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Beautiful Faces Have Variable Reward Value: fMRI and Behavioral Evidence

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Summary

The brain circuitry processing rewarding and aversive stimuli is hypothesized to be at the core of motivated behavior. In this study, discrete categories of beautiful faces are shown to have differing reward values and to differentially activate reward circuitry in human subjects. In particular, young heterosexual males rate pictures of beautiful males and females as attractive, but exert effort via a keypress procedure only to view pictures of attractive females. Functional magnetic resonance imaging at 3 T shows that passive viewing of beautiful female faces activates reward circuitry, in particular the nucleus accumbens. An extended set of subcortical and paralimbic reward regions also appear to follow aspects of the keypress rather than the rating procedures, suggesting that reward circuitry function does not include aesthetic assessment.

Introduction

Beauty in human faces has long been considered within the general category of aesthetic theory (Ruskin, reprinted 1997; Kant, reprinted 1960) and only recently within the domain of biology and neuroscience. Recent research on facial beauty suggests that the perception of beauty is innate (Slater et al., 1998; Langlois et al., 1987, 1991) and universal across race and culture (Jones and Hill, 1993; Cunningham et al., 1995; Perrett et al., 1994). The strong motivational influence of beauty has been shown in studies of labor markets suggesting that there is a "beauty premium" and "plainness penalty" (Hamermesh and Biddle, 1994) such that attractive individuals are more likely to be hired, promoted, and to earn higher salaries than unattractive individuals (Marlowe et al., 1996; Frieze et al., 1990, 1991). Darwinian approaches to the study of facial attractiveness posit that the features of beautiful faces are important biological signals of mate value that motivate behavior in others (Etcoff, 1999; Grammer and Thornhill, 1994; Perrett et al., 1998; Symons, 1995).

Given the association between beauty and motivated behavior in individuals assessing it, it is possible that the brain circuitry implicated in reward function underlying motivated behavior is activated by the social signals contained in beautiful faces. Research with another social stimulus, namely money, has implicated an extended set of brain reward regions with the anticipation and reception of monetary outcomes (Breiter et al., 1996b, 2001; Delgado et al., 2000; Elliott et al., 2000; Knutson et al., 2000, 2001; O'Doherty et al., 2001; Thut et al., 1997). Although money and beautiful faces can both elicit motivated behaviors, money cannot elicit aesthetic evaluations. In contrast, it is possible that beautiful faces may stimulate both reward assessments and aesthetic assessments, each leading to different patterns of brain activity.

Extensive neuroscience research has focused on the visual processing of faces (e.g., Kanwisher, et al., 1997) and facial expression (e.g., Breiter et al., 1996a; Morris et al., 1996; Phillips et al., 1999; Thomas et al., 2001), while other work has evaluated the visual processing of symmetry (Grammer and Thornhill, 1994; Perrett et al., 1999) and attractiveness (Perrett et al., 1998; Bartels and Zeki, 2000; Nakamura et al., 1998). In this study, we wished to evaluate faces as potential objects of reward. Most visual stimuli are not primary reinforcers; indeed, the sensory representation of an object is different from its rewarding properties (Rolls, 1999). When animals or humans respond to rewarding stimuli, they respond to multiple informational features extracted from distinct representations of these goal-objects, including the rate, latency, incidence, intensity, amount, category, and proximity of the reinforcing stimuli (Breiter and Rosen, 1999; Gallistel, 1990; Shizgal, 1999). The response of animals and humans to these features appears to be dependent on their hedonic deficit state regarding such reinforcers (Cabanac, 1971). In the absence of a defined deficit state regarding attractive faces, it remains a salient question whether they could be considered to be rewarding.

To evaluate this issue, we carried out a study with three components, each component using the same categories of faces: beautiful females, average females, beautiful males, and average males (Figure 1A). One component involved a rating measure from 1 ("very unattractive") to 7 ("very attractive") to evaluate the aesthetic quality of these images. Another component used a novel "keypress" task to operationalize the amount of

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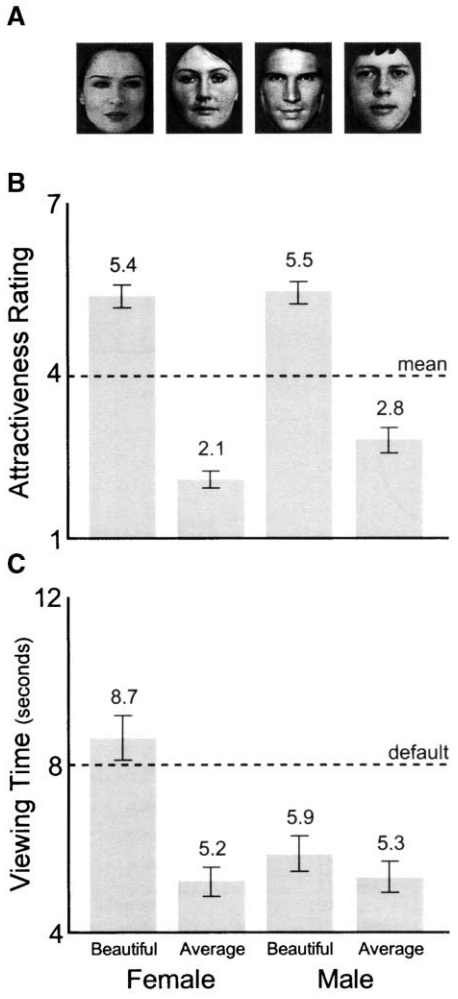

Figure 1. Rating and Keypress Results

(A) A sample of the four picture types used in these tasks (from left to right): beautiful female, average female, beautiful male, and average male.

