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The Neural Response to Facial Attractiveness

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What are the neural correlates of attractiveness? Using functional MRI (fMRI), the authors addressed this question in the specific context of the apprehension of faces. When subjects judged facial beauty explicitly, neural activity in a widely distributed network involving the ventral occipital, anterior insular, dorsal posterior parietal, inferior dorsolateral, and medial prefrontal cortices correlated parametrically with the degree of facial attractiveness. When subjects were not attending explicitly to attractiveness, but rather were judging facial identity, the ventral occipital region remained responsive to facial beauty. The authors propose that this region, which includes the fusiform face area (FFA), the lateral occipital cortex (LOC), and medially adjacent regions, is activated automatically by beauty and may serve as a neural trigger for pervasive effects of attractiveness in social interactions.

Keywords: beauty, neuroaesthetics, face processing, fMRI, reward

Facial attractiveness is likely to be deeply encoded in our biology. Cross-cultural judgments of facial beauty are quite consistent (Etcoff, 1999; Jones & Hill, 1993; Perrett, May, & Yoshikawa, 1994). Adults and children within and across cultures show high rates of agreement in judgments of facial attractiveness (Langlois et al., 2000) suggesting that universal principles of beauty exist. Further evidence for the view that biologic underpinnings drive our response to attractiveness comes from infant studies. Infants look longer at attractive faces within a week of being born, and the effects of attractiveness on infants' gaze generalize across race, gender, and age by 6 months (Langlois, Ritter, Roggman, & Vaughn, 1991; Slater et al., 1998). Thus, the disposition to engage attractive faces is present in brains that have not been modified greatly by experience. These observations do not mean that judgments of beauty are not shaped further by cultural factors (Cunningham, Barbee, & Philhower, 2002), but some components of these judgments are likely to be universal, components that may have distinct neural underpinnings (Chatterjee, 2004).

Theorists postulate two possible (though not mutually exclusive) evolutionary mechanisms for why certain faces are considered more attractive than others (Rhodes, Harwood, Yoshikawa, Miwi, & McLean, 2002). The first possibility is that attractive features represent phenotypic attributes that are desirable in selecting mates, such as genetic health and levels of immunocompetence (Etcoff, 1999; Grammer, Fink, Moller, & Thornhill, 2003; Penton-Voak et al., 2001; Perrett et al., 1998; Symons, 1979; Thornhill & Gangestad, 1999). On this view, the nervous system has evolved to be attracted to specific configurations of facial features that signal "good genes," configurations that we have come to regard as beautiful. The second possibility is that preferences arise as a by-product of a general information-processing mechanism. The leading candidate for such a mechanism is the extraction of a prototype, or the central exemplar of a category. People prefer prototypes of different kinds of stimuli, such as color (Martindale & Moore, 1988) and music (Smith & Melara, 1990). Faces would presumably be another category of stimuli subject to this biased preference for prototypes (Halberstadt & Rhodes, 2000).

How might the nervous system respond to beauty? Such a response might have at least three components. These components are the perceptual processing of the object itself, the emotional response to the object and, when relevant, an explicit judgment about the object's beauty. A few studies have reported that attractive faces activate areas within the orbito-frontal cortex, the nucleus accumbens or the ventral striatum (Aharon et al., 2001; Ishai, 2007; Kampe, Frith, Dolan, & Frith, 2001; Kranz & Ishai, 2006; O'Doherty et al., 2003) and that the amygdala has a nonlinear relationship to attractiveness (Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007). These regional activations, within neural circuitry dedicated to reward systems, are interpreted as reflecting the emotional valence attached to attractive faces (Senior, 2003). The particular emotional valences are those involved in the expectation of rewards and the satisfaction of appetites. The idea that attractive faces are rewarding stimuli, at least for men, is evident behaviorally. Men are willing to discount higher future rewards for smaller immediate rewards when it comes to attractive female faces (Wilson & Daly, 2004). Presumably, these patterns of neural activation reflect ways in which attractive faces influence mate selection (Ishai, 2007). The judgment of beauty, as distinct from its emotional evocations, involves parts of the prefrontal cortex. One positron emission tomography study showed left frontal activation when subjects assessed facial attractiveness (Nakamura et al., 1998). Medial frontal involvement may generalize beyond faces to responses to beauty of even abstract images as reported by Jacobsen and colleagues (Jacobsen, Schubotz, Hofel, & v Cramon, 2005).

