex – in which activity always correlates with the experience of beauty, regardless of source (Ishizu and Zeki, 2011; Kawabata and Zeki, 2004). For faces at least, it is seemingly the joint activity of both components – the sensory on the one hand and the emotional on the other – that lies at the basis of the experience of beauty.

Facial beauty has been classified as belonging to the biological category of beauty (Zeki and Chén, 2020). In the present study, we ask the same question of artifactual beauty, that is, beauty generated by human agency. Many artists, including those belonging to the schools of Abstract Expressionism, Neo-Plasticism and Russian Constructivism, considered that particular arrangements of lines and colours result in aesthetic experiences and consequently made such arrangements central to their art. The English art critic, Clive Bell, believed that "…lines and colours combined in a particular way [to produce] certain forms and relations of forms, stir our aesthetic emotions"; he did not specify what these particular combinations may be but argued that, "It need be agreed only that forms arranged and combined according to some *unknown and mysterious* laws do move us in a particular way and that it is the business of the artist to combine

and arrange them that they shall move us" (Bell, 1914) (our emphasis). Thus, there is, in abstract paintings that arouse the aesthetic emotion, a mysterious and ineffable quality, just as there is in faces. Could that mysterious element also be represented in the form of decodable patterns in sensory areas of the visual brain that process lines and colours, just as happens in sensory face-processing areas when faces that arouse the aesthetic emotion are viewed? And would the emergence of decodable patterns in these sensory areas also correlate with the parallel emergence of decodable activity in medial frontal cortex, thus mirroring the pattern of brain activity during the experience of facial beauty? If so, an overall plausible interpretation would be that, whatever the mysterious qualities that endow stimuli, irrespective of their provenance, with the capacities of arousing the aesthetic emotion of beauty, they are represented in detectable patterns within the sensory areas that are specialized for processing the category of stimuli as well as increased activity within the medial frontal cortex.

To avoid confusion, we begin by giving a brief terminological guide to the area of activation in medial prefrontal cortex. The exact location of activations there has varied across studies of the neural correlates of beauty, and different anatomical terms have been used to refer to the location in the literature, including medial orbitofrontal cortex (mOFC), medial prefrontal cortex (mPFC), ventromedial prefrontal cortex (vmPFC). Ishizu and Zeki (2011) addressed this point and suggested that the region of medial frontal activations related to aesthetic experiences be labelled 'field A1', a functionally defined region which does not necessarily obey anatomical or cytoarchitectonic boundaries; field A1 has its centre at Montreal Neurological Institute (MNI) coordinates [-3 41 -8] mm and a diameter of 15-17 mm. In light of our present studies and those of others, we suggest that the boundaries of A1 be expanded, especially ventrally, to include other areas implicated in the experience of beauty reported in other studies (e.g., Tsukiura and Cabeza, 2011). We believe that this variability is largely caused by fMRI signal quality in that region of the brain, especially across studies using different scanners and acquisition parameters (Weiskopf et al., 2006). We therefore discuss our activations here in terms of field A1.

For this study, we expected that visual areas reported to have large concentrations of orientation-selective and colour selective cells will be active, namely, V1-V4 (including areas V3A and V3B) as well as areas in the intraparietal sulcus (Brouwer and Heeger,

2009, 2013; Cheadle and Zeki, 2014; Hubel and Wiesel, 1968; Montaser-Kouhsari et al., 2007; Zeki, S, Perry, RJ and Bartels, 2003; Zeki, 1978; Zeki and Stutters, 2013), *inter alia*. This would lead to the conclusion that the co-operative emergence of these decodable activities in both sensory areas and in field A1 constitutes the neural selection of objects with qualities that lead to the arousal of the aesthetic emotion and hence the experience of beauty. The experiments that we report here addressed questions based around these issues.

METHODS

Participants

18 healthy subjects (11 females, 7 males; ages 20-31 years, mean age 26.5 ± 3.2) participated in the study; all were right-handed and had normal or corrected-to-normal vision, all gave informed consent, and none was an artist or had art expertise. The experiment was approved by the ethical committee of Ludwig-Maximilians-Universität Munich (LMU) where the imaging experiments were conducted.

Stimuli

The stimuli consisted of 120 images of abstract paintings. The images were obtained from one of our previous studies (Bignardi et al., 2020) and additional paintings were selected from stock image websites. To ensure that the set contained enough paintings belonging to the three categories of "not-beautiful", "average", and "beautiful", a pilot study was undertaken in which 11 participants rated the paintings. The stimuli were scaled to 500 × 500 pixels, presented in their original colour, and were not cropped or modified. The task was programmed in the ''Presentation'' software package (Neurobehavioral Systems, Inc., Albany, CA). We excluded iconic paintings and schools, such as those of the De Stijl school, Russian Constructivists and Suprematists as well as works belonging to artists such as Barnet Newman and Rothko, which contain colours, oriented lines, and edges but which are easily recognizable as belonging to particular artists or schools.

Procedure

Participants were presented with 120 images of abstract paintings inside the MRI scanner and asked to rate them on a scale from one to seven, one corresponding to not beautiful at all and seven to very beautiful. Pressing the left button on a customized button box decreased the rating, while pressing the right button increased it, starting from the neutral rating of four at each trial. The task followed an event-related design in which the stimulus was presented for a duration of 2 s and participants had 4.5 s to respond (Figure 1). The scanning consisted of five fMRI runs, each containing 24 trials. This, in addition to structural scans, amounted to a total scan time of 45 minutes for each subject. After scanning, subjects were asked to complete a 15-minute questionnaire in which the same paintings were rated on familiarity, valence, arousal, and beauty.

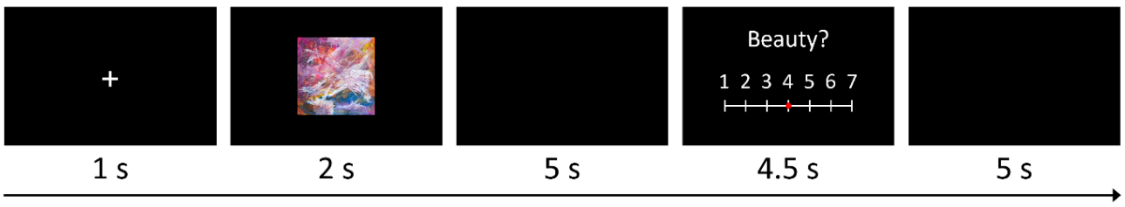

Figure 1. Experimental design.

Each trial started with a 1 s fixation cross, followed by a 2 s stimulus presentation, which was followed by a 5 s blank screen. Subjects then rated the stimulus on aesthetic appeal within 4.5 s on a scale from 1 to 7 (1 – not beautiful at all, 7 – very beautiful). Responses were followed by a 5 s blank screen, amounting to a total trial time of 17.5 s. Each fMRI run consisted of 24 trials, yielding a total of 120 trials.

