

Neural Correlates of Beauty

Hideaki Kawabata and Semir Zeki

JN 91:1699-1705, 2004. doi:10.1152/jn.00696.2003

You might find this additional information useful...

This article cites 29 articles, 10 of which you can access free at:

<http://jn.physiology.org/cgi/content/full/91/4/1699#BIBL>

This article has been cited by 1 other HighWire hosted article:

The Cognitive Neuroscience of Human Decision Making: A Review and Conceptual Framework

L. K. Fellows

Behav Cogn Neurosci Rev, September 1, 2004; 3 (3): 159-172.

[\[Abstract\]](#) [\[PDF\]](#)

Medline items on this article's topics can be found at <http://highwire.stanford.edu/lists/artbytopic.dtl> on the following topics:

Biophysics .. Functional MRI
Neuroscience .. Motor Cortex

Updated information and services including high-resolution figures, can be found at:

<http://jn.physiology.org/cgi/content/full/91/4/1699>

Additional material and information about *Journal of Neurophysiology* can be found at:

<http://www.the-aps.org/publications/jn>

This information is current as of March 12, 2006 .

Neural Correlates of Beauty

Hideaki Kawabata and Semir Zeki

Wellcome Department of Imaging Neuroscience, University College, London WC1E 6BT, United Kingdom

Submitted 18 July 2003; accepted in final form 20 November 2003

Kawabata, Hideaki and Semir Zeki. Neural correlates of beauty. *J Neurophysiol* 91: 1699–1705, 2004; 10.1152/jn.00696.2003. We have used the technique of functional MRI to address the question of whether there are brain areas that are specifically engaged when subjects view paintings that they consider to be beautiful, regardless of the category of painting (that is whether it is a portrait, a landscape, a still life, or an abstract composition). Prior to scanning, each subject viewed a large number of paintings and classified them into beautiful, neutral, or ugly. They then viewed the same paintings in the scanner. The results show that the perception of different categories of paintings are associated with distinct and specialized visual areas of the brain, that the orbito-frontal cortex is differentially engaged during the perception of beautiful and ugly stimuli, regardless of the category of painting, and that the perception of stimuli as beautiful or ugly mobilizes the motor cortex differentially.

INTRODUCTION

The search for the source of beauty, of whether it resides in the object apprehended or in the perceiving subject, has exercised the speculation of philosophers and writers throughout the ages. Plato, whose writings dominated esthetic theories and discourse for much of the last 2,000 years, believed that beauty has an existence of its own that is independent of the subject apprehending it. Even for him, however, participation by the individual was critical. His lofty discourses in *Phaedrus* and *The Symposium*, which emphasize beauty as something with an eternal presence outside the individual, are nevertheless counterbalanced by the concession in *Hippias Major* that the beautiful is that which “is pleasing to the eye and ear,” that is, by participation. It is with the publication of Kant’s work, and especially the *Critique of Esthetic Judgment*, that the emphasis shifted more to a search for the principles of beauty and esthetic value in the perceiver. Kant perspicaciously asked questions that lend themselves to experimental investigation: what are the conditions implied by the existence of the phenomenon of beauty and what are the presuppositions that give validity to our esthetic judgments? This work is an attempt to address the Kantian question experimentally by inquiring into whether there are specific neural conditions implied by the phenomenon of beauty and whether these are enabled by one or more brain structures. The question that we address here is thus at a very basic level. We have not trespassed into more difficult terrain, to address questions such as the difference between the sublime and the beautiful that so exercised the thinking of those who wrote about beauty, among them Winckelmann (1785), Burke (1958), and Kant (1978). Nor have we addressed the important question of how what an individual regards as beautiful is conditioned by culture, upbringing, and inclination. While acknowledging these important issues, we have tried to

circumvent them by allowing subjects to determine themselves what is beautiful and what is not. Our question thus became the simple one of using paintings to ask whether, regardless of how different subjects perceive them, there are brain areas that are consistently active across subjects when they perceive a painting as being beautiful and, conversely, whether there are brain areas that are specifically active when they view paintings that they consider to be ugly.

While many imaging studies have shown the association of specific functions with distinct parts of the brain, such an association is not a priori obvious in the field of esthetics. Beauty and ugliness constitute polar extremes of a continuum. Instead, therefore, of finding distinct cerebral areas whose activities correlate with the experience of beauty or of ugliness, respectively, it seemed to us equally likely that we would find one or more areas in which the intensity of activity reflects linearly the degree of beauty bestowed on an object by the viewer.

METHODS

Subjects

Ten healthy, right-handed subjects (5 females) in the 20- to 31-yr age range participated in the study. They were all fully educated undergraduate or graduate students, and they had no special experience in painting or art theory. All had normal or corrected-to-normal vision, and none had a history of neurological or psychiatric disorder. Informed consent was obtained from all and the study was approved by the Ethics Committee of the National Hospital for Neurology and Neurosurgery, London, UK.