(B) Eight heterosexual males rated picture attractiveness on a 1–7 scale. The overall mean ratings were: beautiful female 5.38 (SD 0.55), beautiful male 5.46 (0.53), average female 2.08 (0.42), average male 2.79 (0.66).

(C) A separate cohort of 15 heterosexual males performed a task where picture viewing time was a function of the number of their keypresses. Within each gender, the 80 faces were always presented in a new random order, with beautiful and average faces intermixed (Ariely et al., 2001). The mean viewing times were: beautiful female 8.67 s (SD 2.1 s), beautiful male faces 5.9 (1.63), average female 5.25 (1.35), average male 5.33 (1.43).

work subjects performed in order to change the relative duration they viewed the different images. The keypress task evaluated whether these categories of faces had reward values that distinguished them (i.e., along the dimension of reward intensity; Shizgal, 1999). For the neuroimaging component of the study, reward region activity was evaluated using fMRI at 3 T to determine if signal changes followed the results of the behavioral tasks. Six brain regions were targeted that have been associated with reward function in animals (Everitt and Robbins, 1992; Rolls, 1999; Schultz and Dickinson, 2000; Shizgal, 1999) and humans (Berns et al., 2001; Breiter et al., 1997, 2001; Delgado et al., 2000; Elliott et al., 2000; Knutson et al., 2000, 2001; Rogers et al., 1999; Small et al., 2001; Stein et al., 1998; Thut et al., 1997), including the nucleus accumbens (NAc), sublenticular extended amygdala (SLEA) of the basal forebrain, amygdala, hypothalamus, orbitofrontal cortex (GOb), and ventral tegmentum (VT) of the midbrain. To control for variable attention to stimuli, BOLD signal in a control region known to be modulated by attention, namely the fusiform gyrus (GF) (Wojciulik et al., 1998), was also evaluated.

Results

Data from Behavioral Measures

Two different groups of heterosexual male subjects were exposed to two distinct behavioral tasks. One group of subjects rated facial attractiveness, and another group used the keypress procedure to control the duration of their exposure to these faces.

Rating Face Attractiveness

Eight young heterosexual males viewed the stimuli sequentially, rating each face's attractiveness on a scale of 1 ("very unattractive") to 7 ("very attractive"). The results (Figure 1B) showed a general effect of beauty [$F(1,7) = 569.9$, $p < 0.0001$], a general effect of gender [$F(1,7) = 23.4$, $p < 0.0001$], and an interaction [$F(1,7) = 5.8$, $p < 0.05$]. Within the male and female sets, the differences between beautiful and average faces were significant ($p < 0.000001$) for each comparison. Most importantly, for our purpose, the difference between the beautiful males and beautiful females was not significant [$t(7) = 0.99$, $p = 0.36$].

The ratings varied with exposure, such that the difference in ratings between average and beautiful female faces increased from 2.96 on the first exposure to 3.39 and 3.54 on the second and third exposures; this trend had a significant linear component, $p < 0.003$. This occurred because the ratings for the average faces decreased (2.33, 2.00, and 1.91 across exposures), while the ratings for the beautiful faces increased slightly (5.29, 5.39, and 5.45). By contrast, for the male faces, ratings of beautiful and average faces both increased slightly with exposure, with the difference remaining fairly steady (2.72, 2.61, and 2.70).

Keypressing Paradigm

A separate cohort of 15 young heterosexual males completed the keypress task with a mean number of keypresses per subject of 6726 (SD 4287), which translated into large effects on image viewing times. The results (Figure 1C) showed that subjects expended effort only to increase the viewing time of beautiful female faces. For all other categories, they keypressed to make the faces disappear faster. There was a significant effect of beauty [$F(1,14) = 21.7$, $p < 0.001$], a significant effect of gender [$F(1,14) = 22.4$, $p < 0.001$], and a significant interaction [$F(1,14) = 24.3$, $p < 0.001$]. Most importantly (and in contrast to the rating task), there was a significant difference between the beautiful males and beautiful females [$t(14) = 5.1$, $p < 0.0002$]. Because the overall duration of the study was fixed (40 min—allowing subjects to control only the allocation of time between the different categories), the number of exposures was not