Image acquisition

Brain images were collected at the University Hospital of the LMU on a 3.0 T Philips Ingenia scanner (Philips Healthcare, Best, The Netherlands). Structural images were acquired with a T1-weighted scan: repetition time (TR) = 9.74 ms; echo time (TE) = 5.66 ms; flip angle = 8°; matrix of 256×256; field of view = 256 mm; voxel size = 1×1×1 mm^3. The blood oxygen level dependent (BOLD) signal was measured with a T2*-weighted Echo Planar Imaging (EPI) sequence: TR = 2500 ms; TE = 30 ms; flip angle = 90°; ascending acquisition; matrix of 80×80; voxel size = 3×3×3 mm^3. A total of five fMRI runs were acquired. Field mapping data were also acquired using a dual-echo GRE sequence to assist with susceptibility distortion correction.

Image preprocessing

The T1w image of each subject was skull-stripped using *optiBET* (Lutkenhoff et al., 2014), bias field corrected (Tustison et al., 2010), and rigidly aligned, using *flirt* (Jenkinson et al., 2002), to the 1 mm MNI T1w brain template (Fonov et al., 2011) as a substitute for AC-PC alignment. This aligned image served as the anatomical reference for subsequent pre-processing of functional images. Additionally, it was normalised to the same MNI template through affine and non-linear transformations (SyN algorithm), computed using ANTs (Avants et al., 2011).

Functional images were first corrected for motion and slice-timing differences using SPM12 (http://www.fil.ion.ucl.ac.uk/spm/software/). The corrected images were then simultaneously corrected for geometric distortions (using the acquired field map) and aligned to the T1w image using FSL's *epireg* tool (Greve and Fischl, 2009; Jenkinson et al., 2002), while maintaining the voxel size at 3×3×3 mm^3. This produced the final fMRI time series images which were used in subsequent modelling steps.

Image space and spatial smoothing

In this study, we analyse the data following the univariate and multivariate frameworks; both rely, in the first instance, on a subject-level (first level) model fitting using the general linear model (GLM). To this end, all first-level analyses were performed in each subject's native space without any image smoothing. For univariate analyses, first-level contrast images were spatially normalised to MNI space (at 3 mm) then smoothed with a Gaussian kernel of a FWHM of 4.5 mm before running the group analysis. For the multivariate analyses, only spatial normalisation was performed, and no smoothing was applied. This was crucial to maintain the spatial specificity of the parameter estimates, which is the main feature at the heart of the multivariate framework.

Univariate analyses

A parametric analysis was performed to identify the brain regions in which activity increased linearly with beauty ratings. A standard GLM was fitted to the time series of each subject, with a single task effect (stimulus presentation) and six motion correction parameters as nuisance regressors. The beauty score given at each trial was used as an additional regressor to account for any variability in the brain oxygen level dependent

(BOLD) signal that is not explained by the other seven regressors. All resulting statistics images were thresholded at a voxelwise level of $p < .005$.

In addition, we looked at the deviation from neutrality. A parametric analysis was performed comparing the neutral ratings (all ratings of four) to both 'not beautiful' and 'very beautiful' ratings, in a V-shaped (linear) fashion. In this model, paintings rated as neutral were predicted to lead to the lowest activations, while paintings given non-neutral ratings were predicted to lead to stronger activations that would scale linearly with the deviation from the neutral point.

Finally, a categorical analysis was conducted to compare baseline activity versus three categories – 'not beautiful' (bottom 15 ratings), 'neutral' (all ratings of 4) and 'very beautiful' (top 15 ratings). Again, a GLM was fitted to each subject's data, with six additional nuisance regressors. The 5 s black screen at the end of each trial was used to register baseline activity.

Multivariate analyses

To investigate whether the experience of abstract paintings as beautiful is associated with specific spatial patterns of neural activity, we used representational similarity analysis (RSA) (Kriegeskorte et al., 2008). To this end, we started by running a GLM in which each trial was treated as an independent condition, thereby generating a parameter estimate (beta) map for each trial. The beta maps corresponding to each subject's 10 highest and 10 lowest rated paintings were selected, and a whole-brain searchlight analysis was performed using cubic regions of interest (ROI) of 3×3×3 voxels. This allowed us to estimate the patterns of neural activity associated with these trials in grey matter. For each searchlight ROI, both the Euclidean distance and Pearson correlation distance were calculated between the patterns associated with these trials. Neural representational dissimilarity matrices (RDMs) were then generated for each subject to capture the (dis)similarity between pairs of trials at each searchlight ROI.

To test whether the similarity was significant only for beautiful trials, the mean group RDM was calculated for each searchlight ROI, and these mean neural RDMs were then compared to a model RDM. The correlation between the neural and model RDMs was assessed with the Spearman rank correlation metric, the statistical significance of which was assessed by way of permutation testing (5000 permutations of the trial labels). This

allowed to us to generate voxelwise correlation and significance maps which could be visually assessed for the purpose of anatomical localisation.

The model RDM assumed a high similarity in the activity patterns associated with viewing beautiful paintings (i.e., a low dissimilarity value), and no similarity when viewing paintings which were deemed not beautiful or between the patterns of beautiful and not beautiful paintings (i.e., a higher dissimilarity value).

Psychophysiological interaction analysis

To further explore the relationship between field A1 and the rest of the brain in the context of aesthetic experiences, we conducted a psychophysiological interaction (PPI) analysis (Friston et al., 1997). A PPI analysis examines how the interaction between two neuronal systems (physiological) is influenced by a contextual factor (psychological). We examined which brain regions exhibit a significantly stronger functional connectivity with field A1 when subjects experienced beautiful abstract paintings compared with paintings that they did not consider beautiful. We placed a spherical seed region with a six mm radius in field A1. We adjusted the exact location of the seed region for each subject to coincide with the location of their peak activations for the 'beautiful' vs. 'not beautiful' contrast; the mean MNI coordinates of the seed region were [3.9, 52.5, 5.0] mm.

RESULTS

Behavioural results

The mean beauty rating for the abstract paintings was 3.97 (*sd* = 0.70). There was a low mean correlation of $r = 0.16$ (lowest $r = -0.34$, highest $r = 0.61$) when comparing each subject's ratings to every other subject's ratings, indicating that there was little agreement among subjects about each painting's beauty score. Moreover, most paintings received, on average, ratings between three and five, and only few ratings of one and seven (Figure 2a), indicating that subjects were rather ambivalent or indifferent to the stimuli. A one-way ANOVA confirmed a very strong variability in the probabilities of each rating: $F(6,119) = 28.63$, $p < .0001$.

For comparison purposes, we reused behavioural data from a previous study on face beauty (Yang et al., 2022) and ran the same behavioural analyses. This revealed that the agreement among subjects is much higher for faces than it is for abstract art, with a mean correlation of $r = 0.72$ (lowest $r = 0.42$, highest $r = 0.88$), which is in accordance with previous studies (Bignardi et al., 2020). Further, it showed that the distribution of ratings when subjects judged the aesthetic appeal of faces was more evenly spread across the rating scale (Figure 2a). A one-way ANOVA confirmed a weak variability in the probability of each rating: $F(6,119) = 2.63$, $p = .01$. This variability was explained by the lower probability of the occurrence of extreme scores (one and seven). This was confirmed by a one-way ANOVA conducted on ratings two through six (excluding the extreme scores of one and seven): $F(4,85) = 0.33$, $p = .86$ (n.s.).