Psychophysical testing and scaling

In psychophysical experiments prior to imaging, each subject viewed 300 paintings for each painting category that were reproductions viewed on a computer monitor. Each painting was given a score, on a scale from 1 to 10. Scores of 1–4 were classified as “ugly,” 5–6 “neutral,” and 7–10 “beautiful.” Each subject thus arrived at an independent assessment of beautiful, ugly, and neutral paintings. Paintings classified as beautiful by some were classified as ugly by others and vice versa with the consequence that any individual painting did not necessarily belong in the same category for different subjects. Based on these psychophysical tests, a total of 16 stimuli in each category (abstract, still life, landscape, or portrait) were viewed by subjects in the scanner, making a total of 192 paintings viewed by each subject (because each category had paintings that had been classified as beautiful, neutral, or ugly) in random order of blocks in the scanner. However, in the ugly and beautiful categories, only paintings classified as 1–2 and 9–10, respectively, were viewed in the

Address reprint requests and other correspondence to: S. Zeki (E-mail: zeki.pa@ucl.ac.uk).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

scanner, whereas for paintings classified as neutral, paintings belonging to both categories 5 and 6 were viewed.

Functional MRI (fMRI) stimulus

Subjects were scanned between 3 and 6 days after the psychophysical determination described above. The stimuli were back-projected onto a screen viewed through an angled mirror. The resolution of the screen was $1,024 \times 768$ pixels, and the height of each stimulus was 18.85° (600 pixels), whereas the width varied. This was an event-related study, in which the rating (e.g., beautiful, ugly, or neutral) was unpredictable to maintain subjects' attention. Subjects were presented with 12 blocks in random order, each block belonging to a different category of painting (e.g., landscape or portrait). Each block contained eight paintings: of these, six belonged to one judgmental category and two to the other two categories. For example, a block contained eight paintings of which six had been classified as beautiful, one as ugly, and one as neutral. The stimuli in each block were presented in random order. Each epoch (block) lasted 20 s, and each painting was shown for 2 s (no fixation required) with an interstimulus interval of ~ 500 ms, during which the subject fixated a central cross. Each of the paintings was presented twice but not in the same or in subsequent epochs, making a total of 384 presentations. Subjects were required to press one of three buttons in the scanner for each painting to indicate whether it was beautiful, ugly, or neutral.

fMRI data acquisition and analysis

The techniques for data acquisition and analysis have been described before (Zeki et al. 2003). Scanning was done in a 2T Magnetom Vision fMRI scanner with a head-volume coil (Siemens, Erlangen, Germany). A gradient echo planar-imaging (EPI) sequence was selected to maximize the blood oxygen level-dependent (BOLD) contrast (TE, 40 ms; TR, 3.65 s). Each functional image volume of the whole brain was acquired in 48 slices, each consisting of 64×64 pixels, 2-mm thickness, with 1-mm gaps between slices. Statistical analysis was done with SPM99 (Wellcome Department of Imaging Neuroscience, London, UK). The EPI images were realigned spatially, normalized to the Montreal Neurological Institute template provided in SPM99, smoothed spatially with a 10-mm Gaussian kernel, and filtered temporally with a band-pass filter with a low-frequency cutoff period of 300 s and a high-frequency cutoff shaped to the spectral characteristics of the canonical hemodynamic response function within SPM99. The images were also realigned in time by using sinc interpolation before spatial normalization. Data from all 10 subjects were analyzed and combined in a fixed-effects analysis. All of the event types were segregated post hoc into a 3×4 event-related design. The two factors were the different response conditions (beautiful, neutral, and ugly) and the four different painting categories (abstract, landscape, still life, and portrait). The statistical maps were thresholded at $P < 0.05$, corrected for multiple comparisons with an extent threshold of 10 voxels. In the scanning session, all subjects viewed all the pictures and classified them into beautiful, neutral, or ugly by pressing a button. There was no significant difference in reaction time to the different stimuli (Fig. 1), most of which were classified as neutral.

RESULTS

Figure 2 shows that, reflecting the functional specialization of the visual brain (Livingstone and Hubel 1988; Zeki 1978; Zeki et al. 1991), viewing different categories of painting produces activity at different sites within it. This is especially so for faces and landscapes and is regardless of whether the paintings are classified as beautiful or not.

We wanted to search for brain areas that responded specif-

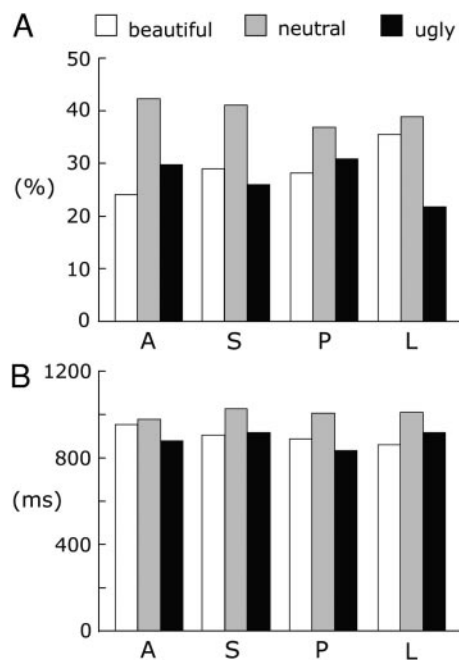


FIG. 1. Behavioral data collected in the functional MRI (fMRI) study. *A*: the proportion of pictures that subjects responded to as beautiful, neutral, or ugly for the picture categories—abstract (A), still life (S), portrait (P), or landscape (L). The proportion for neutral was more than that for beautiful and ugly. *B*: averaged response times by condition and response type. There was no significant difference between categories and between responses in a 2-way ANOVA (4 category \times 3 response type), but the response time for neutral was slower than for other response types.