Table 1A. Random Effects Analysis in A Priori Regions

		Tal Coordinates				
Anatomy	ROI	R/L	A/P	S/I	ANOVA	Paired Contrasts
NAc	A	−6	3	−3	$p < 0.0060$	FBvsFA ($p = 0.07$) FBvsMB ($p = 0.03$)
VT	B	12	−12	−3	$p < 0.0901$	—
SLEA	C	−28	9	−15	$p < 0.0643$	—
SLEA	D	−18	−12	−3	$p < 0.9820$	—
SLEA	E	31	6	−12	$p < 0.9933$	—
GOb	F	−34	21	−21	$p < 0.7860$	—

1B. Random Effects Analysis in Control Region

		Tal Coordinates				
Anatomy	ROI	R/L	A/P	S/I	ANOVA	Paired Contrasts
GF	G	−37	−54	−15	$p < 0.6117$	—
GF	H	34	−75	−6	$p < 0.2991$	—

Region of interest (ROI) based analysis of fMRI data from targeted brain regions. The Talairach coordinates (Talairach and Tournoux, 1988) of maxima for the six a priori and two control ROIs are expressed in mm from the anterior commissure: x, right (+)/left (−); y, anterior (+)/posterior (−); z, superior (+)/inferior (−). ANOVA results from the interaction of Gender and Attractiveness are tabulated; paired contrasts are listed for ANOVA results with $p < 0.05/6$ clusters in hypothesized reward regions = 0.0083. GF clusters were considered separately and had to meet the same threshold. FB stands for beautiful female, FA for average female, and MB for beautiful male.

constant across subjects. On average, subjects viewed the entire set of 80 images three to four times, with the pattern of results not changing with repeated viewing.

Data from Neuroimaging

Initial data analysis focused on six brain regions: the nucleus accumbens (NAc), sublenticular extended amygdala (SLEA) of the basal forebrain, amygdala, hypothalamus, orbitofrontal cortex (GOb), and ventral tegmentum (VT) of the midbrain. For these targeted regions, a region-of-interest based (ROI-based) analysis was initially performed using individual data (henceforth referred to as "random effects analysis"), followed by a voxel-by-voxel post-hoc analysis of data from the averaged cohort. For the ROI-based random effects analysis, we selected all clusters of activated voxels in the targeted regions that were significant in the comparison between the four face categories and the fixation point baseline. These clusters were then used as regions of interest (ROIs) to sample individual data for an analysis of variance. For the ROI-based random effects analysis, type II errors (false negative) might be expected in the case of (1) opponent responses to different face conditions, which would tend to cancel as a result of the averaging of all face categories, or (2) responses confined to a small proportion of face conditions, which would tend to be diluted by such averaging. Thus, a post-hoc parametric analysis (i.e., using t statistics) was performed on a voxel-by-voxel basis using data averaged across the cohort (henceforth referred to as "fixed effects analysis") to determine if differential patterns of reward circuitry activation paralleled results from the two behavioral studies. General effects for beauty and gender were each evaluated, followed by their corresponding specific effects: beautiful female versus average female and beautiful male versus average male (i.e., beauty effects), along with beautiful female versus beautiful male and average female versus average male (i.e., gender effects).

ROI-Based Random Effects Analysis

Foci of Signal Change in Targeted Anatomic Regions. Data obtained at all time points during the face and fixation point phases of the paradigm were evaluated by statistical parametric analysis. Six ROIs were identified, one in the left GOb, two in the left SLEA, one in the right SLEA, one in the left NAc, and one in the right VT. Furthermore, two foci in opposite hemispheres were found in the control region of the fusiform gyrus (GF).

Hypothesis Testing via ANOVA and Contrasts: A Priori Reward Regions. Gender and beauty served as the predictors in the two-way ANOVA of individual time courses sampled from each ROI. The ANOVA results from the interaction of gender and beauty are described in Table 1A. Only the ROI in the left NAc (see Figures 2 and 4) exhibited a significant general effect [$F(1,5) = 20.9$, $p < 0.0060$], although two other ROIs suggested trends toward such an effect [i.e., the VT and SLEA(C)]. The paired contrasts of the NAc time courses were significant for the beautiful female versus average female conditions and for the beautiful female vs. beautiful male conditions (Table 1A). The bar graphs of average percent signal change across subjects for these conditions (Figure 2) supports the results of the paired contrasts in the NAc.

