

Brain correlates of aesthetic judgment of beauty

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Functional MRI was used to investigate the neural correlates of aesthetic judgments of beauty of geometrical shapes. Participants performed evaluative aesthetic judgments (beautiful or not?) and descriptive symmetry judgments (symmetric or not?) on the same stimulus material. Symmetry was employed because aesthetic judgments are known to be often guided by criteria of symmetry. Novel, abstract graphic patterns were presented to minimize influences of attitudes or memory-related processes and to test effects of stimulus symmetry and complexity. Behavioral results confirmed the influence of stimulus symmetry and complexity on aesthetic judgments. Direct contrasts showed specific activations for aesthetic judgments in the frontomedian cortex (BA 9/10), bilateral prefrontal BA 45/47, and posterior cingulate, left temporal pole, and the temporoparietal junction. In contrast, symmetry judgments elicited specific activations in parietal and premotor areas subserving spatial processing. Interestingly, beautiful judgments enhanced BOLD signals not only in the frontomedian cortex, but also in the left intraparietal sulcus of the symmetry network. Moreover, stimulus complexity caused differential effects for each of the two judgment types. Findings indicate aesthetic judgments of beauty to rely on a network partially overlapping with that underlying evaluative judgments on social and moral cues and substantiate the significance of symmetry and complexity for our judgment of beauty.

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Introduction

What are the brain correlates of aesthetic judgment? Previous studies have investigated effects of attractiveness and preference by presenting faces (Aharon et al., 2001; Kampe et al., 2002; O'Doherty et al., 2003) or works of art (Kawabata and Zeki, 2004; Vartanian and Goel, 2004) and yielded evidence for a role of reward-related subcortical and limbic areas. However, these

approaches focus on the particular valences of judgments, e.g., by parametric manipulation of levels of attractiveness or by direct comparison of beautiful versus ugly or neutral pictures. In contrast, none of these studies aimed at identifying the network of aesthetic judgment per se.

Aesthetic judgments can be considered a subset of evaluative judgments such as those made on social, religious, or moral cues. Evaluative judgments as in contrast to descriptive ones were reported to engage frontomedian areas around Brodmann areas (BA) 9 and 10 mostly together with posterior cingulate cortex or precuneus as well as ventral prefrontal cortex around BA 45/47 (Cunningham et al., 2003, 2004; Greene et al., 2001, 2004; Johnson et al., 2002; Moll et al., 2001, 2002; Zysset et al., 2002). It appears plausible to hypothesize aesthetic judgments to engage a similar cerebral network. However, since all considered studies focused on the social or moral evaluation of persons or actions, it remains a fully open issue whether also not-social and non-moral evaluation on abstract entities call for the same network.

The present fMRI study used novel, abstract graphic patterns as stimulus material (Jacobsen and Höfel, 2002) to isolate the neural correlates of aesthetic judgments of beauty (Jacobsen and Höfel, 2003; Jacobsen et al., 2004). Importantly, these stimuli afforded judgments that could not be based on attitudes (Petty et al., 1997) or other memory representations. When using faces or works of art as objects of aesthetic judgment, it cannot be excluded that attitudes like, e.g., financial interests (in case of works of art) or attractiveness (of faces) partly confound identified brain areas. Indeed, an old issue in aesthetics questions whether the evaluation of beauty can be independent of desire, i.e., “disinterested” (Kant, 1764). This is particularly critical as those factors should also affect brain correlates of self-reflection as outlined above. A further confound with a similar effect could result from episodic or semantic memories (Zysset et al., 2002).

Participants performed two judgment tasks and an additional forced choice task. They had to judge either whether a stimulus was beautiful or not (aesthetic judgment task) or whether it was symmetric or not (symmetry judgment task). In many individuals aesthetic judgment is found to be ruled by symmetry (e.g., Jacobsen and Höfel, 2002). Therefore, we expected both the symmetry judgment task and the aesthetic judgment task to trigger

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an assessment of symmetry. In contrast, differences between the brain correlates of aesthetic judgment and symmetry judgment should be solely due to differences of judgment processes per se. Note that stimuli also controlled for effects of symmetry.

Likewise, stimulus complexity has a significant influence on aesthetic judgment of beauty (Eisenman, 1967; Berlyne, 1970; Jacobsen and Höfel, 2002). This factor, again, has not yet been controlled for in studies using faces and works of art as stimulus material, where it also may elude control. While symmetry was a dichotomous stimulus property in the present approach, stimulus complexity was varied as a scalar property. Our design therefore allowed to additionally analyze the parametric influence of perceptual complexity on the considered brain networks.

Materials and methods

Participants

Fifteen right-handed, healthy young volunteers (6 male; age range, 21–33 years; mean age 25.4 years) participated in the study. None of them had received professional training in the fine arts or participated in a similar experiment before. Participants had normal or corrected-to-normal visual acuity and no known neurological condition. After being informed about potential risks and screened by a physician of the institution, subjects gave informed consent

before participating. The experimental standards were approved by the local ethics committee of the University of Leipzig. Data were handled anonymously.

Material

220 black and white patterns from Jacobsen and Höfel (2002, 2003) were used for aesthetic (AJ) and symmetry (SJ) judgment conditions in this experiment (20 for the practice trials, 200 in the main experiment). Each consisted of a solid black circle (8.8 cm in diameter) showing a centered, quadratic, rhombic cutout and 86–88 basic graphic elements (small black triangle) arranged within the rhomb according to a grid and resulting in a graphic pattern. The basic elements were arranged such that geometric figures like triangles, squares, rhombuses, horizontal, vertical, or oblique bars were created. Using this approach of basic elements, the overall luminance was identical for all stimuli. Half (110) were symmetrical, i.e., one mirroring operation given four possible symmetry axes was sufficient to detect symmetry. The other half of the stimuli was clearly not symmetric. Fig. 1 shows examples of the material.

The following features of the patterns were extracted for use in the judgment analysis: mirrored at one axis (one operation sufficient), mirrored at two axes (each one of two possible operations sufficient), regular composition, number of elements, horizontal or vertical bars, large horizontal or vertical bars, small