ically to one category of painting (e.g., portrait) over the others. Such areas can be revealed using a cognitive conjunction approach (CA) (Price and Friston 1997) in which only voxels that show a significant and consistent increase in activity for one class of painting over *any* of the others are included. The contrast portraits versus non-portraits (*A*) produced activity unilaterally in the middle of the fusiform gyrus (fusiform face area (FFA) with Talairach coordinates, 44, -48 , -24 ; $K_E = 383$; $P < 0.001$, corrected), implicated in the recognition of faces (Kanwisher et al. 1997) and bilaterally in the amygdala (left, -34 , -6 , -36 ; $K_E = 26$; $P < 0.001$ corrected; right, 38, -6 , -36 ; $K_E = 43$; $P < 0.001$ corrected), which is also implicated in facial perception (Breiter et al. 1996; Dolan et al. 1996); the CA of landscapes versus non-landscapes (*B*) produced activity in the anterior part of the lingual gyrus (30, -46 , -4 ; $K_E = 204$; $P < 0.001$, corrected), in the para-hippocampal place area (PPA) (Epstein and Kanwisher 1998), extending anteriorly into the hippocampal gyrus, and in area 7 of the parietal cortex of the right hemisphere (18, -72 , 50; $K_E = 16$; $P < 0.005$, corrected); the activity produced by the CA of still life versus non-still life (*C*) was restricted to the lateral and middle occipital gyri, especially centered on left V3 (-26 , -96 , 6; $K_E = 1378$; $P < 0.001$, corrected), but including areas V1 and V2, and extending anteriorly into the posterior lingual gyrus; and at the corrected level, no activity was produced by the CA of abstract versus non-abstract (*D*). This probably reflects the fact that abstract paintings include the same featural and compositional elements that comprise the other paintings but have no additional unique properties, thus canceling out in the subtractions.

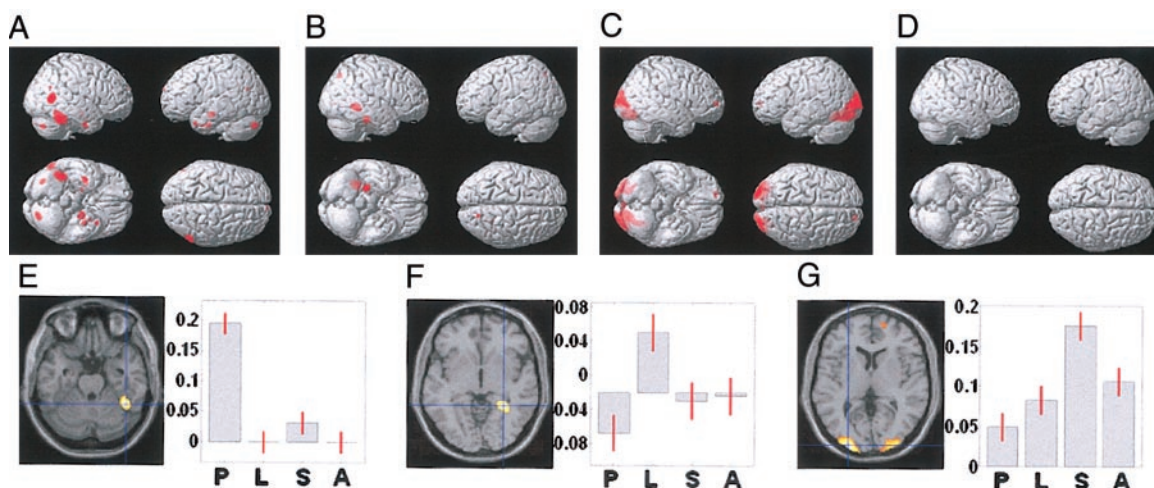


FIG. 2. Statistical parametric maps rendered onto a “standard brain,” showing category-specific activity as assessed by conjunction analysis, in the comparisons of portrait vs. non-portrait (A), landscape vs. non-landscape (B), still life vs. non-still life (C), and abstract vs. non-abstract (D), taken across response categories (corrected, $P < 0.05$). Although abstract paintings produced no activity in the CA-corrected significance level, still life produced the greatest change at V3 (Talairach coordinates, $-26, -96, 6$), portraits in the middle fusiform gyrus (fusiform face area, FFA; $44, -48, -24$), and landscapes at the para-hippocampal place area (PPA; $30, -46, -4$). E–G: averaged parameter estimates for the three different painting categories for portrait (E), landscape (F), and still life (G) with the superimposed slice of the hottest voxel taken through a template brain. Each red bar shows SE of each relative condition.