These results suggest that subjects are more specific and critical in their aesthetic judgment of faces compared to abstract art. To confirm this, we ran a two-way ANOVA to assess whether there was an interaction between stimulus category (faces vs. abstract art) and rating (one to seven) on rating probability. The result confirmed the presence of such an interaction: $F(6,238) = 6.63$, $p < .0001$.

The great variability in the aesthetic ratings of abstract art is also well captured by the distributions of the ratings given by all subjects to the 10 abstract paintings and the 10 faces with the highest and the lowest mean beauty scores (Figure 2b). With faces, the highest rated stimuli (on average) were predominantly given high ratings (higher than the neutral point of four), and those with the lowest mean beauty scores showed a similar trend with most subjects scoring them less than four. However, with abstract art, the highest rated stimuli still received low ratings (as low as one), and the lowest scoring paintings still received scores as high as seven. This indicates that there is greater universal agreement among subjects on the beauty of faces, and much less agreement on the aesthetic status of abstract art paintings. These findings sit well with the theory which proposes a distinction between biological and artifactual stimuli (Zeki and Chén, 2020).

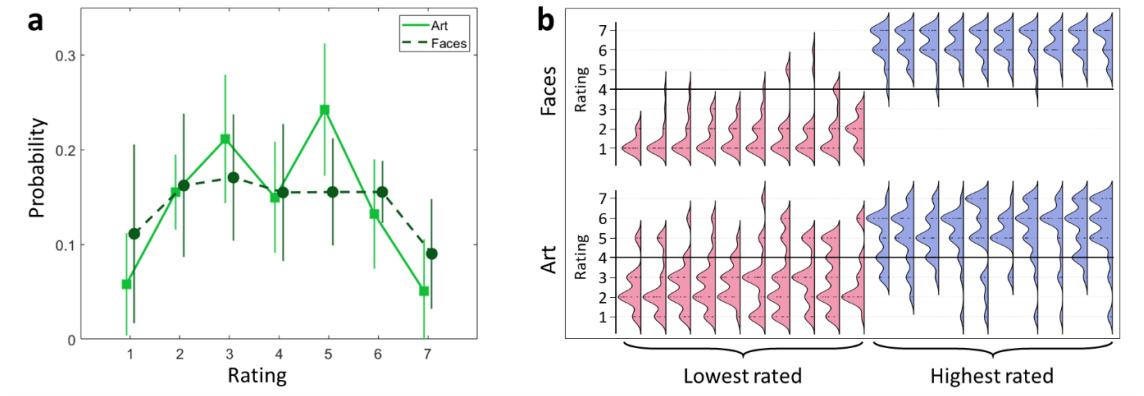

Figure 2. Behavioural results and comparison with data on face beauty.

a) Probability distribution of beauty ratings given for abstract art paintings (this study) and images of faces obtained from Yang et al. (2022). The light green line represents the ratings for abstract art and the dashed dark green line represents the distribution of ratings for faces. The error bars indicate the standard deviation across subjects. **b)** Density plots showing the probability of ratings given to the 10 abstract paintings and faces with the best average (blue) and worst average (pink) scores. Each density plot was constructed using the scores given by all participants for each of these stimuli.

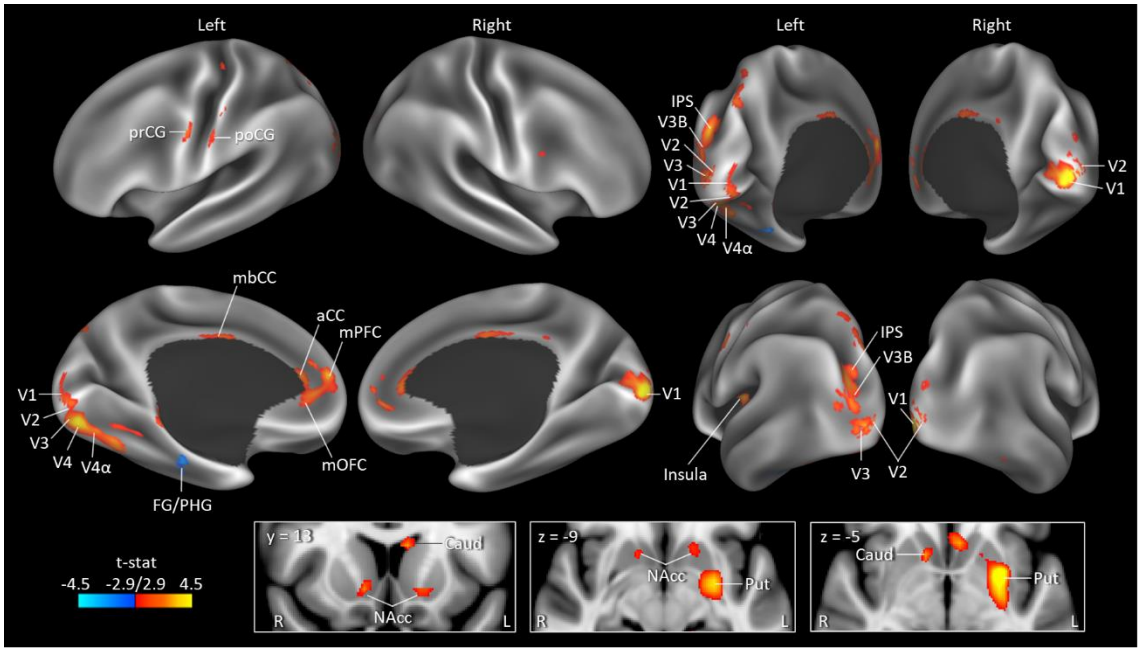

Figure 3. Activations parametrically increasing with beauty.

A linear parametric analysis revealed significant (p_{unc} < .005) increase in activity in visual regions (V1, V2, V3, V4, V4α), intraparietal sulcus (IPS), insula, precentral gyrus (prCG), postcentral gyrus (poCG), mid-body cingulate cortex (mbCC), anterior cingulate cortex (aCC), field A1 (including territories in mPFC and mOFC). There was a decrease in anterior parahippocampal gyrus (PHG) activity as beauty level increased. The bottom three panels show subcortical activations on sections of the MNI template, with the corresponding slice ordinates in the top left of each panel.