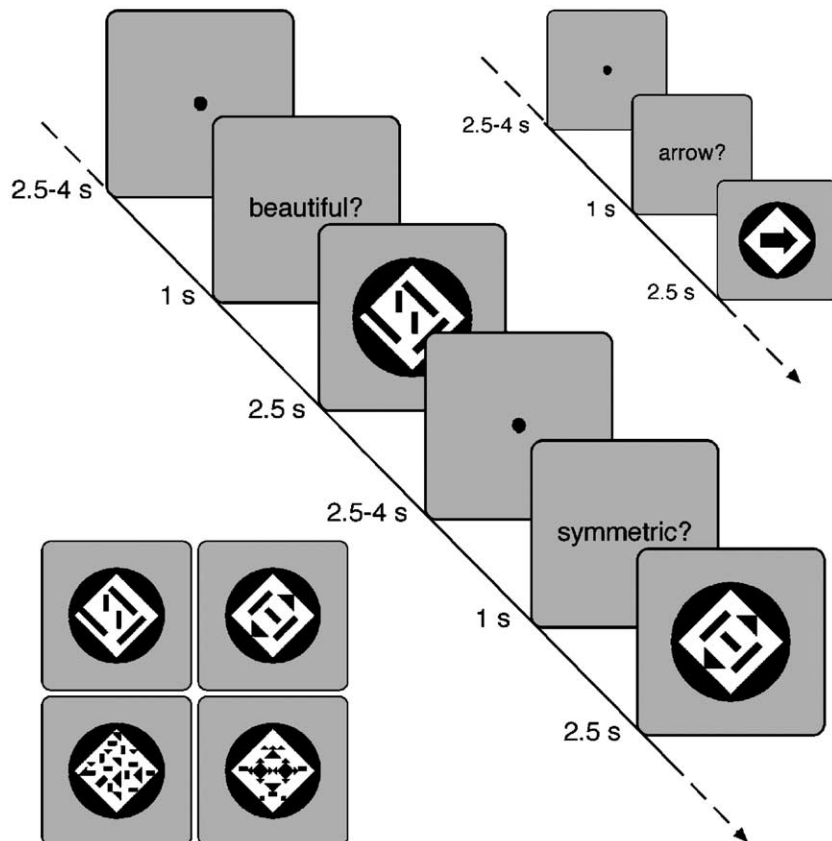


Fig. 1. Exemplary trials for both judgment tasks (middle) and for the control condition (top right). A variable jitter time of 2.5–4 s was followed by a task cue (1 s) and a picture presented at screen center for 2.5 s. Participants were asked to press the selected response button while the picture was presented. They were asked to decide whether or not the presented stimulus was beautiful (aesthetic judgment) or symmetric (symmetry judgment); in the control condition, they were asked to press the left button for arrow pointing left and the right button for arrow pointing right. Stimulus examples (bottom left) depict simple (upper row) and complex (lower row) stimuli which are either symmetric (right column) or not (left column).

horizontal or vertical bars, oblique bars, large oblique bars, small oblique bars, squares, large squares, small squares, rhombuses, large rhombuses, small rhombuses, triangles, large triangles, and small triangles. These were considered to be perceptual cues that could be used by the participants in deriving their judgments. Accordingly, the features were employed in the judgment analysis, i.e., they were introduced as predictors in the multiple regression analysis (Jacobsen, 2004; Jacobsen and Höfel, 2002).

For the control condition (CC), two stimuli (hereafter: arrow patterns) were employed which exactly matched the properties of the judgment stimuli. In these stimuli basic graphic elements were clustered to show an arrow pointing either left or right.

Procedure

This study was conducted in two parts. The first part, the aesthetic threshold test (see below), served to select participants with an aesthetic threshold appropriate for the stimulus set.

Aesthetic threshold test

For the individual beholder, a stimulus needs to have certain properties, in order to elicit aesthetic appreciation. It must exceed the aesthetic threshold (Fechner, 1876). The participants were asked to judge 27 graphic patterns on any number out of six 5-point rating scales (−2 to +2), depending on which scales they considered sensible. Three of these scales were descriptive (round–angular, small–large, not symmetric–symmetric) and three evaluative in character (not harmonic–harmonic, not beautiful–beautiful, not interesting–interesting). Arguably, the beauty scale was only chosen if a given pattern exceeded the aesthetic threshold. Participants of the fMRI experiment were selected on the basis of this test: at least two of the three exemplary patterns that were used in the main experiment had to be judged on the aesthetic scale. The aesthetic threshold of the participant (value on mixed subject–object MDS model) had to be lower than the value of those three patterns.

fMRI experiment

The paradigm comprised two experimental conditions (AJ, SJ), one control condition (CC) and one resting baseline condition (RC) (Fig. 1). Three hundred trials were presented overall, with 100 trials per experimental condition and 50 per control and resting condition. Conditions were presented in random order (mixed-trial design). Background color of the screen was light gray throughout the experimental session. Within each trial of each condition, the screen-centered presentation of the target stimulus (visual angle of 4.3°) lasted 2.5 s including response time and was preceded by a 1-s verbal task cue; stimulation was followed by an intertrial interval that lasted 2.5 s. To enhance the temporal resolution of the blood oxygenation level-dependent (BOLD) signal, variable jitter times of 0, 500, 1000, or 1500 ms were inserted at the beginning of each trial. Stimuli (except arrow patterns) were pseudo-randomly assigned to the experimental conditions AJ and SJ, that is there was no item repetition (Höfel and Jacobsen, 2003). Assignments were counterbalanced across participants. The type of judgment and symmetry status of the stimuli were fully crossed. Participants were asked to judge the patterns with regard to symmetry and aesthetic value contingent on the task cue, answering the question “Is this pattern symmetric?” in the former case and “Is this pattern beautiful?” in the latter. They were instructed to press one of the two response buttons (“yes” or “no”) when they had decided but

still while the stimulus was presented (maximal response time 2.5 s). Participants were randomly assigned to two possible response key assignments (no/yes, yes/no). In CC, participants were presented arrow stimuli pointing equiprobably either to the left or to the right. Participants were asked to press the corresponding response buttons (left button for arrow pointing left, right button for arrow pointing right). In RC, no cue or stimulus was presented but only a black screen-centered fixation cross. Participants were instructed to fixate the cross and to wait for the next trial.

Data acquisition

Participants were instructed before the MRI experiment. Before the experimental session, during acquisition of the anatomical data sets (see below), a block of twenty practice trials was administered using ten symmetric and ten not symmetric patterns. In the MRI session, subjects were supine on the scanner bed with their right index and middle finger positioned on the response buttons. To prevent postural adjustments, the subjects’ arms and hands were carefully stabilized by tape. In addition, form-fitting cushions were used to prevent arm, hand, and head motion. Participants were provided with earplugs to attenuate scanner noise. Imaging was performed at 3T on a Bruker Medspec 30/100 system equipped with the standard birdcage head coil. Twenty-two axial slices (field of view 192 mm; 64 × 64 pixel matrix; thickness 4 mm; spacing 1 mm) parallel to bicommissural line (AC PC) were acquired using a single-shot gradient echo-planar imaging (EPI) sequence (echo time, 30 ms; flip angle, 90°; repetition time, 2 s) sensitive to blood oxygenation level-dependent (BOLD) contrast. A set of two-dimensional (2D) anatomical images was acquired for each subject immediately before the functional experiment, using a modified-driven equilibrium Fourier transformation (MDEFT) sequence (256 × 256 pixel matrix). In a separate session, high-resolution whole-brain images (160 slices and 1 mm slice thickness) were acquired from each subject to improve the localization of activation foci using a T1-weighted three-dimensional (3D) segmented MDEFT sequence covering the whole brain.