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In contrast to these findings about the emotional response to and judgment of facial beauty, little is known about the neural underpinnings of the perceptual apprehension of attractive faces. Winston and colleagues (Winston et al., 2007) found left posterior occipito-temporal activity was enhanced by facial attractiveness, but did not explore this finding further. Similarly, Kranz and Ishai (Kranz & Ishai, 2006) found increased activations for attractive female faces than for unattractive female faces in the lateral fusiform gyrus, but focused their discussion on activations within reward networks. Perceptual features of faces, such as averageness, symmetry, the structure of cheek-bones, the relative size of the lower half of the face and the width of the jaw, influence people's judgments of facial beauty (Enquist & Arak, 1994; Grammer & Thornhill, 1994; Penton-Voak et al., 2001). The influence of such perceptual features suggest that lower-level visual processing that occurs before object processing per se and can affect aesthetic judgments (Chatterjee, 2004) might play a role in facial beauty perception. With this possibility in mind, we paid special attention to ventral visual association areas in this study.

Motivated by the logic that facial attractiveness is likely to have biological underpinnings, we tested two hypotheses using fMRI. First, we tested the hypothesis that explicit judgment of beauty is associated with a distributed neural response to increasing levels of beauty, which includes neural structures involved in visual processing. Specifically, areas of higher visual processing are of interest. We specifically looked at visual association areas associated with processing of faces, places, and objects. Reward circuits, including orbitofrontal, insular medial prefrontal and posterior cingulate cortex, and the ventral striatum, might be activated and we would anticipate that dorsolateral prefrontal and parietal circuits might be involved in the decision making process.

Second, we tested the hypothesis that attractiveness of faces would continue to modulate neural responses within part of the network engaged in explicit judgments, even when subjects are not explicitly considering beauty. Individuals with brain damage may develop prosopagnosia, a deficit in which the ability to recognize faces is impaired. Some prosopagnosics respond differently (e.g., with different autonomic responses) to familiar than unfamiliar faces despite not being able to explicitly recognize either (Bauer, 1984; Tranel & Damasio, 1985). Faces, in general are processed more efficiently than other visual objects and certain attributes such as emotions conveyed in these faces are processed quite rapidly (for a review see Palermo & Rhodes, 2007). With respect to attractiveness, normal subjects apprehend facial beauty at a glance (Olson & Marshuetz, 2005). Finally, Winston and colleagues (Winston et al., 2007) found that parts of medial orbitofrontal cortices responded to facial attractiveness even when subjects made judgments of age rather than attractiveness of faces. They reasonably interpret these activations as related to the rewarding properties of the stimuli that are engaged automatically when viewing attractive faces. However, they did not pursue the hypothesis that perceptual responses to more attractive faces might trigger the activation of these reward circuits.

We should also be clear that despite our interest in the neural response in visual association areas to facial attractiveness, we are not explicitly investigating which visual properties of faces are producing these responses. Our study focuses on what Fechner (Fechner, 1860) referred to as an inner psychophysics (the relationship between subjective experiences and the physical properties of the nervous system) rather than on an outer psychophysics (the relationship between subjective experiences and the physical properties of the stimuli).

Method

Participants

The study was approved by the Institutional Review Board of the University of Pennsylvania. All subjects gave informed consent before participating in the experiments. Thirteen subjects participated in two scanning sessions. There were seven men and six women, age range 18 to 32 (mean 22.6).

Stimuli

Artificial face stimuli were created using commercial software (GenHead by Genemation, http://www.genemation.com/) that was modified for use in our lab. The software allows creation of human faces where the facial identity is determined by settings on each of 114 parameters, each an eigenvector derived from a principal components analysis of a large database of face photographs. Additional parameters allow control over ethnicity, age, and gender. Pilot behavioral studies were used to normalize the perceptual salience of changes in each of the 114 parameters, and to standardize those parameters that had an obvious effect upon the direction of gaze or facial expression. Therefore, all faces appeared in the full frontal position with a neutral expression. Faces could then be created with a normalized measure of distinctiveness, or measured distance from the average face.

We created a set of 100 face sets (50 male, 50 female). Each set initially contained two faces of clearly different identities. All faces were White between the ages of 20 and 30 years, with the same distinctiveness score within the parameterized face space (distance to the average). One face from each pair was arbitrarily designated the "start" face and the other labeled the "end" face. These pairs were then "morphed" to create faces at intermediate points within the parameterized face space. The path between the pairs of faces was computed so that the intermediate points were also at the same distance from the average face. The distance of the intermediate faces from the "start" face were expressed in terms of the % morph toward the "end" face; for example, 33% morph (2/3 "start" face-1/3 "end" face), 66% morph (1/3 "start" face- 2/3 "end" face), and so forth. Therefore, each final face set consisted of four faces: the "start" face, 33% morph, 66% morph, and "end" face (see Figure 1). The face stimuli were full color (32 bits/pixel), and set to be a uniform 288 × 288 pixel size.