These data (Figure 2) support a number of other salient observations. For instance, with regard to the NAc, the signal change in the average male condition is second only to that of the beautiful female faces and is not significantly different than it. It is also notable that signal profiles in the VT and one focus in the SLEA(C) resemble the signal profiles between the beautiful female condition and the average female plus beautiful male conditions in the NAc, even if not significant by the analysis of variance (Table 1A). One other focus of signal change in the SLEA(D) also qualitatively resembles those in the NAc [and VT plus SLEA(C)], but differs with regard to signal change in the average male condition. In general, there is a qualitative resemblance between the keypress results for the beautiful female, average female, and

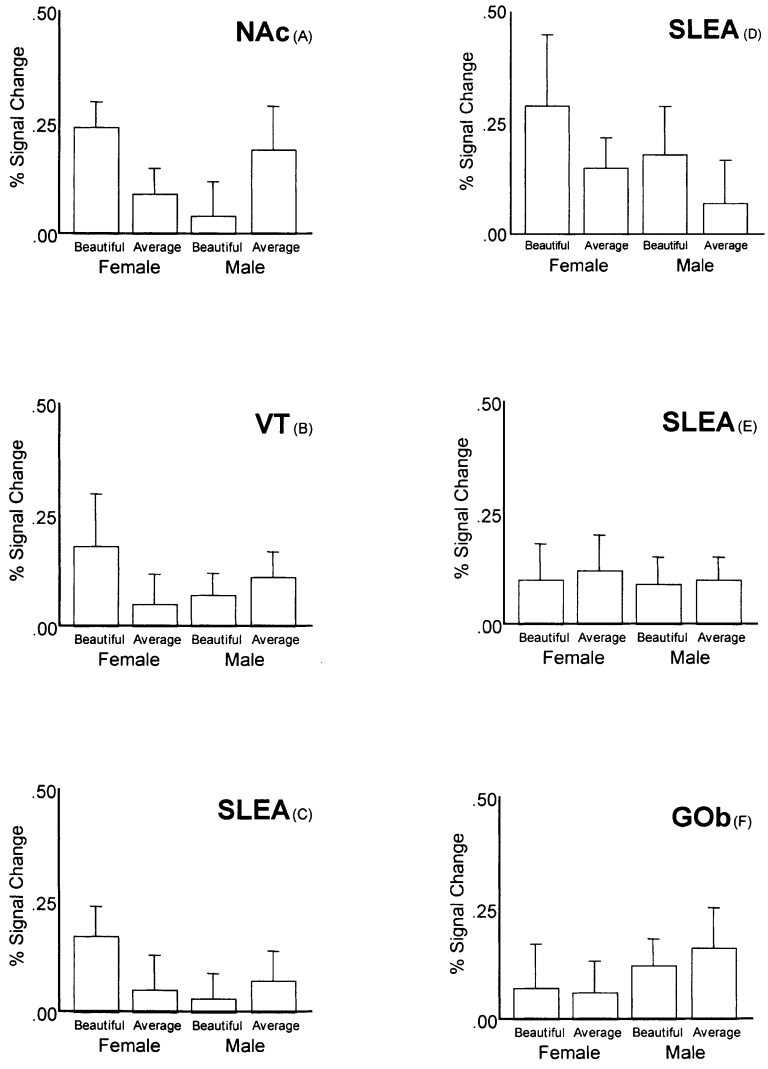

Figure 2. Bar Graphs of Mean Percent Signal Change and Standard Deviation from the Six ROIs Selected for the Random Effects Analysis

Percent signal change is presented, relative to the experimental baseline, for each of the stimulus conditions: beautiful female, average female, beautiful male, and average male faces. Note the similar signal profiles for the first three bars in each graph for the NAc(A), VT(B), SLEA(C), and SLEA(D).

beautiful male conditions, and signal changes for these three conditions in the NAc, SLEA(C), SLEA(D), and VT.

Hypothesis Testing via ANOVA and Contrasts: Control Region. The ANOVA results from the interaction of gender and beauty are described in Table 1B, and no ROIs exhibited a significant general effect.

Fixed Effects (Post-Hoc) Analysis of Average Data

A number of reward regions produced significant signal change ($p < 0.00011$) for the general effects of beauty and gender and the specific effects of the interactions between beauty and gender. The following sections are organized around the general effects with specific effects (interactions) following.

General Effect of Beauty: All Beautiful versus All Average Face Comparison. The general comparison of all beautiful versus average faces revealed four clusters of significant positive signal change in the right GOb, right SLEA, and bilateral VT. One focus of subthreshold positive signal change ($p < 0.001$) was further noted in the left SLEA. Two foci of significant negative signal change were observed in the bilateral SLEA, one of which (row 9 of Table 2) contains ROI C (Table 1A) of the random effects analysis. All of these foci of signal change, with the exception of the right SLEA focus of negative signal change (Table 2, #A8), coincided with foci of signal change observed in the comparisons for the two specific effects that follow.

Specific Effect for Beauty: Beautiful versus Average Female Comparison. For this contrast, four clusters were observed with significant positive signal changes: two in the right GOb, one in the left GOb, and one in the right NAc (Table 2). Four foci of subthreshold positive signal change were further observed in the left NAc, bilateral SLEA, and right VT. Three foci of significant negative signal change were observed: one in the right GOb, and two in the left GOb.