CLUSTER AND/OR REGION	VOXELS	T	Coordinates (mm)		
			x	y	z
Activations increasing with beauty					
Early and association visual cortex	1022				
R V1		4.65	15	-99	3
R V1		4.64	9	-99	-3
L V4		4.58	-27	-81	-18
L fusiform gyrus		3.96	-30	-60	-15
Intraparietal sulcus	92				
L IPS0/IPS1		3.91	-18	-81	45
L IPS2		3.27	-24	-69	57
R fusiform gyrus – lateral	13	3.82	42	-45	-12
L fusiform gyrus – lateral	1	2.99	-39	-45	-12
Hippocampus and parahippocampus	36				
L hippocampus – tail		3.68	-21	-42	3
L posterior parahippocampal gyrus		3.64	-15	-36	-9
R posterior parahippocampal gyrus	1	3.03	15	-33	-9
R collateral sulcus / parahippocampal place area	1	2.92	33	-51	-9
Medial frontal region – Field A1	332				
L medial prefrontal cortex		4.22	-9	54	15
Anterior cingulate cortex		3.96	0	36	12
Medial orbitofrontal cortex		3.95	3	48	-3
R anterior orbital gyrus	6	3.28	24	36	-9
Cingulate cortex – mid-body	47	3.81	3	-6	30
R cingulate cortex – posterior body	12	3.13	3	-39	30
L insula / L frontal operculum	22	4.22	-36	-6	18
L sensorimotor cortex	40				
L precentral gyrus		3.95	-60	-3	39
L postcentral gyrus		3.23	-57	-21	54
L inferior frontal gyrus / frontal operculum	16	3.6	-45	9	6
L central sulcus – ventral	9	3.21	-24	-27	51
R precentral gyrus - ventral	7	3.06	48	6	27
L basal ganglia	116				
L Putamen		4.67	-27	0	-6
L Caudate Head		3.77	-6	18	-3
L Nucleus Accumbens		3.28	-18	12	-6
L caudate nucleus	32				
L caudate body		3.77	-12	3	21
L caudate head		3.69	-9	12	15
L caudate body		3.16	-18	-3	18
R nucleus accumbens	13	3.71	12	12	-6
Activations decreasing with beauty					
L fusiform gyrus – anterior	32	-3.79	-36	-24	-24

Table 1. Results of the parametric fMRI analysis.

Significant clusters of the linear parametric modulation with increasing or decreasing aesthetic appeal and their MNI coordinates. The loci were revealed by a one-sample t-test (*df* = 17) at the group level, with a statistical threshold of $p_{unc.} < .005$.

Parametric activations: linear relationship with beauty

A linear parametric analysis of fMRI data with beauty as a modulator, that is, assuming a linear increase in brain activity as a function of increasing aesthetic appeal, revealed significant clusters in visual cortex, the fusiform gyrus, cingulate cortex, field A1 (straddling mOFC and mPFC), inferior frontal gyrus, insula, putamen, body of the caudate nucleus, and ventral striatum (Table 1 and Figure 3). Only one cortical region, the left anterior fusiform gyrus, showed the opposite trend, i.e., linearly decreasing activity as a function of increasing beauty scores.

Parametric activations: deviation from neutrality

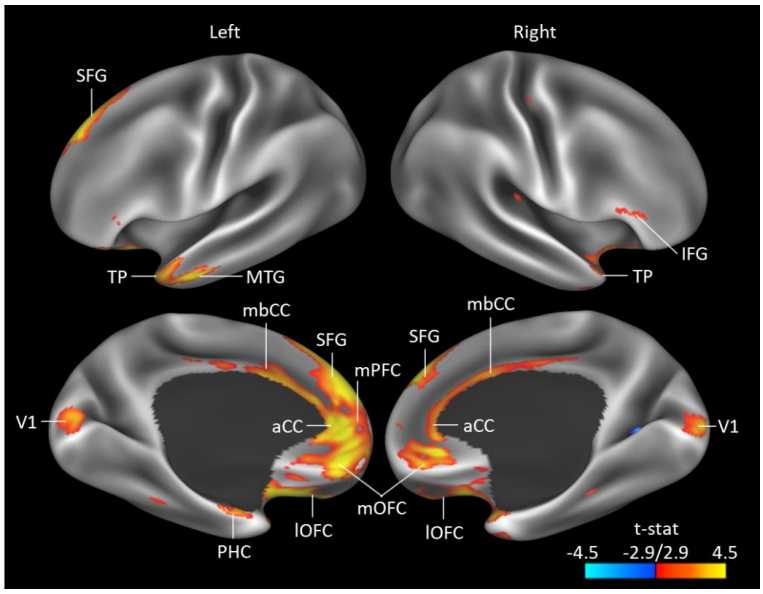

Figure 4. Stronger parametric activations when deviating from neutral ratings.

Significant activations ($p_{unc.}$ < .005) associated with increased deviation in beauty ratings from the neutral point (middle of the scale). Extensive activations are observed in the prefrontal region, including the cingulate cortex, medial prefrontal cortex (mPFC), medial orbitofrontal cortex (mOFC), lateral orbitofrontal cortex (lOFC), superior frontal gyrus (SFG), and temporal pole.

Previous research on the neural correlates of beauty and desire has pointed to a non-linear relationship between the level of the declared experience and BOLD signal changes in medial prefrontal and cingulate cortex (Kawabata and Zeki, 2008; Martín-Loeches et al., 2014; Zeki et al., 2014). To address this question, we also assessed the BOLD signal changes in our study using a parametric analysis that assumed increasing BOLD signals as beauty judgments deviated from neutrality. Our results revealed that a

large portion of the prefrontal cortex (including lOFC, field A1 [mOFC, mPFC], SFG, and frontal pole), cingulate cortex (mid-body [mbCC] and anterior [aCC] cingulate), temporal pole, and V1 showed increased activity with more extreme beauty judgments, both toward the high and low ends of the scale (Figure 4).

Categorical comparisons: task vs. baseline

Next, we sought to assess how activity at different levels of aesthetic appeal compares with activity at rest. To this end, we conducted a categorical fMRI comparison of each of the three categories – 'not beautiful', 'neutral', and 'very beautiful' – against baseline activations. As expected, this revealed extensive increases in activity in the visual cortex for all three categories. Additional common activations included the supplementary motor area (SMA, including the supplementary eye fields), lateral prefrontal cortex, insula, and frontal eye fields (Figure 5).