Procedure

Each subject participated in two separate scanning sessions, with order of scanning sessions randomized across subjects. The time between scanning sessions ranged between 6 and 49 days (mean 27.6).

During both sessions, the stimuli consisted of 500 face pair trials and 200 additional blank trials during which no stimuli were presented and the subjects did not provide responses. During each of the 500 trials, the subject would view two faces in quick succession (each stimulus duration 1 second, ISI 25 milliseconds, ITI 975 milliseconds). The first face was always a "start" face from

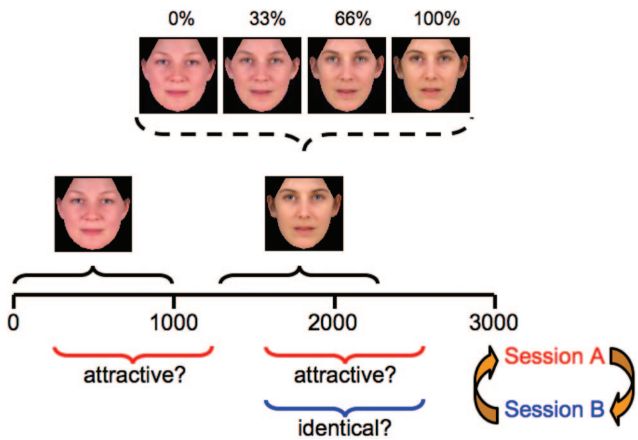

Figure 1. Arrangement of stimulus events and subject responses for the two tasks. During the two separate scanning sessions subjects viewed pairs of face stimuli. These stimuli were either identical or differed to a greater or lesser degree. During one scanning session, subjects judged the attractiveness of each face in the presented pair of faces. During a separate scanning session subjects judged if the second of the pair of faces matched the first.

one of the 100 face sets. The second face was either the same as the first face (both faces the "start" face), completely different (the "start" and "end" face), or a 33% or 66% "morph" between the "start" and "end" faces. As there were 500 trials and only 400 unique crossings of face sets with degree of change, 100 randomly selected trials during each scanning session repeated a particular face pairing. The order of trials was pseudorandom (determined by use of the OptSeq routine; http://surfer.nmr.mgh.harvard.edu/optseq/).

During the *attractiveness* judgment task performed during one scanning session, subjects were asked to judge whether each face was "more or less attractive than average." The subject was explicitly instructed not to judge if they personally found themselves attracted to the presented face, but instead to judge if the face was better or worse looking than an average person. Subjects made a judgment and provided a response for each of the two faces presented in a trial. In the *identity* judgment task performed during the other scanning session, subjects were asked to judge if the second face of each pair of faces was identical to, or in any way different from, the first face. A response was made only after presentation of the second face. In both tasks, subjects indicated their response by pressing either a top pair or bottom pair of buttons using both thumbs. Figure 1 illustrates the structure of the scanning tasks.

In addition to the difference in judgment required by the subject, the tasks also differed in that participants responded to each face during the attractiveness rating session and only to the second of the two faces in the identity judgment. The temporal proximity of face pairs also requires the modeling of facial attractiveness as the average attractiveness of each pair of faces (see below). These limitations result from the design of the study to measure neural adaptation resulting from facial similarity, as opposed to attractiveness; our finding regarding the effects of attractiveness even when subjects were making identity judgments was serendipitous. We submit that the inelegance of the design does not itself invalidate the actual findings regarding the neural effect of facial attractiveness.

MRI Scanning

Scanning was performed on a three Tesla Siemmens Trio using a standard quadrature head coil. Echoplanar BOLD fMRI data were collected at a TR of 3 seconds, with 3 × 3 × 3 mm isotropic voxels covering the entire brain. Head motion was minimized with foam padding, and prospective motion correction (PACE) was performed during image acquisition. A high-resolution anatomical image (3D MPRAGE) with 1 × 1 × 1 mm voxels was also acquired for each subject. Visual stimuli were presented using an Epson 8100 3-LCD projector with Buhl long-throw lenses for rear-projection onto Mylar screens, which subjects viewed through a mirror mounted on the head coil. Subject responses were recorded using a fiber-optic response pad (FORP) (http://www.curdes.com/newforp.htm).

A total of seven BOLD fMRI scanning runs were completed during each scanning session and each composed of 140 images. The first five scans were dedicated to the attractiveness or discrimination tasks. The two additional BOLD scans were used for definition of functional regions of interest (ROIs). Categorical functional ROIs were defined for faces (the fusiform face area or FFA), buildings (the parahippocampal place area or PPA), and general object forms (the lateral occipital cortex or LOC) using previously described methods (Aguirre, Singh, & D'Esposito, 1999).