We next charted, in a fixed effects analysis, areas whose activity correlates with viewing beautiful or ugly paintings regardless of category (Fig. 3). A contrast of beautiful versus ugly produced activity in the medial orbito-frontal cortex alone ($-2, 36, -22$; $K_E = 95$; $P < 0.002$, corrected). A contrast of beautiful versus neutral for all categories produced activity in the orbito-frontal cortex corresponding to BA 11 ($-2, 50, -20$; $K_E = 47$; $P < 0.005$, corrected), and also in the anterior cingulate gyrus, corresponding to BA 32 ($-4, 48, 14$; $K_E =$

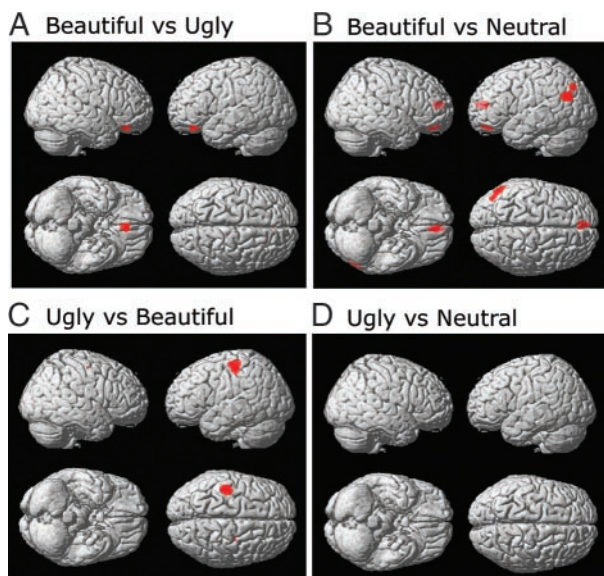


FIG. 3. Statistical parametric maps rendered onto a standard brain showing judgment-specific activity in comparisons of beautiful vs. ugly (A), beautiful vs. neutral (B), ugly vs. beautiful (C), and ugly vs. neutral (D) taken across painting categories (corrected, $P < 0.05$). A: the activity in the medial orbito-frontal cortex only (Talairach coordinates $-2, 36, -22$). B: the activities in medial orbito-frontal cortex ($-2, 50, -20$), anterior cingulate gyrus ($-4, 48, 14$) and left parietal cortex ($-54, -68, 26$). C: somato-motor cortex bilaterally (left $-44, -26, 60$; right $28, -10, 56$). D: no activity at corrected significant level.

148; $P < 0.001$, corrected) and left parietal cortex (BA 39; $-54, -68, 26$; $K_E = 150$; $P < 0.001$ corrected). A comparison of ugly versus beautiful produced activity in the motor cortex bilaterally (left, $-44, -26, 60$; $K_E = 288$; $P < 0.001$ corrected; right, $28, -10, 56$; $K_E = 10$, $P < 0.05$ corrected), whereas the contrast ugly versus neutral produced no activity. Thus the areas that are involved in these contrasts are the medial orbito-frontal cortex, the anterior cingulate, the parietal cortex, and the motor cortex. The activity in motor cortex was more pronounced on the left, possibly reflecting the fact that all our subjects were right-handed. Because the reaction times to beautiful and ugly paintings were the same, the activation of motor cortex is unlikely to be due to differences in reaction times to the two categories (see Fig. 1).

With neutral stimuli acting as a baseline, we were able to chart the strength of activity in these areas as a function of the category of the stimulus. Because the activities in the anterior cingulate and in the parietal cortex only became manifest in the contrast beautiful versus neutral, of greatest interest for our purposes is the activity in the orbito-frontal cortex and the motor cortex. Parameter estimates are shown for all four areas in Fig. 4, in which it can be seen that there is a linear relationship in activity in the orbito-frontal cortex and in the motor cortex, with beautiful pictures producing the highest activity in the former and ugly ones the highest in the latter. No such linear relationship was observed for activity in the anterior cingulate and left parietal cortex. Thus the same areas are involved when stimuli that are considered beautiful or ugly are viewed, but activity in each reflects the judgmental category. The parameter estimates for each subject in the contrast beautiful versus (neutral + ugly) and the contrast ugly versus (beautiful + neutral) are shown in Fig. 5. In Fig. 6, we give the averaged BOLD signal changes for each painting category in the medial orbito-frontal cortex and the left motor cortex. Regardless of the category of painting, the activities show consistent linear relationships in that there is a relative linear