Behavioral data analysis

In the judgment analysis, the judgment values were entered into a constrained stepwise multiple regression as the criterion along with the stimulus features (cues, see above) as predictors. The cue explaining most of the criterion variance was entered into the model first. Other cues, providing incremental explanation of variance, were entered, if they did not show a substantial cue–cue correlation with already entered cues ($r < 0.273$) and yielded a beta weight of 0.1 or more reflecting incremental explanation of variance (Jacobsen, 2004).

fMRI data analysis

The MRI data were processed using the software package LIPSIA (Lohmann et al., 2001). Functional data were corrected for motion using a matching metric based on linear correlation. To correct for the temporal offset between the slices acquired in one scan, a sinc-interpolation based on the Nyquist Shannon theorem was applied. A temporal high-pass filter with a cutoff frequency of 1/72 Hz was used for baseline correction of the signal and a spatial Gaussian filter with 5.652 mm FWHM was applied. To align the functional data slices with a 3D stereotactic coordinate reference

system, a rigid linear registration with six degrees of freedom (3 rotational, 3 translational) was performed. The rotational and translational parameters were acquired on the basis of the MDEFT and EPI-T1 slices to achieve an optimal match between these slices and the individual 3D reference data set. This 3D reference data set was acquired for each subject during a previous scanning session. The MDEFT volume data set was standardized to the Talairach stereotactic space (Talairach and Tournoux, 1988). The rotational and translational parameters were subsequently transformed by linear scaling to a standard size. The resulting parameters were then used to transform the functional slices using trilinear interpolation, so that the resulting functional slices were aligned with the stereotactic coordinate system. Slice gaps were interpolated to generate output data with a spatial resolution of $3 \times 3 \times 3$ mm. The statistical evaluation was based on a least squares estimation using the general linear model (GLM) for serially autocorrelated observations (random effects model; Friston, 1994; Friston et al., 1995a,b; Worsley and Friston, 1995). The design matrix was generated with a synthetic hemodynamic response function and its first and second derivative. Brain activations were analyzed in an event-related design time locked to stimulus onset. The model equation, including the observation data, the design matrix, and the error term, was convolved with a Gaussian kernel of dispersion of 4 s full width at half maximum to deal with the temporal autocorrelation (Worsley and Friston, 1995). In the following, contrast images, i.e., estimates of the raw score differences between specified conditions, were generated for each participant. The single-participant contrast images were then entered into a second-level random effects analysis for each of the contrasts. The group analysis consisted of a one-sample *t* test across the contrast images of all participants that indicated whether observed differences between conditions were significantly distinct from zero (Holmes and Friston, 1998). Subsequently, *t* values were transformed into *z* scores. To protect against false-positive activations, only regions with *z* score > 3.09 ($P > 0.001$; uncorrected) and with a volume > 405 cubic mm (15 contiguous voxels) were considered. All reported activations survived a threshold corresponding to $P > 0.05$ (corrected for multiple comparisons) at the cluster level.

Results

Behavioral results

Judgment analysis

Table 1 gives the paramorphic individual case models for the participants as well as the model for the group average data. Standardized regression coefficients and multiple regression coefficients (*R*) are shown. The following predictors were included in at least one of the models: number of elements (i.e., a measure for complexity, see fMRI analysis), horizontal or vertical bars, large horizontal or vertical bars, oblique bars, large oblique bars, triangles, squares, large squares, small squares, rhombuses, small rhombuses, mirrored at one axis, and mirrored at two axes. No other predictor was included in a model. In addition to these paramorphic individual case models, a group model derived from the mean judgment values for each picture was computed using the same method. For one of the participants, no informative model could be derived.

As predicted, symmetry was found to be the most important stimulus property determining participants' aesthetic judgments. In general, participants showed agreement that symmetric and regular pictures were more beautiful than the others. The group model also reflected this fact. Additionally, the individual case models revealed consistent inter-individual differences. Twelve participants used symmetry cues as the most important stimulus property determining beauty in a positive direction. One of them relied on symmetry cues as the sole substantial factor influencing his judgments. For them, a symmetric pattern was more beautiful. Moreover, individual beta weights of symmetry cues ranged from 0.35 to 0.90 revealing considerable variation of cue use, that is the importance of symmetry cues for individual judges differed. These inter-individual differences were leveled by the group model. Hence, detailed capturing of individual judgment policies provides a more thorough account of aesthetic judgment policies for these stimuli.

At the group level, the number of elements in a pattern, a measure for complexity, accounted for the second-most amount of

Table 1

Paramorphic individual case models (rows: participant nos. 1–15) and model for the group average data (last row: mean) as computed in the judgment analysis

	A	B	C	D	E	F	G	H	I	J	K	L	M	R
1										0.191		0.733		0.774
2					–0.285								0.5	0.545
3									0.162			0.903		0.915
4														/
5				–0.167									0.69	0.714
6			0.201										0.577	0.56
7	0.52													0.52
8								0.174					0.638	0.696
9				–0.223									0.482	0.511
10	0.176	–0.161										0.7		0.749
11							0.164					0.696		0.717
12	0.224												0.347	0.407
13												0.526		0.526
14	–0.213									0.261				0.3
15						0.147					0.251	0.706		0.705
mean	0.219											0.782		0.795

Standardized regression coefficients and multiple regression coefficients (*R*) are shown. Columns show all predictors (A–M, abbreviations as given below) included in at least one model. Most important predictors are in bold font.

Abbreviations: A = number of elements; B = horizontal or vertical bars; C = large horizontal or vertical bars; D = oblique bars; E = large oblique bars; F = triangles; G = squares; H = large squares; I = small squares; J = rhombuses; K = small rhombuses; L = mirrored at one axis; M = mirrored at two axes.

variance. One of the participants relied on this predictor as the sole substantial factor influencing his judgments. Three participants considered a larger number of elements in a pattern more beautiful. Conversely, one participant had the opposite strategy. To him, patterns with fewer elements were more beautiful. One participant relied on a shape cue for the judgment. This participant found patterns with rhombuses more beautiful than other patterns. This predictor was found to be the most important predictor, followed by number of elements.

A number of stimulus features (e.g., small triangles or small oblique bars) were not used by the participants to derive their judgments. Participants revealed differences in linear predictability. Multiple R 's ranged from 0.3 to 0.92, that is, a range of explained judgmental variance from 9% to 85%. The group model showed 63.2% of linearly explained variance, thus leveling the inter-individual differences and hiding that fact. Averaging procedures treat individual differences as noise and therefore cancel them out which was not adequate for the present data. Furthermore, differences in explained variance are typically interpreted as an index of strategy use (Stewart, 1988). Participants with a high linear predictability used systematic judgment strategies, while linearly unpredictable judges most likely employed highly configural cue combinations (Brehmer and Joyce, 1988; Cooksey, 1996).

Behavioral performance

92.1% of all symmetry judgment responses were correct. There were 2.9% non-responses and 5.1% of the given answers were erroneous. Aesthetic judgment responses showed 1.9% non-responses. Mean response times for correct trials only and standard deviations (in parenthesis) were as follows: symmetry judgment "yes" 1274 ms (271 ms), 8.1% errors; symmetry judgment "no" 1289 ms (288 ms), 6.6% errors; aesthetic judgment "yes" 1401 ms (246 ms); and aesthetic judgment "no" 1263 ms (233 ms). A repeated-measures analysis of variance (ANOVA) over the judgment latencies with the factors judgment TASK (symmetry/aesthetic) and ANSWER (yes/no) revealed an interaction ($F(1,14) = 9.46$, $MSE = 9405.03$, $P = 0.008$). No other effect was significant (TASK, $F(1,14) = 1.42$, $MSE = 27,185.17$, $P = 0.25$; and ANSWER, $F(1,14) = 3.15$, $MSE = 17,968.47$, $P = 0.1$). Further investigation of the interaction TASK by ANSWER showed an effect for the judgment latencies for ANSWER under the aesthetic task, with beautiful patterns being slower to be answered ($F(1,14) = 13.76$, $MSE = 10,439.1$, $P = 0.002$). Summarized judgment latencies for the tasks symmetry and aesthetics were significantly slower than those for the baseline trials ($F(1,14) = 149.43$, $MSE = 23,909.4$, $P < 0.0001$). An ANOVA over the symmetry judgment errors revealed no significant effect ($F < 1$). Summarized judgments errors for the symmetry task were significantly higher than those for the baseline trials ($F(1,14) = 7.15$, $MSE = 0.002$, $P = 0.02$). 42.2% of the stimuli under the aesthetic judgment task were judged as beautiful, 57.8% as not beautiful, the difference being statistically significant ($F(1,14) = 6.09$, $MSE = 298.9$, $P = 0.03$).