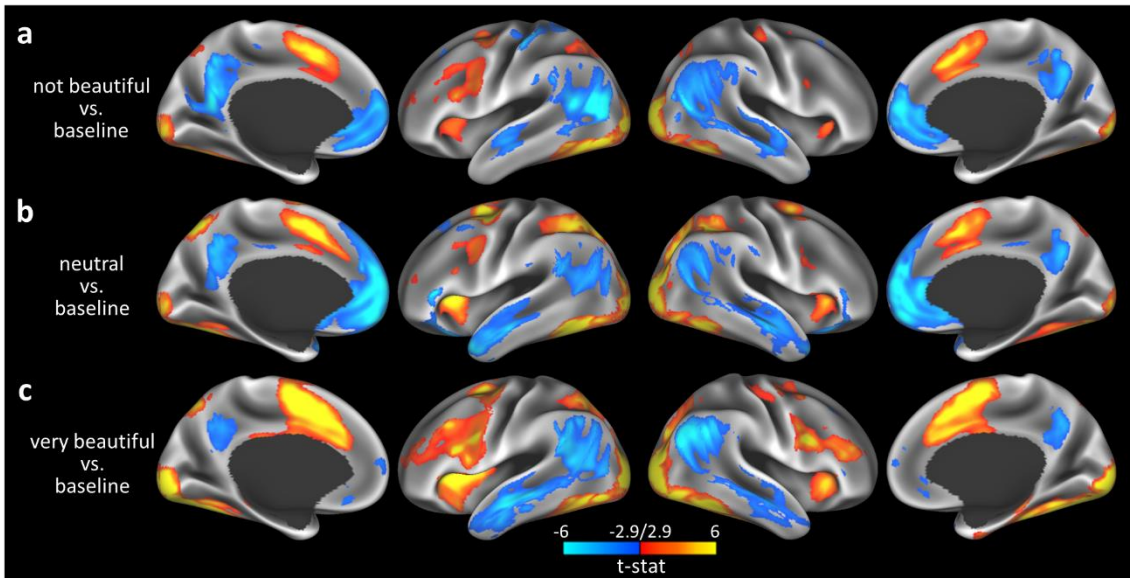

Figure 5. Categorical comparison between task conditions and baseline activity.

BOLD signal changes associated with viewing a) not beautiful, b) neutral, and c) very beautiful abstract art were compared with the baseline signal. All three conditions activate a wide array of cortical regions, including extended visual cortex, the supplementary motor area, frontal eye fields and insula. All visualisations here are significant at $p_{unc.} < .005$.

The largest difference between the three categories was observed in field A1 and the aCC. Specifically, there was a strong deactivation of this region in the 'neutral' condition. The 'not beautiful' condition resulted in a moderate activation, whereas the 'very

beautiful' condition strongly activated this area. These findings have been observed before (Zeki et al., 2014) and agree with the results of the deviation from neutrality analysis reported earlier. It is also worth noting that increased activity was observed in the reticular formation (MNI: [0, -33, -39], t = 4.54) only for the 'very beautiful versus baseline' comparison.

Representational similarity analysis

A whole-brain searchlight representation similarity analysis (RSA) using the Pearson correlation distance revealed clusters in visual areas with common patterns in response to beautiful stimuli. More specifically, Spearman correlations between the neural RDMs for these regions and the model RDM revealed the following significant (p < .0001) correlations after permutation testing: left V3, r = 0.39; left V4, r = 0.49; left precentral sulcus (prcs), r = 0.39; left inferior frontal sulcus (ifs), r = 0.27; right ifs, r = 0.39; left insula, r = 0.36 (Figure 6).

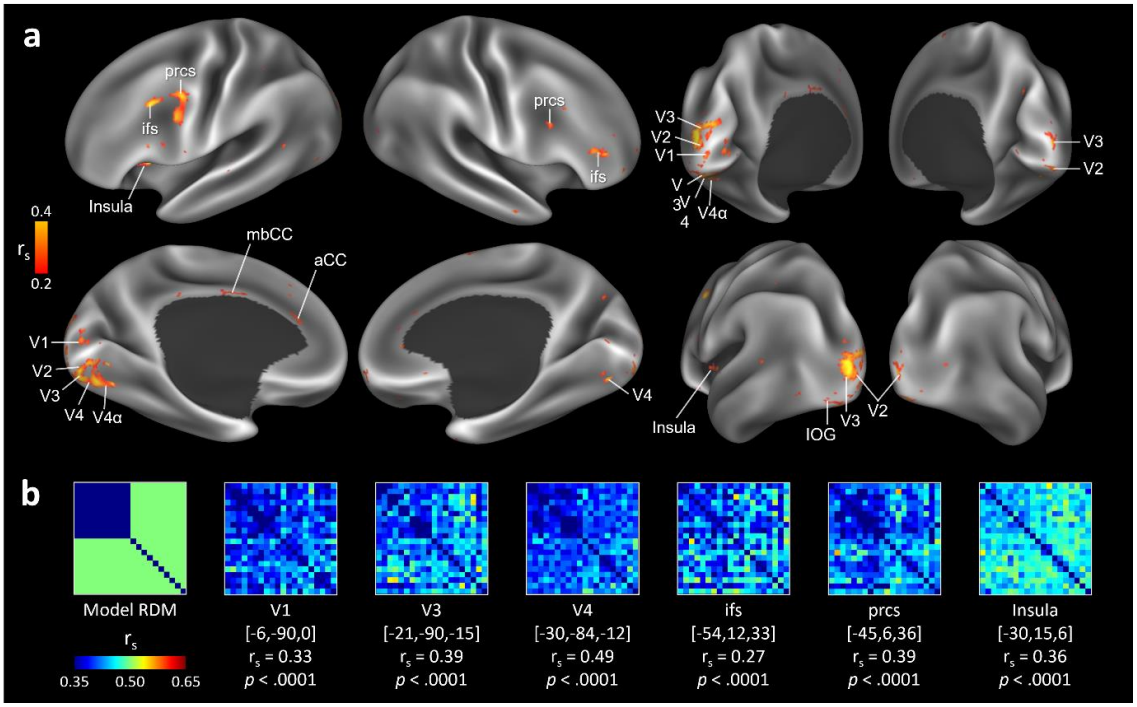

Figure 6. Results of the representational similarity analysis.

RSA results using the Pearson correlation distance metric. A) Brain regions which showed significant correlations (thresholded at r = 0.2) with the model RDM. B) The model RDM (most left panel), which assumes similar patterns for beautiful paintings, and the significantly correlating neural RDM's of V1, V3, V4, the inferior frontal sulcus (ifs), the precentral sulcus (prcs), and the insula. The numbers in square brackets under each RDM correspond to MNI coordinates.

A whole-brain searchlight using the Euclidean distance as a similarity metric revealed clusters in frontal areas including field A1 (r = 0.40, p < .0001) and frontal pole (r = 0.46, p < .0001), and visual areas including V3 (r = 0.41, p < .0001) and the left IOG (r = 0.41, p < .0001). Overall, the only area revealed by both methods was V3, which is known to be important in form perception and contains many orientation selective cells (Larsson and Heeger, 2006; Larsson et al., 2006; Shigihara and Zeki, 2014; Tong et al., 2012; Zeki, 1978, *inter alia*). Note that the Euclidean distance is sensitive to the amplitude of the parameter estimates as well as the spatial pattern of the activations, whereas the Pearson correlation is only sensitive to the spatial pattern (Kriegeskorte et al., 2008). Given that the aim here is to find a specific pattern of activity regardless of amplitude, the Pearson correlation is the preferred distance metric for our purposes.

Psychophysiological interaction

Given that field A1 and sensory areas showed increased activity in the univariate analyses when comparing beautiful versus non-beautiful stimuli, we asked whether the interaction between these areas changed as a function of the level of the aesthetic experience. To this end, we conducted a PPI analysis for each subject with a seed region at MNI coordinates of [3.9, 52.5, 5.0] mm based on the univariate analyses, then ran a one-sample t-test at the group level. The PPI analysis revealed such an interaction; there was increased connectivity between the seed region at one end, and V1, V2, and V3 at the other, when subjects experienced beautiful abstract paintings compared to those that they did not consider beautiful (Table 2).