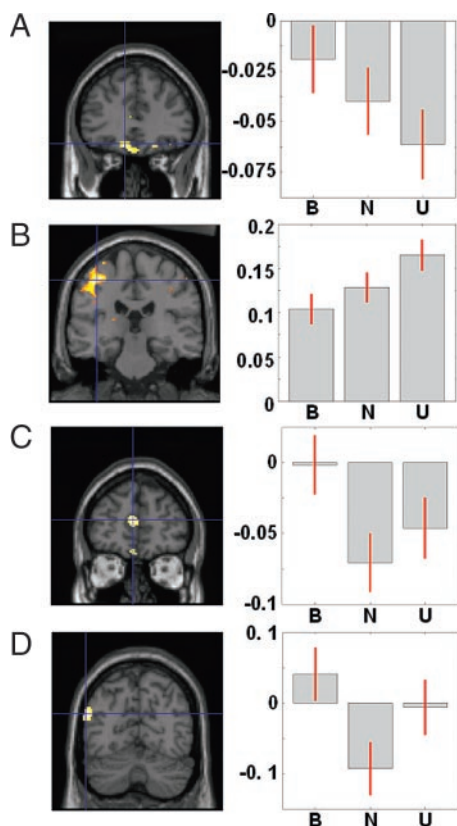


FIG. 4. Averaged parameter estimates for all 3 response categories at medial orbito-frontal cortex (A; Talairach coordinates, $-4, 36, -20$), left motor cortex (B; $-4, 38, -20$), anterior cingulate (C; $-54, -68, 26$), and left parietal cortex (D; $-54, -68, 26$). The medial orbito-frontal cortex and the motor cortex show a significant linear modulation of their response with esthetic judgment (F test, corrected, $P < 0.05$), whereas the anterior cingulate and the parietal cortex show no linear modulation. Each red bar shows SE of each condition.

increase of activity during the viewing of beautiful stimuli, and a decrease with ugly stimuli, even for abstract paintings.

The association of each of the first three category of paintings, regardless of esthetic judgment, with activity in a specific part of the visual brain naturally raised the question of whether it is additional activity in these specialized areas that leads to a painting in the corresponding category being perceived as beautiful or whether other areas are engaged as well. Using portraits and landscapes, which gave the most robust activity in two separate areas corresponding to regions implicated in the perception of faces and of places respectively, we conducted a psychophysiological interaction analysis (Friston et al. 1997) between the medial orbito-frontal cortex and the hottest voxels in the two areas, in a fixed effect analysis. The results, given in Fig. 7, show that there is no consistent relationship in the activity produced by beautiful, neutral, or ugly paintings in the two areas. This implies that it is not extra activity within a center that is specialized for a particular type of stimulus that correlates with whether it is ugly or beautiful.

DISCUSSION

To the simple question of whether there are any specific brain areas that are engaged when subjects perceive something as beautiful, we obtained answers that are partly predictable

and partly not. Predictably, sight of a painting that is to be classified as beautiful or not engages, not the entire visual brain, but only the area(s) that is specialized for the processing and perception of that category of stimulus (Moutoussis and Zeki 2002). Implicit in this demonstration therefore is that a functional specialization lies at the basis of esthetic judgments (Zeki 1995). By this we mean that to be judged as beautiful or not, the picture must be processed by the area specialized for processing that category of work. Predictably too, and in accordance with the mass of imaging data showing the association of specific feelings and emotional states with specific brain structures, the judgment of a painting as beautiful or not correlates with specific brain structures, principally the orbito-frontal cortex, known to be engaged during the perception of rewarding stimuli (Aharon et al. 2001; Francis et al. 1999; Rolls 2000; Small et al. 2001) and, perhaps surprisingly, the motor cortex. Less predictably, the results also tell us that there is no separate structure that is specifically engaged when stimuli are perceived as ugly. Parameter estimates show that it is rather a change in relative activity in the orbito-frontal cortex that correlates with the judgment of beauty and of ugliness. Much the same pattern, though in reverse order, is characteristic of the motor cortex, where stimuli judged to be ugly produced the greatest activity and the beautiful ones the least, although both lead to a change from baseline activity. That the judgmental categories of beautiful and of ugly should not engage separate areas but relative changes of activity in the same areas is supported by previous electrophysiological evidence. Kawasaki et al. (2001) have shown that single neurons in human orbito-frontal cortex increase their responses more to aversive than to pleasant stimuli compared with the neutral state, although they do not give reverse examples. Another

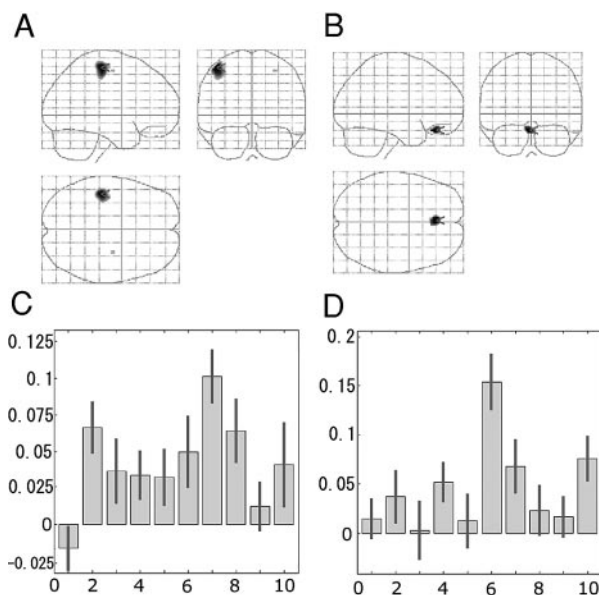


FIG. 5. Brain activities in motor cortex and in orbito-frontal cortex in individual subjects. A and B: glass-brain presentations of group results produced in comparisons of ugly vs. neutral plus beautiful (A) and beautiful vs. ugly plus neutral (B). C and D: averaged-parameter estimates for 10 subjects at the hottest voxel of the somato-motor and the orbito-frontal produced the activities by contrast of B and A. C: consistently higher BOLD responses for beautiful compared with non-beautiful judgments. D: 5 of 10 subjects had significantly more activity for ugly compared with non-ugly judgments in their motor cortex. Each bar shows SE of each condition.