Imaging results

Aesthetic and symmetry judgments versus control condition

In both judgment tasks, assessed separately versus the control condition CC (AJ–CC, SJ–CC), activity was observed in the dorsal frontomedian cortex with a maximum probably within mesial BA 8, the intraparietal sulcus, the inferior precentral gyrus

(ventral premotor cortex), the anterior inferior frontal sulcus, fusiform gyrus, pulvinar nucleus of the thalamus (dorsomedial nucleus), superior anterior insula, ventral tegmental area, and extrastriate visual cortex. While frontomedian activation extended more anteriorly for aesthetic judgments (AJ–CC) than for symmetry judgments (SJ–CC), symmetry judgments but not aesthetic judgments caused activation in the bilateral dorsal premotor cortex at the crossing between superior precentral sulcus and superior frontal sulcus.

Aesthetic judgments versus symmetry judgments

The direct contrast revealed that a number of areas were differentially activated by the two categories of judgment tasks under investigation (Fig. 2, Table 2). Aesthetic judgments (AJ–SJ) elicited activation within the right frontomedian cortex (BA 9 and 10), extending bilaterally onto the convexity of superior frontal gyri, and in adjacent areas of the anterior cingulate cortex (BA 32). Other foci were observed within the posterior cingulate cortex, the inferior precuneus, the right and left inferior frontal gyrus (BA 45/47) extending into the lateral orbitofrontal cortex in the left hemisphere, the left temporal pole, and the temporoparietal junction. In contrast, symmetry judgments (SJ–AJ) caused bilateral activation within dorsal premotor cortex and the superior parietal lobule, the intraparietal sulcus, left ventral premotor cortex, left fusiform gyrus probably corresponding to the so-called fusiform face area (FFA; Kanwisher et al., 1997), and the visual cortex.

Beautiful versus not-beautiful judgments, and symmetric versus not-symmetric judgments

In order to identify valence effects within the networks specifically engaged for either aesthetic or symmetry judgments, BOLD signal changes were extracted from voxels with maximal activation in areas identified by direct task contrasts AJ–SJ and SJ–AJ. Considering firstly areas with higher activation for aesthetic as compared to symmetry judgment (AJ–SJ), some of them showed a higher signal for beautiful as compared to not-beautiful judgments (dorsal frontomedian cortex, BA 45/47 and temporal pole), whereas all others were indifferent. Selected t tests revealed, however, that the signal difference beautiful versus not-beautiful reached significance only in BA 10 ($x/y/z = 2/53/27$; $P = 0.03$), which is in accordance to this areas' connectivity with BA 45/47 and temporal pole (Ramnani and Owen, 2004). All of these areas were indifferent with respect to the two symmetry judgments. Considering areas with higher activation for symmetry as compared to aesthetic judgment (SJ–AJ), no differences were found for signal changes of either symmetric or not-symmetric judgments. Interestingly, however, judged-as-beautiful pictures showed a higher signal than judged-as-not-beautiful pictures in the left intraparietal sulcus ($x/y/z = -31/-85/32$), though with a t test reaching only marginal significance ($P = 0.09$). Overall, hence, symmetry had no significant influence on signal changes, whereas beautiful judgments led to higher signal changes than not-beautiful judgments in frontomedian BA 10, i.e., an area which was specifically engaged in aesthetic judgments, as well as in the left intraparietal sulcus, i.e., an area which was specifically engaged in symmetry judgments (Fig. 2).

Since each stimulus was presented only once to a participant over the course of the experiment, the assessment of mere valence effects was restricted by this fact. Contrasting beautiful