Data Preprocessing and Statistical Analysis

BOLD fMRI data were processed using the VoxBo (http://www.voxbo.org/) software package. After image reconstruction the data were sinc interpolated in time to correct for the fMRI acquisition sequence (Aguirre, Zarahn, & D'Esposito, 1997), motion corrected, transformed to a standard spatial frame (using SPM2; http://www.fil.ion.ucl.ac.uk/spm), and spatially smoothed with a three voxel FWHM 3D Gaussian kernel.

The relative attractiveness of each of the 400 face stimuli was determined by the proportion of agreement of "better than average" judgments across the 13 subjects for each face (see Figure 2). The highest possible score for a face was therefore unity if all 13 subjects indicated that the face was better looking than average, and zero if all subjects felt the subject was worse looking than average. We confirmed that this measure of a dichotomous judgment produces similar attractiveness ratings as obtained with a Likert scale. Thirty different subjects (mean age 22.7) rated the faces presented in the fMRI study for the same duration using a 5-point scale. The averaged Likert judgments of attractiveness for each face correlated highly (r = .85) with the proportion of agreement scores obtained during the scanning experiment, suggesting that these methods of ascribing levels of attractiveness to each of the faces in this set are comparable.

Within-subject statistical models of the fMRI data were created as follows. Trials in which subjects made a correct response (correct in the beauty judgment session defined as any response within the response-time window) were identified. As the two faces in each trial were presented in close temporal proximity (preventing measurement of the BOLD response unique to each face), the average of the attractiveness rating scores of the two faces was assigned to the trial. An attractiveness covariate was then constructed by modeling a step function of linear effect of attractiveness score upon neural response for the 3 seconds of the

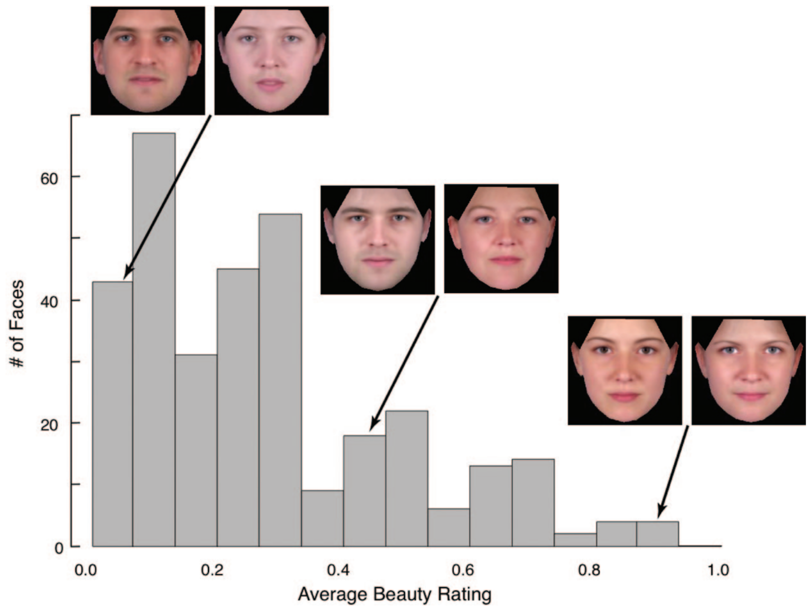

Figure 2. Frequency histogram of subjects' agreement for facial attractiveness, with examples. Subject judgments of face attractiveness were aggregated to produce an attractiveness score for each face. Faces considered less attractive than average by all subjects would be rated 0.0. Faces considered more attractive than average by all subjects would be rated 1.0.

trial, convolved by a standard hemodynamic response function (Aguirre, Zarahn, & D'Esposito, 1998). The attractiveness scores were mean centered before convolution, to render the covariate orthogonal to the main effect of stimulus presentation versus the null-trials. In other words, the attractiveness covariate modeled the variation in neural response to the presentation of a face that could be linearly related to the attractiveness of the face.

Additional covariates, not of interest here, modeled the main effect of stimulus presentation versus null-trials, the similarity of pairs of faces, a polynomial expansion of this similarity covariate, and the average reaction time of subject responses in each trial. Nuisance covariates for effects of scan and global signals were also included. Time series data were subjected to a high-pass (0.0075 Hz) filter, and serial correlation of error terms was modeled as previously described (Zarahn, Aguirre, & D'Esposito, 1997). Second order (random effect) analyses were based upon the beta values measured for the particular covariate of interest. Whole-brain statistical maps were prepared as "effect size maps," in which the average beta value attributed to the effect of facial beauty was scaled by the average beta value attributed to the effect of the presentation of a face versus null-trials. This permits the assessment of continuous effects across the cortex and the magnitude of the effect of attractiveness. Mapwise significance was also estimated using permutation testing (Nichols & Holmes, 2002).