Of these activation foci, four directly correspond to foci observed in the general contrast for beauty. In particular, activation in the VT, SLEA (see Figure 3), and GOb (Table 2, #B5, B7, B9, B11) is common to both, although one SLEA focus is countered by an activation of opposite valence from the beautiful male versus aver-

Table 2. Post-Hoc Fixed Effects Analysis

		Contrast																					
		A				B				C				D				E				F			
		General Beauty				BF–AF				BM–AM				General Gender				BF–BM				AF–AM			
Anatomy	Number	R–L	A–P	S–I	p Value	R–L	A–P	S–I	p Value	R–L	A–P	S–I	p Value	R–L	A–P	S–I	p Value	R–L	A–P	S–I	p Value	R–L	A–P	S–I	p Value
NAc and other VS	1					16	18	−5	3.3E−6	7	12	2	−6.4E−6					7	9	−2	1.4E−4*	16	18	−5	−1.0E−4
	2					−6	15	−2	5.9E−4*	−12	9	2	−3.3E−7					−9	9	5	6.6E−7	−9	6	2	−4.0E−5
	3																	−12	3	−2	3.8E−5				
VT	4	−3	−8	−15	1.4E−5					−3	−18	−11	3.0E−6	−6	−18	−8	3.4E−4*					−6	−18	−8	1.9E−5
	5	3	−18	−15	4.4E−5	13	−15	−5	2.4E−4*									13	−15	−5	4.9E−6	10	−24	−5	2.5E−4*
	6																	19	−21	−2	4.8E−5				
SLEA	7	16	−9	−8	2.2E−5	16	−9	−8	2.1E−4*																
	8	22	3	−15	−5.3E−6													19	9	−15	5.9E−6				
	9	−15	9	−11	−2.1E−7	−24	3	−18	2.5E−4*	−18	9	−15	−1.5E−10					−18	9	−15	1.4E−5	−18	9	−15	−1.4E−5
	10									−12	0	−8	−2.0E−6					−30	−3	−8	−2.2E−5				
GOb	11	16	45	−11	1.0E−4	19	48	−11	8.5E−6									28	45	−5	−1.4E−7	22	51	−2	3.3E−6
	12					−21	33	−8	2.0E−6									−21	18	−8	9.5E−8				
	13					−21	45	−5	−3.9E−9									−18	45	−5	−7.8E−9	−24	42	2	1.2E−6
	14					34	42	−2	−8.6E−11													34	42	−2	5.1E−5
	15					13	54	−8	1.9E−8																
	16					−33	24	2	−6.2E−5													−33	24	−5	1.9E−6
Amyg	17													−12	−3	−24	−2.3E−4*					−18	0	−15	−6.3E−4*
	18													−27	−6	−21	9.2E−4*					−27	−6	−21	5.0E−4*
	19																					28	3	−28	1.6E−4*
	20																	0	3	−15	−1.9E−4*				
Hypo	21													7	−12	−8	5.6E−4*					3	−12	−8	2.4E−5

Activation clusters are identified by post-hoc voxel-by-voxel analysis. "Anatomy" lists the six targeted reward regions, including putative Brodman Area (BA) where appropriate. Activations are identified by row number (Number) and specific subtraction (A–F). These subtractions include the general comparisons for beauty and gender and their associated specific contrasts: beautiful female versus average female (BF–AF), beautiful male versus average male (BM–AM), beautiful female versus beautiful male (BF–BM), and average female versus average male (AF–AM). Talairach coordinates (Talairach and Tournoux, 1988) of these activation foci are listed, and maxima p values are tabulated, where "E" stands for exponent, such that 1.0E−4 means 1.0×10^{-4}. Activation clusters are listed that produced significant post-hoc effects per a p value threshold corrected for the volume of voxels sampled in a priori targeted regions. Activations with asterisks did not meet this corrected threshold but had maxima with $1.1 \times 10^{-4} < p < 9.9 \times 10^{-4}$. Activations are recorded in the same row if their foci are within 2 cm of each other; some contrasts have multiple foci proximate to foci in other contrasts, in which case, the focus with the closest maximum to the others is placed in the row with them.