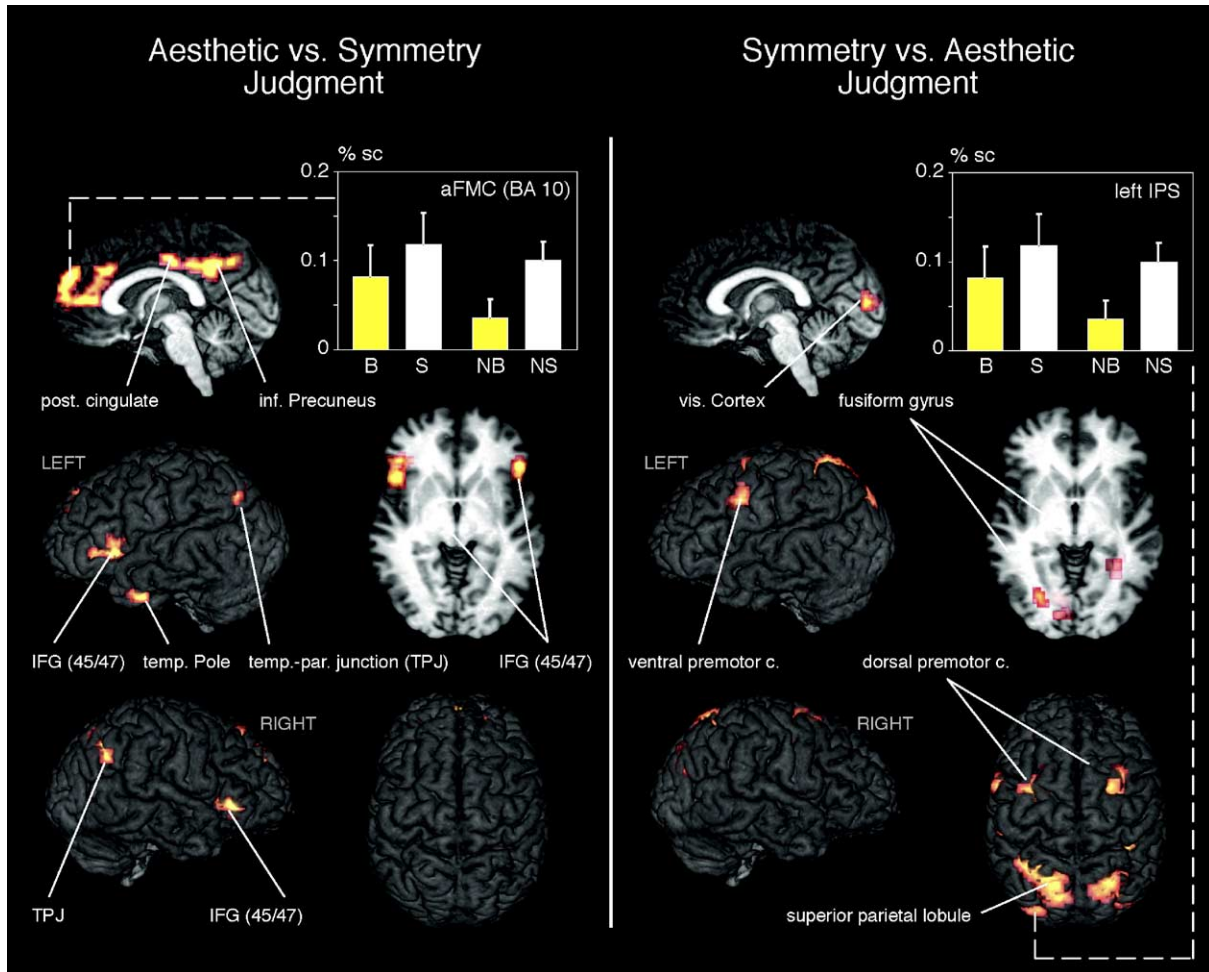


Fig. 2. Brain correlates of experimental tasks. Group-averaged ($n = 15$) statistical maps of significantly activated areas for aesthetic judgments as opposed to symmetry judgments (left panel) and for symmetry as opposed to aesthetic judgments (right panel). Z-maps were thresholded at $z = 3.09$ ($P < 0.05$ corrected). Bar charts depict maximal signal changes (% sc) for the two areas in which beautiful judgments (B) caused a higher BOLD signal than not-beautiful (NB) judgments (aFMC = frontomedian cortex at BA 10, and left IPS = intraparietal sulcus). In contrast, no significant differences were found between symmetric (S) and not-symmetric (NS) judgments. Further abbreviations: IFG (45/47) inferior frontal gyrus at BA 45/47.

versus not-beautiful judgments (under this restriction), we found the left junction of the inferior frontal sulcus and inferior precentral sulcus ($x/y/z = -40/9/26$) and extrastriate visual areas ($x/y/z = 31/-80/5$ and $13/-87/7$) to be more engaged when subjects judged a stimulus to be beautiful (no activation was found for the reverse contrast). Activation in these areas may owe to the particularly extended visual analysis preceding the beautiful judgment (1401 ms versus 1263 ms) and thereby the shortly postponed assignment of the key to the currently evaluated stimulus. Note, however, that viewing time was the same for all conditions, as stimulus presentation was not response-dependently aborted (cf. analysis in Vartanian and Goel, 2004).

Parametric effects of complexity

Finally, a parametric contrast was calculated to test for the correlates of stimulus complexity. Complexity was measured by the number of separate elements in a stimulus pattern (see Materials and methods section). The complexity value was 13.4 elements on average (± 7.6 SD) and ranged from 3 to 44. These values entered the parametric analysis testing for the effect of

stimulus complexity separately for aesthetic and symmetry judgments. For both judgment conditions, increasing complexity caused significant activation within the fusiform gyri (aesthetic judgment: $x/y/z = -22/-80/-3$, $-25/-56/-3$, $25/-66/-3$, and $34/-74/-3$; symmetry judgment: $-22/-89/-3$, $-28/-59/-3$, $28/-51/0$, and $16/-89/0$). This effect was descriptively dominant for symmetry judgments. Condition-specific effects of complexity were observed in the right lateral fronto-orbital cortex for aesthetic judgments ($x/y/z = 31/35/-6$), and within the right anterior inferior frontal gyrus ($x/y/z = 43/29/17$) and the right ventral premotor cortex ($x/y/z = 40/2/35$) for symmetry judgments (Fig. 3).

Discussion

The present fMRI study aimed at identifying the neural correlates of genuine aesthetic judgments of beauty. Novel, abstract graphic patterns were employed to minimize influences of attitudes or memory-related processes. As aesthetic judgments are known to be often guided by criteria of symmetry, evaluative aesthetic

Table 2

Anatomical area, hemisphere (R right, L left), Talairach coordinates (x, y, z), and maximal Z scores (Z) of significant activations of the direct contrasts

Anatomical area	Hemisphere	x	y	z	Z
Aesthetic judgment versus symmetry judgment					
Frontomedian/anterior cingulate cortex (BA 9/32)	R	1	23	32	4.77
Frontomedian cortex (BA 10)	R	1	54	26	4.99
Superior frontal gyrus (BA 10)	R	22	45	26	4.32
Posterior cingulate cortex	R	1	-18	41	4.02
Inferior precuneus	L	-4	-47	32	4.35
Inferior frontal gyrus (BA 45/47)	L	-46	17	0	4.03
	R	46	24	0	5.06
Temporal pole	L	-43	2	-29	4.07
Temporoparietal junction	R	46	-56	32	4.03
	L	-41	-59	35	3.51
Symmetry judgment versus aesthetic judgment					
Superior parietal lobule	L	-19	-56	55	6.13
	R	22	-59	58	4.70
Intraparietal sulcus	L	-31	-83	32	4.21
Precentral gyrus (dorsal premotor cortex)	L	-25	0	52	4.64
	R	25	8	44	4.44
Precentral gyrus (ventral premotor cortex)	L	-49	3	32	4.14
Fusiform gyrus (face area, FFA)	L	-25	-71	0	3.98
Extrastriate visual cortex	L	-7	-80	11	4.59

judgments were moreover compared with descriptive symmetry judgments on the same stimulus material. Results revealed both types of judgment to rely on a set of areas supporting high-level visual analysis. As hypothesized, however, direct contrasts showed specific activations for aesthetic judgments; these were located in the medial wall (BA 9/10 and inferior precuneus) and bilateral ventral prefrontal cortex (BA 45/47), i.e., regions which have been previously reported for social or moral evaluative judgments on persons and actions (Cunningham et al., 2003; Greene et al., 2001; Johnson et al., 2002; Moll et al., 2001; Zysset et al., 2002). Aesthetic judgments also engaged the left temporal pole and the temporoparietal junction. In contrast, symmetry judgments elicited specific activations in several areas related to visuospatial analysis, including superior parietal lobule and intraparietal sulcus as well as dorsal premotor cortex (Wager and Smith, 2003; Schubotz and von Cramon, 2003). Interestingly, when participants judged a pattern to be beautiful (as in contrast to not beautiful), not only areas dominant in aesthetic judgments, but also one area specifically engaged in symmetry judgments (left intraparietal sulcus) showed

an enhanced BOLD signal. Moreover, the parametrically manipulated and a second important factor of aesthetic judgment, stimulus complexity, caused differential effects for each of the two judgments types, including right lateral fronto-orbital cortex (BA 47/11) for high complexity during aesthetic judgments. Against the background of the literature, present findings indicate that aesthetic judgments of beauty recruit partially overlapping networks with social and moral judgments, but also specific areas which have not yet been reported for the latter. Moreover, the behaviorally established significance of stimulus symmetry and complexity for our judgment of beauty was found to be reflected also by brain correlates.