The ROI localization scans were analyzed using a fixed-effects analysis across subjects. A fixed-effects analysis was felt to be appropriate for this purpose as no hypothesis was being tested regarding the existence of these well-established functional regions. Instead, maximal sensitivity was desired for identifying their average location within this set of subjects. The fusiform face area (FFA) was identified by the voxels within the fusiform gyrus that demonstrated substantially greater response to faces than to pictures of objects and buildings, and the parahippocampal place area (PPA) identified with the complementary contrast. A region was generated for "form responsive cortex" by identifying those voxels that had a greater response for faces, objects, or buildings versus the scrambled stimuli. The lateral occipital cortex (LOC) was identified as the region with the largest average difference between the formed stimuli and the phase-scrambled stimuli (see Figure 3).

Results

No significant differences according to gender were found for either task. Therefore, we performed the following analyses with data collapsed across gender. There was a modest correlation ($r = .270$) between the attractiveness scores and reaction times (RT) when subjects performed explicit judgments of facial beauty. Table 1 provides the average RTs for the different sessions binned by facial attractiveness. The analysis of the fMRI data included a covariate that modeled each subject's average reaction time to each pair of faces, so that any relationship between the attractiveness covariate and neural activity would not be a first-order effect of how long the subjects looked at the faces.

ROI analyses revealed neural activity correlated with attractiveness ratings in the FFA and LOC bilaterally (for all four ROIs, p values <0.02), but not in the PPA (both p values > 0.8). An ANOVA showed that the effects of beauty interacted with the ROIs ($F(2,72) = 6.029$, $p = .004$) but not by hemisphere ($F(1,72) = 0.525$, p = NS). Post hoc tests showed effects in LOC > PPA ($p = .003$), a trend toward FFA > PPA ($p = .054$) and no difference between FFA and LOC. Whole brain analyses showed that the ventral activations extended between and adjacent to FFA and LOC (see Figure 3). Additional correlated activity was

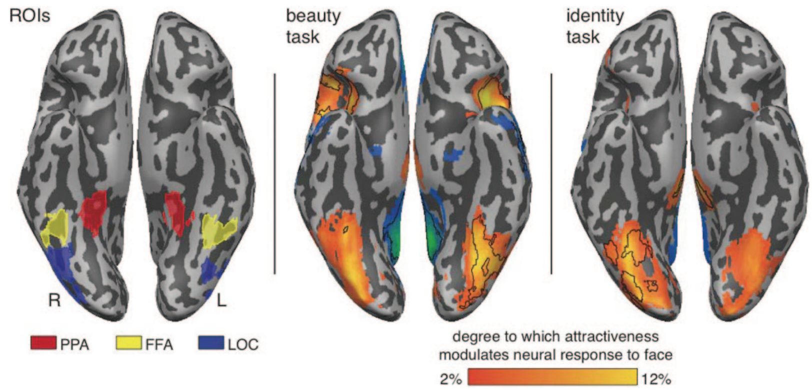

Figure 3. Ventral cortical neural responses to facial beauty. Ventral surface of the inflated brain showing regions in which neural activity across subjects varied parametrically with the rated attractiveness of presented faces. The image on the left shows functionally defined ROIs: PPA in red, FFA in yellow and LOC in blue. The central figure shows effects of explicit judgments of facial beauty. The right figure shows effects of facial attractiveness during identity judgments. The color scale (red-yellow) indicates the degree to which facial beauty positively modulated neural responses, scaled by the average magnitude of neural response to face presentation within visual areas (blue-green indicates a greater response to unattractive than attractive faces). The map was arbitrarily thresholded at 2%. Outlined in black are those areas of signal change that were significant at a whole-brain level (determined by permutation analysis, $p < .05$ corrected for multiple comparisons, t(12 *df*) = 3.6, cluster = 100 voxels). We present these data in this manner because the unilateral appearance of the significant areas is belied by the results of ROI analyses and the clearly continuous appearance of the underlying effect sizes.

found in the dorsal posterior parietal cortex, anterior insula, inferior and medial prefrontal regions bilaterally (see Figure 4). Negatively correlated activity was seen in the anterior and posterior cingulate cortex. See Table 2 for details of whole brain activation results.

In the identity judgment task, no correlation between the beauty ratings and RT was found (r = −0.024), reflecting that facial attractiveness was irrelevant to performance of the task (see also Table 1). Nonetheless, neural activity was correlated with facial attractiveness within the LOC bilaterally ($p < .007$ in both cases) and the FFA on the left ($p < .003$), but not the right ($p > .1$). There was no significant effect of facial beauty within the PPA (for both, $p > .5$). Again, whole brain analyses revealed that this ventral activation extended across the FFA (see Figure 5) and LOC as well as in adjacent medial regions, and did not represent two distinct activation peaks (see Figure 3). The distribution of activity was similar to the pattern seen when subjects made explicit attractiveness judgments. Significant activation was also seen in the pulvinar bilaterally, but not in parietal or prefrontal regions. We did not have adequate signal within the orbitofrontal cortex to test the hypothesis that this region was activated explicitly or automatically by facial attractiveness.