CLUSTER AND/OR REGION	VOXELS	T	Coordinates (mm)		
			x	y	z
R V1/V2	24	4.72	12	-99	0
R V2/V3	8	3.06	24	-90	15
L visual cortex	92				
L V2/V3		3.32	-15	-96	12
L V1/V2		3.25	-9	-102	6

Table 2. Psychophysiological interaction.

Results of a psychophysiological interaction analysis with a seed region in the field A1, with mean MNI coordinates at [3.9, 52.5, 5.0] mm. The only regions that showed an increased interaction with the seed during the experience of beauty were V1, V2 and V3. The loci were revealed by a one-sample t-test (df = 17) at the group level, with a statistical threshold of $p_{unc.}$ < .005. Coordinates are given in MNI space.

DISCUSSION

Biological vs. artifactual beauty

We enquired into whether the experience of beauty derived from viewing abstract works of art – consisting of arbitrary assemblies of lines and colours – leads to broadly similar neural activity as that resulting from viewing beautiful human faces based on previous studies. Though both can arouse an experience of beauty, the two categories of stimuli differ significantly. While the experience of facial beauty is mediated through inherited or rapidly acquired concepts and is resistant to revision through peer opinion, the experience of works created through human agency, in which we include abstract works of art, is much less resistant to revision in light of peer opinion and is probably not interfaced through any known inherited brain concept (Bignardi et al., 2020; Chen and Zeki, 2011; Glennon and Zeki, 2021; Zeki, 2009; Zeki and Chén, 2020). Yet the fact that they can both arouse the "aesthetic emotion", or the experience of beauty, implies that aesthetic experiences aroused through a combination of lines and colours in abstract paintings may engage broadly similar brain mechanisms. It thus became interesting to learn whether the experience of beauty in abstract works of art would result in decodable activity within sensory visual areas on the one hand and within field A1 on the other.

When we place abstract art in the artifactual category, we do not mean to imply that the constituents that go into making up abstract art may not be the result of inherited physiological mechanisms. It is almost certain, for example, that orientation selectivity is inherited (Zeki and Chén, 2020); but the assembly of lines and colours in different works is not. This is distinct from faces where the constituent elements usually have to take their correct place in an overall composition in order to be recognised as a face.

Consistent with previous results (Bignardi et al., 2020), our present behavioural evidence shows that there is much greater variability in assigning particular abstract works to particular aesthetic categories, making of the experience of beauty in abstract art a more subjective one than the experience of facial beauty. Despite these differences, a similar strategy is used by the brain for the two categories; both involve the emergence of decodable patterns in sensory areas; with facial beauty the decodable activity was in the sensory areas known to be critical for the perception of faces (Yang

et al., 2022), while for beautiful abstract art it was in sensory visual areas known to contain large concentrations of orientation selective and chromatic cells. In addition, both experiences have, as a correlate, decodable activity in field A1.

The neural correlates of the experience of abstract beauty

We compared the neural activity associated with the perception of works of abstract art at three levels of aesthetic experience – 'beautiful', 'neutral', and 'not beautiful' – against baseline activity (Figure 5). All categories engaged a wide array of visual areas, but this engagement was strongest when the stimuli were deemed beautiful, which was confirmed by a parametric activation analysis (Figure 3, Table 1). Further, we observed important differences within the medial prefrontal region: only beautiful stimuli fully engaged field A1, while the other categories did not, or did so to a limited degree. The aesthetic category that resulted in the weakest activations of field A1 was the 'neutral' category. Indeed, when we modelled brain activity following a V-shaped curve in response to beauty ratings, that is, when we looked for increasingly stronger activity with more extreme beauty scores (positive or negative), we found very strong activations in a large swath of medial frontal cortex (Figure 4). This region included field A1 (mPFC and mOFC), the aCC, and medial SFG, among others. This indicates that the medial prefrontal region plays a general role in deciding whether a stimulus is aesthetically evocative, in the positive and negative senses of the word. Within this broad region, the more ventral part, i.e., field A1, is further involved in specifically assigning a positive aesthetic attribute to a stimulus, though we do not intend to imply that that is its only function. We found more support for the specificity of this involvement through a PPI analysis with a seed placed in that region (Table 2): activity in field A1 had a significantly stronger influence on activity in early visual cortex (V1-V3) during the experience of beautiful stimuli compared with those not deemed beautiful. The activated region broadly resembled the activations described by Vessel et al. (2019) as being part of the default mode network. However, the connection between field A1 and these sensory areas is not part of this network, and these same sensory areas are ones in which specific patterns of neural activity emerge only during the experience of beautiful stimuli (Figure 4).

We can draw at least three conclusions from these results.

The selective function of sensory areas

The sensory areas of the visual brain, in addition to the sensory functions attributed to them – of processing visual stimuli according to their specializations – also have the function of selecting stimuli according to certain arrangements of their constituent elements, endowing them with aesthetic appeal. Clive Bell (1914) referred to such arrangements, dictated by "unknown laws" as "Significant Forms"; we prefer to generalise the term and refer instead to "Significant Configurations" (Zeki, 2013); the former term sits uneasily with, for example, harmonious colours or beautiful facial expressions, while the latter term does not.

Our results, and those of Yang et al. (2022) show that the so-called visual "sensory" areas cannot be mere passive recipients of signals related to their specialities. Rather, the ineluctable conclusion seems to be that these sensory areas are also able to distinguish between stimuli according to their aesthetic appeal. This seems to be true regardless of whether the viewed stimuli belong to the biological category (faces) or the artifactual one (abstract art). This is because decodable patterns emerge in the sensory areas only with stimuli that are experienced as beautiful, regardless of category, and it is only when such patterns emerge that there is, as a correlate, activity in field A1.

It is tempting to suggest that it is the emergence of such decodable patterns in sensory areas that engages field A1. We do not do so and deliberately use the term 'as a correlate' instead because, in the absence of temporal studies, we cannot exclude the possibility that field A1 is activated prior to the sensory areas and that the latter are only activated through feedback. A precedent for this may be found in studies which have shown, for example, that activity in the amygdala precedes activity in face-processing sensory areas when fearful stimuli are viewed (Méndez-Bértolo et al., 2016). Whatever the precedence in activity between the sensory areas and field A1, we cannot escape the conclusion that, in addition to registering the characteristics of the stimulus, the sensory areas are also involved – either before, simultaneously with, or after activation of field A1 – in ordering the stimuli according to criteria that give them an aesthetic status. They are therefore involved in a selective process.