Common activations of the aesthetic and the symmetry judgment reflected that participants encountered decisions under uncertainty, as indicated by activation of mesial BA 8, anterior insula, and ventral tegmental area (Volz et al., 2003, 2004). In contrast, direct comparisons revealed a cortical network for aesthetic judgments, parts of which are reported for social (Cunningham et al., 2003; Johnson et al., 2002), moral (Moll et

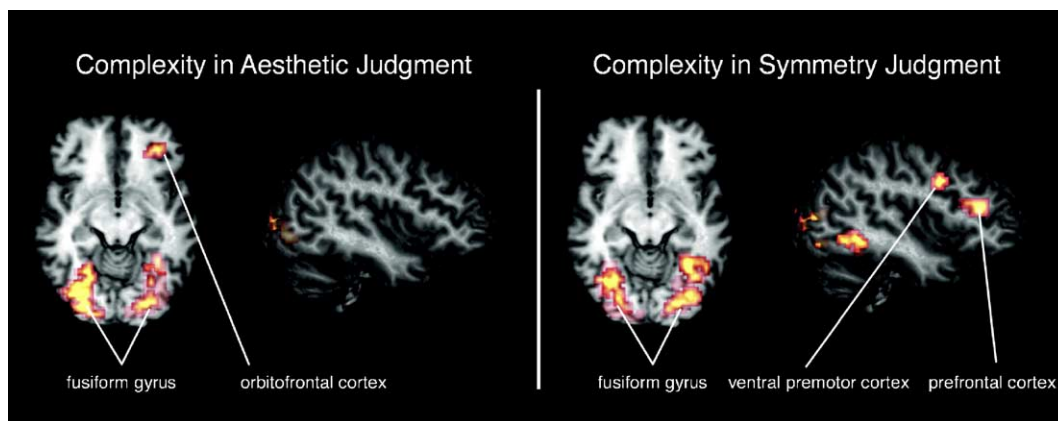


Fig. 3. Brain correlates of parametric effects of stimulus complexity in aesthetic judgments (left panel) and symmetry judgments (right panel). For both conditions, activation was enhanced by high complexity in fusiform gyri. Differential effects were observed in the right orbitofrontal cortex for aesthetic judgments, and in the right prefrontal and premotor area for symmetry judgments.

al., 2001; Greene et al., 2001), or other (Zysset et al., 2002) evaluative judgments.

One of these areas, frontomedian BA 9/10, has attracted particular interest in recent years as almost no functional models exist for this area in the non-human primate. BA 10 is a very large brain region in humans: in volumetric terms probably the largest single architectonic region of the frontal lobes (Christoff et al., 2001). Rostral prefrontal cortex (BA 10 included) is in relative terms twice as large in the human brain as in many great apes (Semendeferi et al., 2001). This region is possibly the last to achieve myelination, and it has been argued that tardily myelination areas engage in complex functions highly related to the organism's experience (Fuster, 1997; Burgess et al., 2005).

In our aesthetic versus symmetry judgment, the center of activation was located within BA 10/9, and BA 10 activation was restricted to its polar subdivision (BA 10p; Ongur et al., 2003). Functionally, this region has been related to the explicit processing or introspective evaluation of internal mental states, i.e., one's own thoughts and feelings (Christoff and Gabrieli, 2000). The notion of evaluation of internally generated information (as in contrast to externally available information) takes into account that the same area and networks were found in tasks related to mentalizing (Happé, 2003) which requires self-reference as well (Vogeley et al., 1999; Gusnard et al., 2001; Gallagher, 2000). Our present findings are in accord with this account. Thus, to give a candid answer in the aesthetic judgment task, subjects had to ask themselves "Do I find this pattern beautiful?" In contrast, to judge upon symmetry all relevant information could be derived directly from the stimulus itself without explicit reference to one's own thoughts or feelings. Ramnani and Owen (2004) in their review on area BA 10 propose it more generally to be involved when integration of the outcomes of two or more separate cognitive operations is required in the pursuit of a higher behavioral goal. It is an open issue, however, whether the notion, as put forward by Christoff and Gabrieli (2000), that the lateral portion of BA 10 supports relational integration, i.e., binding a large number of independent sources of variance, applies to the medial portion of area BA 10, too. It appears plausible, at least, that evaluative judgments necessitate complex relational integration in terms of multiple relations between external entities and mental states (Kroger et al., 2002; Christoff et al., 2001), or holding in mind goals while exploring and processing secondary goals (Koechlin et al., 1999).

Mesial BA 10 is known to be reciprocally connected with several areas which were also activated in aesthetic as compared to symmetry judgment, including the ventrolateral prefrontal cortex (BA 45/47), temporal pole, posterior cingulate cortex, and precuneus (Barbas, 1992; Pandya and Yeterian, 1996; for a literature synopsis, see Ramnani and Owen, 2004). Comparing our data with other findings on evaluative judgment so far, BA 45/47 in the ventral prefrontal area was found to be unilaterally activated in previous studies. Zysset et al. (2002) reported left BA 45/47 for evaluative in contrast to either semantic or episodic judgments. Cunningham et al. (2003) found right BA 45/47 for good–bad in contrast to factual judgments made on famous people, and signal in this area was found to particularly increase for ambivalent judgments. Authors take this effect to support that evaluative judgments reflect a constructed online process rather than a controlled activation of a memory representation. In accordance with this view, and because probably most of the stimuli were not judged to be absolutely beautiful or absolutely not beautiful, bilateral BA 45/47 activation in our study may reflect a

particular demand of the aesthetic judgments, namely to map a non-dichotomous judgment onto a binary decision (for involvement of both hemispheres in aesthetic judgment, see also Regard and Landis, 1988). Indirect evidence for this interpretation comes from the finding that the BOLD signal of a directly adjacent orbitofrontal area was found to positively co-vary with stimulus complexity during aesthetic judgments only. Furthermore, work by Cunningham et al. (2004) suggests that the stronger recruitment of areas BA 9/10, BA 45/47, anterior cingulate, and the left temporal pole in the present evaluative judgment task depended on the intentional nature of the processes (as in contrast to implicit processes of evaluation). With regard to aesthetic judgments, complexity was found to account for the second-most amount of variance at the group level, as outlined in the judgment analysis. Overall, pictures that contained more elements were considered more beautiful. The parametric effect in this area may hence reflect the particular conflict arising when subjects evaluated a complex stimulus, and often against the principal bias for not-beautiful judgments.

A further area specifically co-activated with BA 10 in aesthetic judgment, the temporal pole, has been suggested to be concerned with generating, on the basis of past experience, a wider semantic and emotional context for the material currently being processed (Frith and Frith, 2003). Finally, the potential contribution of posterior cingulate cortex and precuneus to aesthetic judgment may relate to their role in memory retrieval (Fletcher et al., 1998; Shallice et al., 1994; Buckner et al., 1996; Dobbins et al., 2002; Nakamura and Kubota, 1996), particularly successful episodic memory retrieval (Cabeza and Nyberg, 2000). As outlined in the introduction, we aimed to minimize or even rule out memory-related confounds by using a non-referential, abstract stimulus material. What may be the particular role of memory retrieval in aesthetic judgment as compared to symmetry judgment? One possibility is that participants, in order to give an appropriate answer according to their subjective valence system, engaged in a spontaneous comparison of the graphic patterns with patterns they were already familiar with. This could be done in two ways. Firstly, participants could have spontaneously associated the graphic stimuli they were presented with to the similar patterns they were already familiar with before the experimental session, as e.g., grandma's bobbin lace. Secondly, participants could try to retrieve their own judgments on prior patterns in the experiment, or run a comparison to facilitate their judgment, saying e.g., that the present pattern is more or less beautiful than the preceding one. In this context, it is particularly interesting that the precuneus responds to the repeated exposure to stimuli (Maguire et al., 1999; Dolan et al., 1997). Together with posterior cingulate cortex, this region is hence suggested for fitting new information into an established mental framework of prior knowledge (Maguire et al., 1999). In either way, present effects in memory-related networks signify a strong behavioral bias to use episodic or semantic memories to guide aesthetic judgment.