Table 1
Reactions Times to Face Presentations During Scanning

	Attractiveness rating		
	0–0.3	0.3–0.7	0.7–1
Identity task			
Face 1	602 ± 169	604 ± 167	583 ± 172
Face 2	598 ± 173	610 ± 161	617 ± 150
Both	600 ± 170	600 ± 166	660 ± 163
Beauty task			
Face 1	629 ± 58	680 ± 53	677 ± 50
Face 2	512 ± 78	551 ± 72	564 ± 75
Both	570 ± 92	619 ± 85	608 ± 106

Note. Each cell presents the average (±*SD*) reaction time in msecs across subjects measured during the two scanning. Tasks, binned by the attractiveness rating of the two faces presented during each trial. As participants responded to each face during the beauty judgment task session, the reaction time to each face was binned by the attractiveness of the face that was presented. The average reaction time to the two faces is presented. In the "both" row, binned by the average attractiveness of the two faces in the trial. During the identity judgment task session, participants made a single response after both faces were presented. Accordingly, the reaction time for each trial was binned by the attractiveness of the first face or the attractiveness of the second face, or the average attractiveness of the two faces to produce the values in the table.

Discussion

Our results confirm that the apprehension of facial beauty is associated with an identifiable neural response. When subjects make explicit judgments of attractiveness, neural activity within a distributed network involving ventral visual association cortices and parts of dorsal posterior parietal and prefrontal cortices varied parametrically with the degree of attractiveness of the faces viewed. The response to beauty did not represent a general activation of visual association areas, as the effects were not evident in brain regions that process buildings and landscapes. We interpret the ventral occipito-temporal activations as being involved in the visual processing of attractive faces. Recently, Winston and colleagues (Winston et al., 2007) found a similar region activated more robustly when subjects judged facial attractiveness as com-

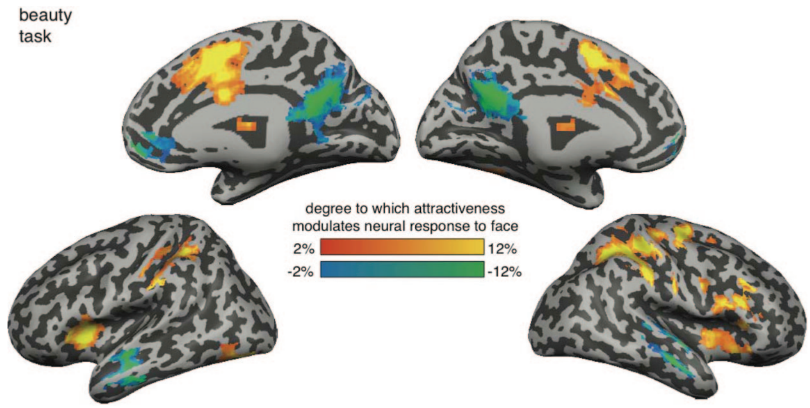

Figure 4. Lateral and medial neural responses to explicit judgments of beauty. Lateral and medial surface of the inflated brain showing regions in which there was a significant effect of facial beauty during explicit judgment of attractiveness. The color scale indicates the size of the statistical effect, thesholded at a mapwise level (determined by permutation analysis, $p < .05$ corrected for multiple comparisons, $t(12\ df) = 3.6$, cluster = 100 voxels).

pared to facial age. However, they did not explore the implications of activation within this region further.

The parietal, medial, and dorsolateral frontal activations were present only during explicit judgments of beauty. We propose that these areas represent neural correlates of the attention and decision-making components of this task. The positively correlated insular activations and negatively correlated anterior and posterior cingulate activations are likely to represent emotional responses to attractiveness. The frontomedian activation pattern, also reported by O'Doherty and colleagues in response to attractive faces (O'Doherty et al., 2003) are similar to activation patterns reported by Jacobsen and colleagues found to beauty judgments of abstract geometric images (Jacobsen et al., 2005). Jacobsen and colleagues emphasized that frontomedian activity is probably involved in the evaluative component of aesthetic judgments, and might turn out to be involved regardless of the domain in which these judgments are being made. This interpretation is consonant with the view that this region is involved when one's evaluation draws on an inter-

Table 2
Anatomic Regions Demonstrating Activity That Correlated Parametrically With Attractiveness Ratings of Faces in the Whole Brain Analyses for Both the Explicit Beauty and the Identity Judgment Task