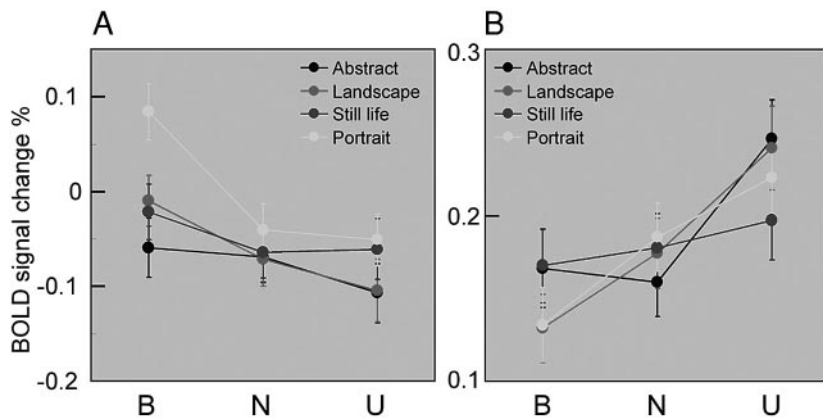


FIG. 6. Averaged blood oxygen level-dependent signal changes taken across all 10 subjects for the 4 different painting categories (abstract, landscape, still life, portrait) and the 3 response categories (beautiful, neutral, ugly) at medial orbito-frontal cortex (A), produced by the contrast of beautiful vs. ugly, and left motor cortex (B) by ugly vs. beautiful. Regardless of painting categories, the signals increase for beautiful judgment at the orbito-frontal cortex and for ugly judgment at the motor cortex.

example of a direct relationship between cell response and reward expectation has been documented for anterior cingulate cortex in the monkey (Shidara and Richmond 2002). If one were able to obtain a good quantification of response vigor, one might be able to study the relationship between neural activity and esthetic judgment (as a function of reward) in a more quantitative way. It is hard to imagine, from these results, the possibility that stimuli judged to be beautiful or ugly engage different types of cell because one would then have expected equivalent responses in orbito-frontal cortex, not relative increases or decreases.

We do not suggest that any of the areas described here act in isolation. Not only do the results suggest a reciprocal interaction between motor and orbito-frontal cortex, but the widespread cortical connections that each of these areas has with other cortical regions makes it likely that each can influence, and be influenced, by widespread regions of the cortex. Of particular interest is the anterior cingulate and the left parietal

cortex, both of which were prominent in the contrast of beautiful versus neutral. Of these, the former is a large cortical zone that has often been associated with a variety of emotional states, such as romantic love (Bartels and Zeki 2000a), pleasurable response to music (Blood and Zatorre 2001), and the viewing of sexually arousing pictures. Although the activations obtained in these studies are not identical in location to the one that we report here, nevertheless the general site of activation is not un-interesting, in that it implies a connection between the esthetic sense and emotions. Also interesting is the activation in the parietal cortex, in a region associated with spatial attention (Corbetta and Shulman 2002). In our studies, this zone was only active in the comparison beautiful versus neutral, which may have placed a greater load on the attentional system.

It is of course important to emphasize that, by its nature, an fMRI study only reveals areas that are especially active during the paradigm used. It does not follow that undetected areas do not contribute in some way to the question under study, a point that is important in assessing all fMRI results. Hence it is possible that, though undetected, many more areas and cortical zones may have been active during the tasks that we have studied although experience with other systems, such as the motion and color system, indicates that the fMRI method is a powerful guide to areas that are especially involved in a given task. It is also important to emphasize that the conclusions drawn here are derived from studies of visual beauty alone. Only future studies using other stimuli and different experimental paradigms will tell whether these conclusions are true of other esthetic experiences—in music, poetry, literature, drama and other human endeavors that have had esthetic appeal.