Co-activity between sensory areas and field A1 is the basis of the experience of beauty

Our second conclusion is that only under conditions when decodable patterns of activity emerge in sensory areas, with activity in field A1 as a correlate, that the observer experiences stimuli as beautiful. On the sensory side, V3 was the only area that both the Pearson correlation distance and the Euclidean distance multivariate analyses point to as being critically involved, but it is possible that the other sensory areas which our Pearson correlation distance metric revealed – V1, V2, V4 – also play an important role. A large segment of visual sensory cortex was active in the comparison of very beautiful vs baseline as well as in the parametric analysis charting increasing activity with increasing intensity of the declared experience of beauty, even though we did not detect any decodable activity in them with our multivariate analyses. Areas such as IPS or V3B, in which no specific patterns were observed, could nevertheless influence areas in which decodable patterns emerged – especially V3 – through connections between them, thus expressing their contribution through V3 or the other sensory areas which my act as a "final common pathway" in the interaction with A1. Such a conclusion is similar to that drawn in the Yang et al. (2022) study, in which it was posited that some areas such as the fusiform face area (FFA) and the occipital face area (OFA) may act as a sort of "final common pathway" that mediates interactions with field A1.

Our RSA results shows that there are areas besides field A1 with decodable patterns with stimuli that are experienced as beautiful. We do not know what role to assign to these areas at present; if we concentrate on field A1 and its interaction with sensory areas, it is because it is the only area that has been found to be invariably active when subjects experience beauty regardless of its source. But the activity in field A1 itself also raises interesting questions. Whether the same or different sub-regions of it are active with different aesthetic experiences is not clear (see also Pegors et al. (2015)). Hence, one pointer to future work that emerges from these studies is the importance of detailing the pattern of anatomical connectivity within field A1 and between it and other areas in both the sensory and frontal cortices.

The demonstration of experience-dependent connections in the human brain

Over a quarter of a century ago, Crick and Jones (1993) considered it "intolerable" and "shameful" that we do not have as much information about human neuroanatomy as we

do about that of monkey; they were in a search for anatomical techniques that can be used in the post-mortem human brain, based around tract-tracing; this, they hoped, might reveal a connectivity pattern in the human brain which could come close to the anatomical tracing methods used in live monkeys. Since then, many advances have been made in the study of the human brain's anatomy and function owing to advances in non-invasive brain imaging techniques, and these are of two kinds.

The first revolves around diffusion MRI and tractography which, together, have advanced our knowledge of the brain's anatomical connectivity. They have demonstrated, for example, the existence of direct anatomical connections between the posterior occipital cortex and the prefrontal cortex in the human brain, and have linked them to conscious visual processing and face perception (ffytche and Catani, 2005; Forkel et al., 2014; Rokem et al., 2017). These studies (and others) have established that the polar occipital cortex is directly connected with the lateral and polar frontal cortex, but no direct connections have been established with the medial anatomical areas overlapping field A1. Despite these advances, the descriptions of the exact terminations of these connections are vague with respect to the many specific visual areas of the occipital lobe. It is hard to learn from what is available which visual areas such as V3, V3A, V4, FFA, or OFA are connected with which part of the frontal cortex.

The second approach is illustrated by the present results and those of Yang et al. (2022), among many others, which demonstrate that connections, whether direct or indirect, between the areas enumerated above do exist in the human brain but are currently only demonstrable during certain experiential states – in our instance during the experience of beauty. We refer to these as *experience-dependent connections in the human brain* which, otherwise, remain occult. The results also show that our experience dependent connections are selective, in that parallel activity in sensory areas and in field A1 depends upon the nature of the stimulus that elicits the experience of beauty.

We use the examples provided in this study and in that of Yang et al. (2022) although of course any number of previous fMRI studies could serve our purpose just as well. We also do not mean that these connections can only become evident with the experience of beauty; other affective experiences may also render them visible. For example, in a previous study (Ishizu and Zeki, 2014) we showed that ambiguous visual stimuli, in

addition to engaging visual areas such as V1 and V3, also engage the mid-cingulate cortex, which had been implicated in conflict monitoring (Botvinick et al., 2001), though no direct connections between these visual areas and the mid-cingulate cortex have been anatomically demonstrated. Such connections also exist in other domains, such as that of motor learning (Laureys et al., 2001). But it is important to emphasize that there are such highly specific state dependent connections that become demonstrable with specific aesthetic experiences.

Limitations

Our study does not come without limitations. For instance, we used RSA as a method for multivariate analysis, and this method relies on the distribution of activity across voxels. This, of course, opens the results to variability with a different imaging resolution. Perhaps higher resolution in future imaging experiments could reveal patterns in other areas and help refine the ones we found in our study. Further, we based our results on 18 subjects, and future studies with larger samples may see an increase in statistical power and reveal a larger set of regions involved in the task.

Conclusion

We have demonstrated that the experience of beauty derived from abstract art leads to specific patterns of neural activity in a set of visual regions involved in processing orientations and colours, and to activity in medial frontal regions involved in affective processing. We have further demonstrated that the connection between these geographically distant regions is specific, in that it is only established during the experience of works of art which the subjects deemed beautiful (in our experimental context). Our results, taken in conjunction with those of Yang et al. (2022), bring us closer to understanding the neural determinants of the experience of beauty; they also bring us a little, but not much, closer to understanding the nature of beauty itself.

ACKNOWLEDGEMENTS

This work was supported by the Leverhulme Trust grant RPG-2017-341 to Semir Zeki. We thank Professor Ernst Pöppel for facilitating these experiments and Dr Taoxi Yang for expert advice on several aspects of the study.

REFERENCES

Avants, B.B., Tustison, N.J., Song, G., Cook, P.A., Klein, A., and Gee, J.C. (2011). A reproducible evaluation of ANTs similarity metric performance in brain image registration. Neuroimage *54*, 2033–2044.

Bell, C. (1914). Art (London: Chatto & Windus).

Bignardi, G., Ishizu, T., and Zeki, S. (2020). The differential power of extraneous influences to modify aesthetic judgments of biological and artifactual stimuli. PsyCh J. pchj.415.

Botvinick, M.M., Carter, C.S., Braver, T.S., Barch, D.M., and Cohen, J.D. (2001). Conflict monitoring and cognitive control. Psychol. Rev. *108*, 652.

Brouwer, G.J., and Heeger, D.J. (2009). Decoding and reconstructing color from responses in human visual cortex. J. Neurosci. *29*, 13992–14003.

Brouwer, G.J., and Heeger, D.J. (2013). Categorical clustering of the neural representation of color. J. Neurosci. *33*, 15454–15465.

Cheadle, S.W., and Zeki, S. (2014). The role of parietal cortex in the formation of color and motion based concepts. Front. Hum. Neurosci. *8*, 1–10.

Chen, C.-H., and Zeki, S. (2011). Frontoparietal activation distinguishes face and space from artifact concepts. J. Cogn. Neurosci. *23*, 2558–2568.

Crick, F., and Jones, E. (1993). Backwardness of human neuroanatomy. Nature *361*, 109–110.

ffytche, D.H., and Catani, M. (2005). Beyond localization: from hodology to function. Philos. Trans. R. Soc. B Biol. Sci. *360*, 767–779.