Effects of beauty during explicit beauty judgments							
Area	Voxel count	Tal X	Tal Y	Tal Z	Max $t_{(12)}$	Min $t_{(12)}$	Avg $t_{(12)}$
Inferior fusiform (L)	171	−26	−53	−23	5.6	3.7	4.2
Inferior fusiform (L)	97	−33	−75	−19	5.5	3.7	4.4
Inferior fusiform (R)	98	21	−51	−27	5.3	3.7	4.2
Anterior cingulate (R)	686	1	5	41	10.1	3.7	4.8
Post cingulate (L)	649	−1	−57	20	−3.7	−6.9	−4.7
Inferior parietal lobule (R)	573	34	−39	40	7.3	3.7	4.7
Inferior parietal lobule (L)	178	−41	−36	38	5.9	3.7	4.2
Insula (R)	352	34	12	2	6.4	3.7	4.3
Insula (L)	239	−34	14	5	6.6	3.7	4.6
Inferior anterior cingulate (R)	114	1	43	1	−3.7	−8.2	−5.0
Middle temporal (L)	149	−50	−13	−14	−3.7	−6.8	−4.6
Middle temporal (R)	150	47	−15	−14	−3.7	−8.7	−4.6
Thalamus (R)	307	12	−14	9	8.5	3.7	4.9
Thalamus (L)	184	−11	−14	10	5.4	3.7	4.3
Effects of beauty during identity judgments							
Area	Voxel count	Tal X	Tal Y	Tal Z	Max t	Min t	Avg t
Inferior occipital (R)	157	23	−86	−5	4.9	3.5	4.0
Inferior fusiform (R)	88	27	−65	−12	5.7	3.5	4.1
Central sulcus (L)	119	−40	−25	49	−3.5	−6.7	−4.2

Note. Talairach coordinates show the geometric center of activations in these different anatomic regions.

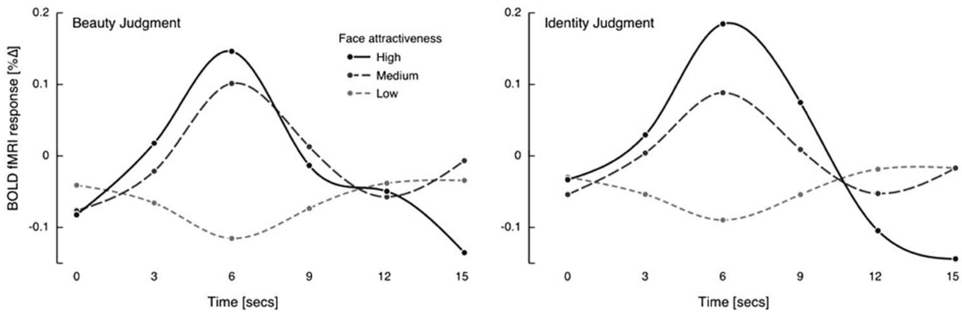

Figure 5. Time course of BOLD responses within FFA to faces binned into high medium and low attractiveness for both the beauty and the identity judgment conditions. Similar response patterns occurred within LOC, but not within PPA.

nally generated and self-referential processes (Christoff & Gabrielli, 2000), such as "what do I think of the beauty of this object?" Our observations that activity in posterior cingulate region correlates negatively with degree of attractiveness, raises the possibility that these neural structures are engaged in the negative evaluation of the beauty of an object. In that regard, it is of particular interest that these regions are part of a paralimbic neural system that is dysregulated and overactive in the resting state in depressed individuals (Mayberg, 1997; Mayberg et al., 1999). These patients are often anhedonic and do not derive pleasure from objects that others find pleasurable (Snaith, 1993). Thus, a predisposition to negatively evaluate attractive objects may be a component of these patients' anhedonia.

When our participants judged facial identity, specific regions within visual association cortices continued to respond to facial attractiveness. Despite the irrelevance of beauty to the task, facial beauty modified evoked neural response to faces by as much as 10% in some areas (see Figure 3). Again, the FFA and LOC and not the PPA, were sensitive to degrees of facial attractiveness. Whole brain analyses revealed that this activity occurred in a contiguous area within and adjacent to the FFA and LOC across the fusiform and inferior occipital gyrus. Our findings suggest that this ventral occipital region responds to beauty automatically, regardless of the task in which the subject is engaged. This region may be involved in visual processing before object identification, such as the apprehension of symmetry and grouping, which also occur automatically and influence aesthetic judgment (Chatterjee, 2004). The fact that this ventral occipital region of activation extended beyond parts of cortices especially sensitive to faces raises the possibility that this area may be responsive to aesthetic objects more generally. Consistent with this possibility, in an fMRI study Vartanian and Goel (Vartanian & Goel, 2004) found that activity within this area correlated with preferences for paintings, especially for representational ones and Jacobsen and colleagues (Jacobsen et al., 2005) found this area to be responsive to symmetry and aesthetic judgments for novel graphic abstract images.