These results lead us to draw a distinction between two different kinds of brain activation. On the one hand is activity related to a particular types of stimulus—e.g., color or motion—that engages principally a specific area specialized for processing that attribute—in these instances, V4 or V5, respectively. This is so whether these stimuli are presented in isolation (Bartels and Zeki 2000b; Zeki et al. 1991) or as part of a more complex and freely viewed scene (Bartels and Zeki 2004). But unlike an attribute such as motion, which may or may not be present, beauty is part of a continuum, representing a value attributed to it by the brain, a value that, incidentally, can change from one viewing to another and differs between individuals. Here we show that that value correlates with the intensity of activity in the same areas of the brain, and the shift

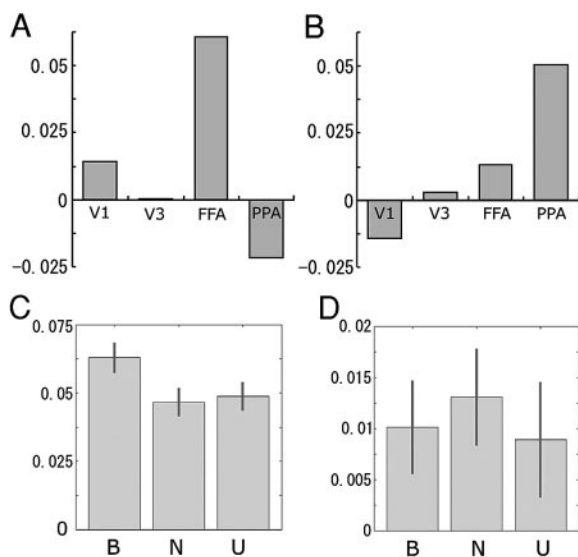


FIG. 7. Psychophysiological interactions between the hottest voxel of the medial orbito-frontal cortex and the peak points (V1, V3, FFA, and PPA) revealed in category-specific analyses (see Fig. 2). The bars show the difference in correlation between these areas in the context of portraits vs. non-portraits (A) and landscape vs. non-landscape (B). The panels show that the activity in the FFA correlates with activity in the medial orbito-frontal cortex in judgments of portraits, and with the activity in PPA for landscape judgments. C and D: averaged parameter estimates for FFA (C) and for PPA (D) for the 3 response categories. Each red bar shows SE for each condition.

from beautiful to ugly does not engage different areas. That both beautiful and ugly stimuli modulate activity in the same cortical area(s) implies that it is the modulation of activity within those areas that correlates with the judgment of a stimulus as being beautiful or not. The distinction between the two types of activation is not, however, exclusive. For example, a graded response in area V5 has been observed when the visibility of a pattern of moving dots is increased by increasing the coherence of the motion of the dots (Rees et al. 2000). As well, an increase in activity within an area can render the individual conscious of a stimulus (Zeki and ffytche 1998). Both naturally raise the primordial question of what determines the increase in activity.

The activation of motor cortex is of special interest. It is not unique to our study. Previous studies on the perception of ugly or fearful faces or other emotionally charged stimuli have also found either unilateral or bilateral activity here even though neither the activity nor its relevance is discussed in these papers. The area is activated, for example, in studies of transgressions of social norms (Berthoz et al. 2002), of fear inducing visual stimuli (Armory and Dolan 2002), of congruent fearful voices and faces, and of anger (Dougherty et al. 1999). It has also been observed during states of visual consciousness (Pinns and ffytche 2003), when it succeeds activity in the occipital lobe. It would therefore seem that activation of motor cortex may be a common correlate not only of the perception of emotionally charged stimuli but also of stimuli of which we become conscious. Why this should be so is conjectural, but it suggests that perception of visual stimuli in general and of emotionally charged stimuli in particular mobilizes the motor system, either to take some action to avoid the ugly or aversive stimulus or, in the case of beautiful stimuli, to make a response toward them. We are puzzled that perception of the beautiful does not mobilize the motor system to the same extent as the perception of the ugly. It is possible that the motor cortex has functions besides the one that is usually attributed to it.

The parallel that we emphasize in the preceding text, between strength of activity and conscious awareness of a stimulus, and strength of activity and its categorization into beautiful or not, is of more than passing interest. Although much studied in the past two decades, no study has been able to pinpoint with certainty what constitutes consciousness in neural terms. The same is true here, where we cannot be said to have been able to determine what constitutes beauty in neural terms. Instead, the more meaningful question for both would currently seem to be the Kantian question outlined in the INTRODUCTION, namely what are the conditions implied by the existence of the phenomenon of beauty (or its absence) and of consciousness (or its absence) and what are the presuppositions that give validity to our esthetic judgments. In esthetics, the answer to both questions must be an activation of the brain's reward system with a certain intensity. The definition of the activity of neural structures that are implicated in the judgment of beauty or in conscious experiences opens up the possibility of studying what in turn determines the strength of activity within the implicated structures.

ACKNOWLEDGMENTS

We are grateful to Drs. M. Self and Andreas Bartels for comments on this paper.

GRANTS

This work was supported by the Wellcome Trust, London.