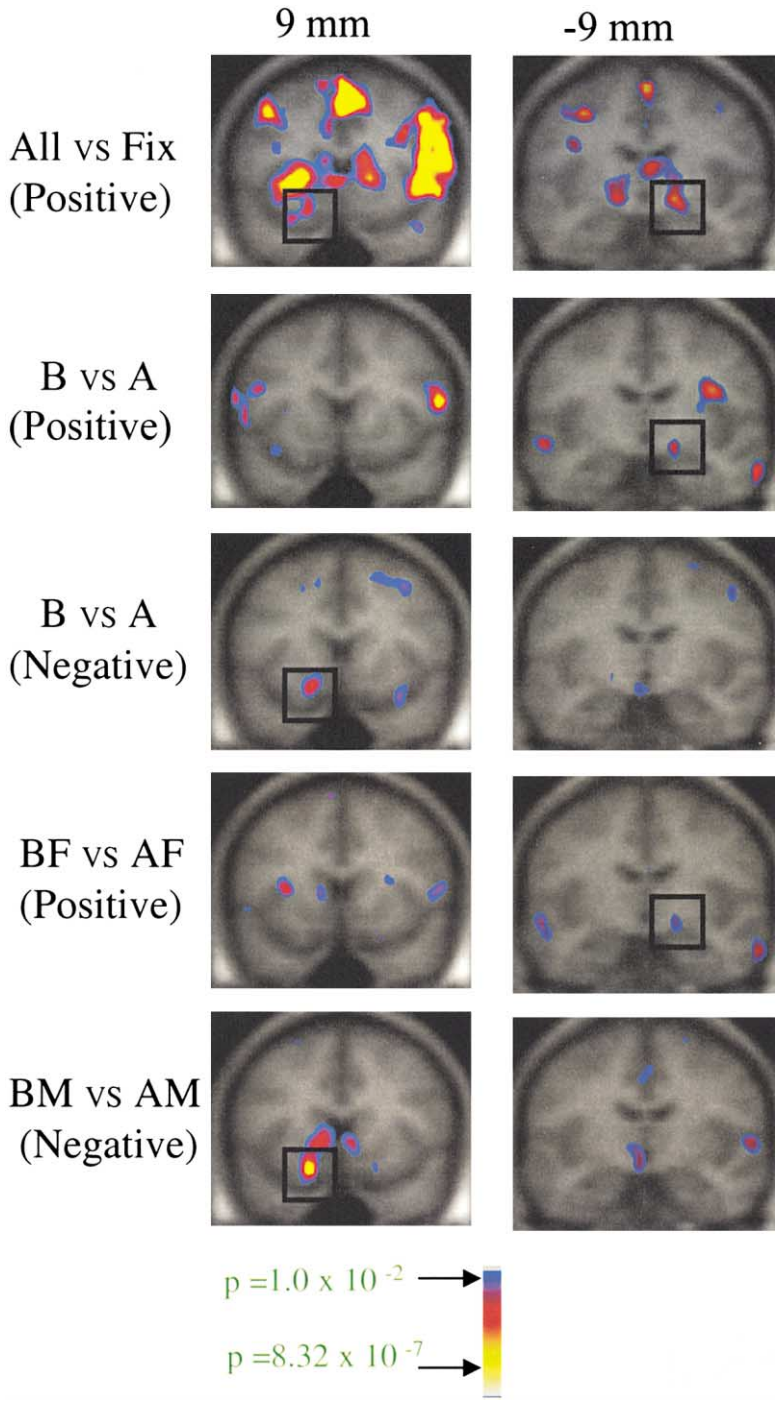

Figure 3. Post-Hoc Analysis (for General Effects of Beauty, along with Its Specific Contrasts)

Bilateral activation of the SLEA in the general contrast of all faces versus baseline (first row) and the general and specific effects of beauty (rows 2–5). Rows 2 and 3 are the positive and negative results of the general effect of beauty (B versus A). Row 4 shows the positive activation for the comparison of beautiful female faces versus average female faces (BF versus AF), and the negative activation (row five) for the comparison of beautiful male faces versus average male faces (BM versus AM). The SLEA activation (rectangles) in the contrast of all faces versus baseline and the general effect B versus A, coincided with the foci of signal changes observed in the comparison for the specific effects (BF versus AF, and BM versus AM). Note that activations in the specific contrasts are additive and are thus observed in the general contrast.

age male conditions. Also, clusters in rows 2, 5, and 9 (Table 2) contain ROIs A–C (Table 1A) of the random effects analysis.

Specific Effects for Beauty: Beautiful versus Average Male Comparison. For this comparison, one focus of significant positive signal change was identified in the left VT (Table 2). Four clusters of significant negative signal change were further observed in the left SLEA (n = 2), and the bilateral NAc/ventral striatum. The NAc/ventral striatum foci had maxima in the ventral striatum with their clusters covering the NAc (e.g., see Figure 3, bottom row images for one such example).

One focus of positive signal change and one focus of negative signal change directly correspond to foci of positive and negative signal change observed in the general contrast for beauty. In particular, activation in the VT and SLEA (see Figure 3 and Table 2, #C4 and C9) is common to both. Also, clusters in rows 2 and 9 (Table 2) contain ROIs A and C (Table 1A) of the random effects analysis.

General Effect of Gender: All Female versus All Male Face Comparison. The general comparison of all female versus all male faces revealed no foci of significant activation. Subthreshold foci of positive signal change were

observed in the left amygdala, right hypothalamus, and left VT. A subthreshold focus of negative signal change was also observed in the left amygdala (Table 2). All of these foci of signal change coincided with foci of signal change observed in the comparisons for the specific effects that follow.

Specific Effect for Gender: Beautiful Female versus Beautiful Male Comparison. For this contrast, seven clusters were observed with significant positive signal change in the left GOb, bilateral SLEA, left NAc/ventral striatum, left NAc, and right VT (n = 2) (Table 2). One focus of subthreshold signal change was observed in the right NAc. Three foci of significant negative signal change were observed in the bilateral GOb and left SLEA, while one focus of subthreshold signal change was noted in the amygdala.