Could this ventral occipital activation be the neural signature of the extraction of facial prototypes? On this account, the FFA responses to attractiveness would simply be a reflection of increased activity to facial averageness. This hypothesis is unlikely to be accurate, since activity within FFA correlates with facial distinctiveness rather than averageness (Loffler, Yourganov, Wilkinson, & Wilson, 2005). Furthermore, the neural response to facial beauty was not confined to face processing areas, and extended to area LOC. Further research will be needed to determine which perceptual attributes (such as symmetry, or relative sizes of different facial features) drive the increased activity within LOC.

Is it possible that the ventral-occipital activations reflect greater attention to attractive faces rather than a response to beauty per se? For two reasons, we think this explanation is unlikely. First, regions traditionally associated with attention, such as the posterior parietal cortex were activated by the explicit beauty judgment conditions and not the identity judgment condition, suggesting attentional engagement with attractive faces in the former condition but not the latter. Second, one could test these alternate hypotheses directly by using faces in which attractiveness and attentional salience are not monotonically correlated. For example, especially unattractive faces also engage attention. Winston and colleagues (Winston et al., 2007) did use faces that covered a wide range and found amygdala rather than the ventral occipital activations were activated by both highly attractive and highly unattractive faces.

The stimuli used in our experiment on the whole did not contain faces at either extreme of an attractiveness continuum, super model faces or extremely unattractive faces. Such faces might be more likely to evoke automatic activity within the amygdala and reward circuitry than our stimuli as Winston and colleagues found (Winston et al., 2007). We remain agnostic about orbitofrontal involvement, because we did not have adequate signal within these regions to test the hypothesis that attractiveness engages these areas.

Attractiveness has pervasive social effects beyond its specific role in mate selection. Attractive children are considered more intelligent, honest, and pleasant, and are thought to be natural leaders (Kenealy, Frude, & Shaw, 1988; Lerner, Lerner, Hess, & Schwab, 1991; Ritts, Patterson, & Tubbs, 1992). Attractive adults are judged to have socially desirable traits, such as strength and sensitivity (Dion, Berscheid, & Walster, 1972). They are considered more competent as politicians (Lewis & Bierly, 1990), professors (Romano & Bordiere, 1989), and counselors (Green, 1986). Attractive people are preferred in hiring decisions (Rynes & Gerhart, 1990), earn more money (Hamermesh & Biddle, 2001), and receive lesser punishments for transgressions (Dion, 1972). Thus, a person's attractiveness influences social interactions in ways that extends far beyond domains in which attractiveness per se is directly relevant.

The fact that people are often unaware of the extent to which attractiveness influences social judgments suggests that facial beauty may be one of a number of facial attributes apprehended automatically (Palermo & Rhodes, 2007). Facial beauty can be apprehended at a glance and can bias subsequent cognitive judgments (Olson & Marshuetz, 2005). The cascade of neural events that result in biases in high-level social decisions is likely to be triggered by an early perceptual response to attractiveness. We propose that neural activity within ventral visual cortices in response to facial attractiveness, which occurs even when subjects are not considering beauty explicitly, serves as the initial trigger for this cascade. Further along this cascade, medial orbitofrontal mediation (an area in which we had poor signal detection) may support the emotional valence engendered by attractive faces automatically (Winston et al., 2007). Senior (Senior, 2003) suggested that the neural underpinning of face perception has a core system (the inferior occipital gyri, the lateral fusiform gyri, and the superior temporal sulcus) dedicated to perceptual processing, and an extended system (the extended amygdala and reward circuitry) dedicated the appraisal of beauty and its rewarding and aesthetic consequences. This speculation, which he considered provisional, was motivated by two studies of facial attractiveness (Aharon et al., 2001; O'Doherty et al., 2003). Our findings suggest that the initial automatic appraisal of facial beauty occurs earlier than Senior anticipated, within what he referred to as the core system.

In summary, we confirm that facial beauty evokes a widely distributed neural network involving perceptual, decision-making and reward circuits. In our experiment, the perceptual response across FFA and LOC remained present even when subjects were not attending explicitly to facial beauty. A general and testable hypothesis generated by these results is that the perceptual response to visual beauty involves patterns of domain specific and nonspecific regional activations. Thus, other objects, such as attractive bodies or beautiful landscapes might be accompanied by greater activity that extend from domain specific cortical regions such as the extrastriate body area or the parahippocampal place area into LOC.

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