The valence of aesthetic judgments had a significant influence on the BOLD signal in several of these areas and, interestingly, also on the left intraparietal sulcus involved in symmetry judgments. On the one hand, signal boost in areas related to aesthetic judgment may reflect the particularly intensive evaluation before assigning a stimulus to the category of beautiful items. This view is substantiated by the general and statistically significant tendency of the participants to find patterns not beautiful (42.2% "beautiful" as compared to 57.8% "not beautiful") and to need significantly

more time for beautiful (1401 ms) than for not-beautiful judgments (1263 ms). On the other hand, beautiful judgments caused higher signal changes than not-beautiful judgments in left intraparietal sulcus engaged in symmetry judgments. One might argue that this effect cannot be unambiguously attributed to the (subjective) beauty of the stimulus, since symmetric items were more frequently judged to be beautiful (66.4%, SD 23.2). However, symmetric judgments did not cause higher signals than not-symmetric ones in this very area. It can therefore be ruled out that the “beauty-induced” signal boost in left intraparietal sulcus was due to (the perception of) a higher ratio of symmetric patterns among those judged as beautiful. This effect may rather reflect, in our view, that the analysis of stimulus symmetry was boosted whenever participants found a stimulus beautiful. Metabolic findings hence nicely parallel the behavioral finding that, in many participants, symmetry guides aesthetic judgments of beauty.

Conclusion

The present study shows, for the first time, that aesthetic judgments of beauty trigger activation in a brain network that generally underlies evaluative judgments, and hence share neural substrate with, e.g., social and moral judgments. Since judgments of beauty often base on the analysis of stimulus symmetry, a descriptive symmetry judgment was employed for comparison. The differential patterns of metabolism demonstrate that brain activations during aesthetic judgment cannot be reduced to an assessment of symmetry but are actually due to a particular mode of judgment.

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References

- Aharon, I., Etcoff, N., Ariely, D., Chabris, C.F., O'Connor, E., Breiter, H.C., 2001. Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron* 32, 537–551.
- Barbas, H., 1992. Architecture and cortical connections of the prefrontal cortex in the rhesus monkey. *Adv. Neurol.* 57, 91–115.
- Berlyne, D.E., 1970. Novelty, complexity and hedonic value. *Percept. Psychophys.* 8, 279–286.
- Brehmer, B., Joyce, R.B., 1988. *Human Judgment: The SJT View*. North-Holland, Amsterdam.
- Buckner, R.L., Raichle, M.E., Miezin, F.M., Petersen, S.E., 1996. Functional anatomic studies of memory retrieval for auditory words and visual pictures. *J. Neurosci.* 16, 6219–6235.
- Burgess, P.W., Simons, J.S., Dumontheil, I., Gilbert, S.J., 2005. The gateway hypothesis of rostral prefrontal cortex (area 10) function. In: Duncan, J., McLeod, P., Phillips, L. (Eds.), *Measuring the Mind: Speed, Control, and Age*. Oxford Univ. Press, pp. 215–246.
- Cabeza, R., Nyberg, L., 2000. Neural bases of learning and memory: functional neuroimaging evidence. *Curr. Opin. Neurol.* 13, 415–421.
- Christoff, K., Gabrieli, J.D.E., 2000. The frontopolar cortex and human cognition: evidence for a rostrocaudal hierarchical organization within the human prefrontal cortex. *Psychobiology* 28, 168–186.
- Christoff, K., Prabhakaran, V., Dorfman, J., Zhao, Z., Kroger, J.K., Holyoak, K.J., Gabrieli, J.D., 2001. Rostrolateral prefrontal cortex involvement in relational integration during reasoning. *NeuroImage* 14, 1136–1149.
- Cooksey, R.W., 1996. *Judgment Analysis: Theory, Methods, and Applications*. Academic Press, San Diego.
- Cunningham, W.A., Johnson, M.K., Gatenby, J.C., Gore, J.C., Banaji, M.R., 2003. Neural components of social evaluation. *J. Pers. Soc. Psychol.* 85, 639–649.
- Cunningham, W.A., Raye, C.L., Johnson, M.K., 2004. Implicit and explicit evaluation: fMRI correlates of valence, emotional intensity, and control in the processing of attitudes. *J. Cogn. Neurosci.* 16, 1717–1729.
- Dobbins, I.G., Foley, H., Schacter, D.L., Wagner, A.D., 2002. Executive control during episodic retrieval: multiple prefrontal processes subserve source memory. *Neuron* 35, 989–996.
- Dolan, R.J., Fink, G.R., Rolls, E., Booth, M., Holmes, A., Frackowiak, R.S., Friston, K.J., 1997. How the brain learns to see objects and faces in an impoverished context. *Nature* 389, 596–599.
- Eisenman, R., 1967. Complexity-simplicity: I. Preference for symmetry and rejection of complexity. *Psychon. Sci.* 8, 169–170.
- Fechner, G.T., 1876. *Vorschule der Aesthetik [Experimental Aesthetics; “Pre-school” of aesthetics]*. Breitkopf and Härtel, Leipzig.
- Fletcher, P.C., Shallice, T., Frith, C.D., Frackowiak, R.S.J., Dolan, R.J., 1998. The functional roles of prefrontal cortex in episodic memory: II. Retrieval. *Brain* 121, 1249–1256.
- Friston, K.J., 1994. Statistical parametric mapping. In: Thatcher, R.W., Hallet, M., Zeffiro, T., John, E.R., Huerta, M. (Eds.), *Functional Neuroimaging*. Academic, San Diego, pp. 79–93.
- Friston, K.J., Holmes, A.P., Poline, J.B., Grasby, B.J., Williams, C.R., Frackowiak, R.S.J., 1995a. Analysis of MRI time-series revisited. *NeuroImage* 2, 45–53.
- Friston, K.J., Holmes, A.P., Worsley, K.J., Poline, J.P., Frith, C.D., Frackowiak, R.S.J., 1995b. Statistical parametric maps in functional imaging: a general linear approach. *Hum. Brain Mapp.* 2, 189–210.
- Frith, U., Frith, C.D., 2003. Development and neurophysiology of mentalizing. *Philos. Trans. R. Soc. Lond., B Biol. Sci.* 358, 459–473.
- Fuster, J.M., 1997. *The Prefrontal Cortex: Anatomy, Physiology, and Neuropsychology of the Frontal Lobe*. Lippincott-Raven, Philadelphia, PA.
- Gallagher, S., 2000. Philosophical conceptions of the self: implications for cognitive science. *Trends Cogn. Sci.* 4, 14–21.
- Greene, J.D., Sommerville, R.B., Nystrom, L.E., Darley, J.M., Cohen, J.D., 2001. An fMRI investigation of emotional engagement in moral judgment. *Science* 293, 2105–2108.
- Greene, J.D., Nystrom, L.E., Engell, A.D., Darley, J.M., Cohen, J.D., 2004. The neural bases of cognitive conflict and control in moral judgment. *Neuron* 44, 389–400.
- Gusnard, D.A., Akbudak, E., Shulman, G.L., Raichle, M.E., 2001. Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. *Proc. Natl. Acad. Sci. U. S. A.* 98, 4259–4264.
- Happe, F., 2003. Theory of mind and the self. *Ann. N. Y. Acad. Sci.* 1001, 134–144.
- Höfel, L., Jacobsen, T., 2003. Temporal stability and consistency of aesthetic judgments of beauty of formal graphic patterns. *Percept. Mot. Skills* 96, 30–32.
- Holmes, A.P., Friston, K.J., 1998. Generalisability, random effects and population inference. *NeuroImage* 7, S754.
- Jacobsen, T., 2004. Individual and group modeling of aesthetic judgment strategies. *Br. J. Psychol.* 95, 41–56.
- Jacobsen, T., Höfel, L., 2002. Aesthetic judgments of novel graphic patterns: analyses of individual judgments. *Percept. Mot. Skills* 95, 755–766.
- Jacobsen, T., Höfel, L., 2003. Descriptive and evaluative judgment processes: behavioral and electrophysiological indices of processing symmetry and aesthetics. *Cogn. Affect. Behav. Neurosci.* 3, 289–299.
- Jacobsen, T., Buchta, K., Köhler, M., Schröger, E., 2004. The primacy of beauty in judging the aesthetics of objects. *Psychol. Rep.* 94, 1253–1260.