Fonov, V., Evans, A.C., Botteron, K., Almli, C.R., McKinstry, R.C., and Collins, D.L. (2011). Unbiased average age-appropriate atlases for pediatric studies. Neuroimage *54*, 313–327.

Forkel, S.J., Thiebaut de Schotten, M., Kawadler, J.M., Dell'Acqua, F., Danek, A., and Catani, M. (2014). The anatomy of fronto-occipital connections from early blunt dissections to contemporary tractography. Cortex *56*, 73–84.

Friston, K.J., Buechel, C., Fink, G.R., Morris, J., Rolls, E., and Dolan, R.J. (1997). Psychophysiological and modulatory interactions in neuroimaging. Neuroimage *6*, 218–229.

Glennon, M.J., and Zeki, S. (2021). The power of external influences to modify judgments of facial and moral beauty. PsyCh J.

Greve, D.N., and Fischl, B. (2009). Accurate and robust brain image alignment using boundary-based registration. Neuroimage *48*, 63–72.

Hubel, D.H., and Wiesel, T.N. (1968). Receptive fields and functional architecture of monkey striate cortex. J. Physiol. *195*, 215–243.

Ishizu, T., and Zeki, S. (2011). Toward a brain-based theory of beauty. PLoS One *6*, e21852.

Ishizu, T., and Zeki, S. (2014). Varieties of perceptual instability and their neural correlates. Neuroimage *91*, 203–209.

Jenkinson, M., Bannister, P., Brady, M., and Smith, S. (2002). Improved optimization for the robust and accurate linear registration and motion correction of brain images. Neuroimage *17*, 825–841.

Kawabata, H., and Zeki, S. (2004). Neural correlates of beauty. J. Neurophysiol. *91*, 1699–1705.

Kawabata, H., and Zeki, S. (2008). The neural correlates of desire. PLoS One *3*, e3027.

Kriegeskorte, N., Mur, M., and Bandettini, P. (2008). Representational similarity analysis – connecting the branches of systems neuroscience. Front. Syst. Neurosci. *2*.

Larsson, J., and Heeger, D.J. (2006). Two Retinotopic Visual Areas in Human Lateral Occipital Cortex. J. Neurosci. *26*, 13128–13142.

Larsson, J., Landy, M.S., and Heeger, D.J. (2006). Orientation-selective adaptation to first- and second-order patterns in human visual cortex. J. Neurophysiol. *95*, 862–881.

Laureys, S., Peigneux, P., Phillips, C., Fuchs, S., Degueldre, C., Aerts, J., Del Fiore, G., Petiau, C., Luxen, A., Van der Linden, M., et al. (2001). Experience-dependent changes in cerebral functional connectivity during human rapid eye movement sleep. Neuroscience *105*, 521–525.

Lutkenhoff, E.S., Rosenberg, M., Chiang, J., Zhang, K., Pickard, J.D., Owen, A.M., and Monti, M.M. (2014). Optimized brain extraction for pathological brains (optiBET). PLoS One *9*, e115551.

Martín-Loeches, M., Hernández-Tamames, J.A., Martín, A., and Urrutia, M. (2014). Beauty and ugliness in the bodies and faces of others: An fMRI study of person esthetic judgement. Neuroscience *277*, 486–497.

Méndez-Bértolo, C., Moratti, S., Toledano, R., Lopez-Sosa, F., Martínez-Alvarez, R., Mah, Y.H., Vuilleumier, P., Gil-Nagel, A., and Strange, B.A. (2016). A fast pathway for fear in human amygdala. Nat. Neurosci. *19*, 1041–1049.

Montaser-Kouhsari, L., Landy, M.S., Heeger, D.J., and Larsson, J. (2007). Orientation-selective adaptation to illusory contours in human visual cortex. J. Neurosci. *27*, 2186–2195.

Pegors, T.K., Kable, J.W., Chatterjee, A., and Epstein, R.A. (2015). Common and unique representations in pFC for face and place attractiveness. J. Cogn. Neurosci. *27*, 959–973.

Rokem, A., Takemura, H., Bock, A.S., Scherf, K.S., Behrmann, M., Wandell, B.A., Fine, I., Bridge, H., and Pestilli, F. (2017). The visual white matter: the application of diffusion MRI and fiber tractography to vision science. J. Vis. *17*, 4.

Shigihara, Y., and Zeki, S. (2014). Parallel processing in the brain's visual form system: an fMRI study. Front. Hum. Neurosci. *8*, 506 doi: 10.3389/fnhum.2014.00506.

Tong, F., Harrison, S.A., Dewey, J.A., and Kamitani, Y. (2012). Relationship between BOLD amplitude and pattern classification of orientation-selective activity in the human visual cortex. Neuroimage *63*, 1212–1222.

Tsukiura, T., and Cabeza, R. (2011). Shared brain activity for aesthetic and moral judgments: implications for the Beauty-is-Good stereotype. Soc. Cogn. Affect. Neurosci. *6*, 138–148.

Tustison, N.J., Avants, B.B., Cook, P.A., Zheng, Y., Egan, A., Yushkevich, P.A., and Gee, J.C. (2010). N4ITK: Improved N3 bias correction. IEEE Trans. Med. Imaging *29*, 1310–1320.

Vessel, E.A., Isik, A.I., Belfi, A.M., Stahl, J.L., and Gabrielle Starr, G. (2019). The default-mode network represents aesthetic appeal that generalizes across visual domains. Proc. Natl. Acad. Sci. U. S. A. *116*, 19155–19164.

Weiskopf, N., Hutton, C., Josephs, O., and Deichmann, R. (2006). Optimal EPI parameters for reduction of susceptibility-induced BOLD sensitivity losses: A whole-brain analysis at 3 T and 1.5 T. Neuroimage *33*, 493–504.

Yang, T., Formuli, A., Paolini, M., and Zeki, S. (2022). The neural determinants of beauty. Eur. J. Neurosci. *55*, 91–106.

Zeki, S, Perry, RJ and Bartels, A. (2003). The processing of kinetic contours in the brain. Cereb. Cortex *13*, 189-202 doi:10.1093/cercor/13.2.189.

Zeki, S. (2009). Splendors and Miseries of the Brain: Love, Creativity and the Quest for Human Happiness (Oxford: Wiley-Blackwell).

Zeki, S. (2013). Clive Bell's "Significant Form" and the neurobiology of aesthetics. Front. Hum. Neurosci. *7*, 730.

Zeki, S.M. (1978). Uniformity and diversity of structure and function in rhesus monkey prestriate visual cortex. J. Physiol. *277*, 273–290.

Zeki, S., and Chén, O.Y. (2020). The Bayesian-Laplacian brain. Eur. J. Neurosci. *51*, 1441–1462.

Zeki, S., and Stutters, J. (2013). Functional specialization and generalization for grouping of stimuli based on colour and motion. Neuroimage *73*, 156–166.

Zeki, S., Romaya, J.P., Benincasa, D.M.T., and Atiyah, M.F. (2014). The experience of mathematical beauty and its neural correlates. Front. Hum. Neurosci. *8*, 68.