Although none of these activation clusters account for the foci observed for the general effect of gender, five of them directly overlap foci of opposite signal change observed in the contrast of average female versus average male faces described below. An example of this countervalanced signal change in the left NAc/ventral striatum can be observed in Figure 4. Also, clusters in rows 2, 5, and 9 (Table 2) contain ROIs A–C (Table 1A) of the random effects analysis.

Specific Effects for Gender: Average Females versus Average Males. For this comparison, six foci of significant positive signal change were identified in the right GOb (n = 2), left GOb (n = 2), right hypothalamus, and left VT (Table 2). Subthreshold positive signal change is observed in the bilateral amygdala and right VT. Regarding significant foci of negative signal change, three foci are observed: in the right NAc, left NAc/ventral striatum, and left SLEA. One focus of subthreshold negative signal change is noted in the left amygdala.

Of these activation foci, three foci of positive signal change and one of negative signal change directly correspond to foci of subthreshold signal change observed in the general contrast for gender. In particular, activation in the amygdala, hypothalamus, and VT (Table 2, #F4, F17, F18, F21) is common to both. The negative signal change in the right NAc and left NAc/ventral striatum (Table 2, #F1 and F2; see Figure 4), along with three other foci of negative and positive signal change (Table 2, #F9, F11, F13), directly overlay oppositely valanced foci of signal change in the contrast of attractive female versus attractive male faces described above. It is also notable that clusters in rows 2, 5, and 9 (Table 2) contain ROIs A–C (Table 1A) of the random effects analysis.

Discussion

Overview

The goal of this study was to provide evidence for separable measures of aesthetic versus rewarding qualities in beautiful faces and to provide an initial understanding of the neural mechanisms that underlie these qualities. To reach this goal, we carried out both behavioral and fMRI experiments involving the visual assessment of beautiful and average faces. The results of these experiments produced five primary points.

First, the rating and keypress tasks revealed a dissociation between assessments of attractiveness and quantified measures of reward valuation, particularly for beautiful male faces. This dissociation between assessments of attractiveness and quantified measures of reward resembles that described by Berridge (1996, 2000) regarding the processes of "liking" and "wanting" (also see Ariely and Loewenstein, 2000). Second, the keypress procedure revealed that a category of visual stimulus that is not linked to any post experiment asset or reward, namely beautiful female faces, can be rewarding without being associated with any clear hedonic deficit state.

Third, the fMRI experiment revealed a significant response in the nucleus accumbens to the beautiful female faces by both random effects and fixed effects analyses. The fixed effects analysis further indicated that regions such as the ventral striatum proximate to the NAc, along with the VT, SLEA, and GOb, also produced significant activation with regard to the same stimulus conditions. Both the random effects (Figure 2) and fixed effects analyses (Table 2) revealed relative positive signal changes in the NAc for heterosexual males viewing rewarding faces (i.e., beautiful female versus average female conditions) and relative negative signal changes for nonrewarding faces (i.e., beautiful male versus average male conditions). These results have some analogy to the negative deflection in BOLD signal reported for part of the NAc in response to painful thermal stimulation versus a nonaversive baseline (Becerra et al., 2001).

In conjunction with results of human neuroimaging work using drug, gustatory, tactile, and monetary stimuli, these beauty results strongly support a fourth point, that at the spatial scale of subcortical nuclei and their cortical projection fields, there appears to be a generalized circuitry processing rewarding stimuli.

Lastly, the fMRI data suggest a hypothesis for further study regarding the potential effect of "liking" and "wanting" on these brain reward regions (Berridge, 1996, 2000). Specifically, we observed patterns of activation from four of six ROIs in the NAc, SLEA, and VT that generally follow the keypress results for the beautiful female, average female, and beautiful male conditions (Figures 1C and 2). The observation of similar signal profiles across multiple reward regions resembles reports of similar signal changes across a distributed set of reward regions with money (Breiter et al., 2001). Although the outcomes for the behavioral tasks and fMRI procedure were not perfectly symmetric, no reward region per se mirrored the outcomes of the rating experiment (Figure 5). The fixed effects analysis supported the random effects analysis by showing that components of the NAc, SLEA, and VT paralleled the keypress data with regard to subtractions between the beautiful female, average female, and beautiful male conditions (Figure 5). These results suggest that reward regions respond primarily to the reinforcing characteristics of a subgroup of the faces rather than to their aesthetic components.