- Johnson, S.C., Baxter, L.C., Wilder, L.S., Pipe, J.G., Heiserman, J.E., Prigatano, G.P., 2002. Neural correlates of self-reflection. *Brain* 125, 1808–1814.
- Kampe, K.K., Frith, C.D., Dolan, R.J., Frith, U., 2002. Reward value of attractiveness and gaze. *Nature* 413, 589.
- Kant, I., 1764. *Beobachtungen über das Gefühl des Schönen und Erhabenen*. Königsberg. Translation J.T. Goldthwait, *Observations on the feeling of the beautiful and sublime*. Berkeley and Los Angeles, Univ California Press.
- Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17, 4302–4311.
- Kawabata, H., Zeki, S., 2004. Neural correlates of beauty. *J. Neurophysiol.* 91, 1699–1705.
- Koechlin, E., Basso, G., Pietrini, P., Panzer, S., Grafman, J., 1999. The role of the anterior prefrontal cortex in human cognition. *Nature* 399, 148–151.
- Kroger, J.K., Sabb, F.W., Fales, C.L., Bookheimer, S.Y., Cohen, M.S., Holyoak, K.J., 2002. Recruitment of anterior dorsolateral prefrontal cortex in human reasoning: a parametric study of relational complexity. *Cereb. Cortex* 12, 477–485.
- Lohmann, G., Mueller, K., Bosch, V., Mentzel, H., Hessler, S., Chen, L., Zysset, S., von Cramon, D.Y., 2001. Lipsia—A new software system for the evaluation of functional magnetic resonance images of the human brain. *Comput. Med. Imaging Graph.* 25, 449–457.
- Maguire, E.A., Frith, C.D., Morris, R.G.M., 1999. The functional neuro-anatomy of comprehension and memory: the importance of prior knowledge. *Brain* 122, 1839–1850.
- Moll, J., Eslinger, P.J., Oliveira-Souza, R., 2001. Frontopolar and anterior temporal cortex activation in a moral judgment task: preliminary functional MRI results in normal subjects. *Arq. Neuro-Psiquiatr.* 59, 657–664.
- Moll, J., de Oliveira-Souza, R., Bramati, I.E., Grafman, J., 2002. Functional networks in emotional moral and nonmoral social judgments. *Neuroimage* 16, 696–703.
- Nakamura, K., Kubota, K., 1996. The primate temporal pole: its putative role in object recognition and memory. *Behav. Brain Res.* 77, 53–77.
- O’Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D.M., Dolan, R.J., 2003. Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia* 41, 147–155.
- Ongur, D., Ferry, A.T., Price, J.L., 2003. Architectonic subdivision of the human orbital and medial prefrontal cortex. *J. Comp. Neurol.* 460, 425–449.
- Pandya, D.N., Yeterian, E.H., 1996. Comparison of prefrontal architecture and connections. *Philos. Trans. R. Soc. Lond., B Biol. Sci.* 351, 1423–1432.
- Petty, R.E., Wegener, D.T., Fabrigar, L.R., 1997. Attitudes and attitude change. *Ann. Rev. Psychol.* 48, 609–647.
- Ramnani, N., Owen, A.M., 2004. Anterior prefrontal cortex: insights into function from anatomy and neuroimaging. *Nat. Rev. Neurosci.* 5, 184–194.
- Regard, M., Landis, T., 1988. Beauty may differ in each half of the eye of the beholder. In: Rentschler, I., Herzberger, B., Epstein, D. (Eds.), *Beauty and the Brain: Biological Aspects of Aesthetics*. Birkhäuser, Basel, pp. 243–257.
- Schubotz, R.I., von Cramon, D.Y., 2003. Functional–anatomical concepts of human premotor cortex: evidence from fMRI and PET studies. *Neuroimage* 20, 120–131.
- Semendeferi, K., Armstrong, E., Schleicher, A., Zilles, K., Van Hoesen, G.W., 2001. Prefrontal cortex in humans and apes: a comparative study of area 10. *Am. J. Phys. Anthropol.* 114, 224–241.
- Shallice, T., Fletcher, P., Frith, C.D., Grasby, P., Frackowiak, R.S., Dolan, R.J., 1994. Brain regions associated with acquisition and retrieval of verbal episodic memory. *Nature* 368, 633–635.
- Stewart, T.R., 1988. Judgment analysis. In: Brehmer, B., Joyce, C.R.B. (Eds.), *Human Judgment: The SJT View*. North Holland, Amsterdam, pp. 41–74.
- Talairach, J., Tournoux, P., 1988. *Co-Planar Stereotaxic Atlas of the Human Brain*. Thieme, New York.
- Vartanian, O., Goel, V., 2004. Neuroanatomical correlates of aesthetic preference for paintings. *NeuroReport* 15, 893–897.
- Vogeley, K., Kurthen, M., Falkai, P., Maier, W., 1999. Essential functions of the human self model are implemented in the prefrontal cortex. *Conscious. Cogn.* 8, 343–363.
- Volz, K.G., Schubotz, R.I., von Cramon, D.Y., 2003. Predicting events of varying probability: uncertainty investigated by fMRI. *Neuroimage* 19, 271–280.
- Volz, K.G., Schubotz, R.I., von Cramon, D.Y., 2004. Why am I unsure? Internal and external attributions of uncertainty dissociated by fMRI. *Neuroimage* 21, 848–857.
- Wager, T.D., Smith, E.E., 2003. Neuroimaging studies of working memory: a meta-analysis. *Cogn. Affect. Behav. Neurosci.* 3, 255–274.
- Worsley, K.J., Friston, K.J., 1995. Analysis of fMRI time-series revisited—Again. *NeuroImage* 2, 173–181.
- Zysset, S., Huber, O., Ferstl, E., von Cramon, D.Y., 2002. The anterior frontomedian cortex and evaluative judgment: an fMRI study. *Neuroimage* 15, 983–991.