REFERENCES

- Aharon I, Etcoff N, Ariely D, Chabris CF, O'Connor E, and Breiter HC.** Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron* 32: 537–551, 2001.
- Armory JL and Dolan RJ.** Modulation of spatial attention by fear-conditioned stimuli: an event-related fMRI study. *Neuropsychologia* 40: 817–826, 2002.
- Bartels A and Zeki S.** Neural basis of romantic love. *Neuroreport* 11: 3829–3834, 2000a.
- Bartels A and Zeki S.** The architecture of the colour centre in the human visual brain: new results and a review. *Eur J Neurosci* 12: 172–193, 2000b.
- Bartels A and Zeki S.** The chronoarchitecture of the cerebral cortex. In: *Human Brain Function* (2nd ed.), edited by Frackowiak RSJ, Friston KJ, Frith CD, Dolan RJ, Zeki S, and Price CJ. San Diego, CA: Elsevier, 2003, p. 201–229.
- Berthoz S, Armory JL, Blair RJR, and Dolan RJ.** An fMRI study of intentional and unintentional (embarrassing) violations of social norms. *Brain* 125: 1696–1708, 2002.
- Blood AJ and Zatorre RJ.** Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proc Natl Acad Sci USA* 98: 11818–11823, 2001.
- Breiter HC, Etcoff NL, Whalen PJ, Kennedy WA, Rauch SL, Buckner RL, Strauss MM, Hyman SE, and Rosen BR.** Response and habituation of the human amygdala during visual processing of facial expression. *Neuron* 17: 875–887, 1996.
- Burke E.** *A Philosophical Enquiry into the Origin of Our Ideas of the Sublime and Beautiful* Edited with notes by J. T. Boulton. London, UK: Routledge and K. Paul, 1958.
- Corbetta M and Shulman GL.** Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3: 201–215, 2002.
- Dolan RJ, Fletcher P, Morris J, Kapur N, Deakin JF, and Frith CD.** Neural activation during covert processing of positive emotional facial expressions. *Neuroimage* 4: 194–200, 1996.
- Dougherty DD, Shin LM, Alpert NM, Pitman RK, Orr SP, Lasko M, Macklin ML, Fischman AJ, and Rauch SL.** Anger in healthy men: a PET study using script-driven imagery. *Biol Psychiatry* 46: 466–472, 1999.
- Epstein R and Kanwisher N.** A cortical representation of the local visual environment. *Nature* 392: 598–601, 1998.
- Fan J, Flombaum JI, McCandliss BD, Thomas KM, and Posner MI.** Cognitive and brain consequences of conflict. *Neuroimage* 18: 42–57, 2003.
- Francis S, Rolls ET, Bowtell R, McGlone F, O'Doherty J, Browning A, Clare S, and Smith E.** The representation of pleasant touch in the brain and its relationship with taste and olfactory areas. *Neuroreport* 10: 453–459, 1999.
- Friston KJ, Buechel C, Fink GR, Morris J, Rolls E, and Dolan RJ.** Psychophysiological and modulatory interactions in neuroimaging. *Neuroimage* 6: 218–229, 1997.
- Kant I.** *The Critique of Judgment* translated from the German with analytical indexes by James Creed Meredith. Oxford, UK: Clarendon, 1978.
- Kanwisher N, McDermott J, and Chun MM.** The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J Neurosci* 17: 4302–4311, 1997.
- Kawasaki H, Kaufman O, Damasio H, Damasio AR, Granner M, Bakken H, Hori T, Howard MA, and Adolphs R.** Single-neuron responses to emotional visual stimuli recorded in human ventral prefrontal cortex. *Nat Neurosci* 4: 15–16, 2001.
- Livingstone M and Hubel M.** Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science* 240: 740–749, 1988.
- Moutoussis K and Zeki S.** The relationship between cortical activation and perception investigated with invisible stimuli. *Proc Natl Acad Sci USA* 99: 9527–9532, 2002.
- Pins D and ffytche D.** The neural correlates of conscious vision. *Cereb Cortex* 13: 461–474, 2003.
- Price CJ and Friston KJ.** Cognitive conjunction: a new approach to brain activation experiments. *Neuroimage* 5: 261–270, 1997.
- Rees G, Friston K, and Koch C.** A direct quantitative relationship between the functional properties of human and macaque V5. *Nat. Neurosci* 3: 716–723, 2000.
- Rolls ET.** The orbitofrontal cortex and reward. *Cereb Cortex* 10: 284–294, 2000.

- Shidara M and Richmond BJ.** Anterior cingulate: single neuronal signals related to degree of reward expectancy. *Science* 296: 1709–1711, 2002.
- Small DM, Zatorre RJ, Dagher A, Evans AC, and Jones-Gotman M.** Changes in brain activity related to eating chocolate: from pleasure to aversion. *Brain* 124: 1720–1733, 2001.
- Winckelmann JJ.** *Geschichte der Kunst des Alterthums*. Dresden, Walther: 1764.
- Zeki S.** Functional specialization in the visual cortex of the rhesus monkey. *Nature* 274: 423–428, 1978.
- Zeki S.** The motion vision of the blind. *NeuroImage* 2: 231–235, 1995.
- Zeki S and ffytche D.** The Riddoch syndrome: insights into the neurobiology of conscious vision. *Brain* 121: 25–45, 1998.
- Zeki S, Perry RJ, and Bartels A.** The processing of kinetic contours in the brain. *Cereb Cortex* 13: 193–203, 2003.
- Zeki S, Watson JD, Lueck CJ, Friston KJ, Kennard C, and Frackowiak RSJ.** A direct demonstration of functional specialization in human visual cortex. *J Neurosci* 11: 641–649, 1991.