Dissociation of Rewarding and Aesthetic Behavioral Responses

Heterosexual male subjects rated beautiful male faces as very attractive but did not expend effort to increase the viewing times of these faces. The most reasonable inference is that they found them aesthetically pleasing

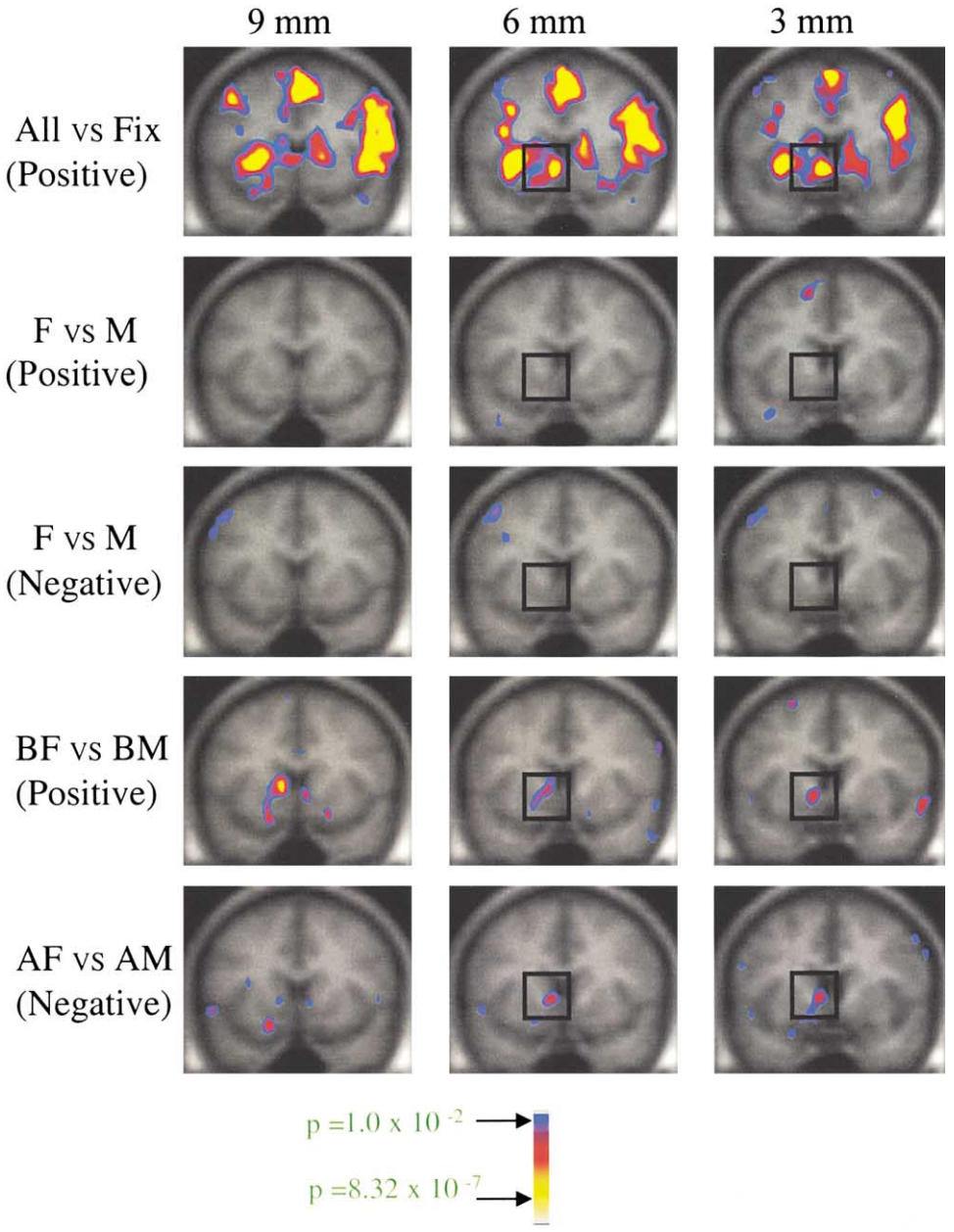

Figure 4. Post-Hoc Analysis (for General Effects of Gender, along with Its Specific Contrasts)

Activation of the left NAc in at least two of three contiguous brain slices for the contrast of all faces versus baseline (row 1) but not the general effect of gender (rows 2 and 3 for positive and negative signal changes, respectively). Row 4 shows the positive signal changes from the comparison of beautiful female faces versus beautiful male faces (BF versus BM), while row 5 shows the negative signal changes of the comparison of average female faces versus average male faces (AF versus AM). Activation in the left NAc (in boxes) can be observed as foci of opposite signal change (positive BF versus BM, and negative AF versus AM). This explains the absence of this activation in the general effect of gender.

but not rewarding, in contrast to their ratings and behavior regarding beautiful female faces. These observations suggest that the ratings procedure and the keypress procedure measure aesthetic value and reward value respectively. The keypress results further indicate that visual stimuli can have reward value by an objective measure, namely work performed to increase or decrease exposure time to different images. In general, the reward value associated with a stimulus is not a static, intrinsic property, but is rather a function of the animal's internal state at the time and of its past experience with the stimulus. Primary homeostatic functions lead to drives such as eating, drinking, and thermal regulation on the basis of deficit states, or changes in physiological conditions. In the current study, the beautiful female faces were rewarding without reference to a specific deficit state, post experiment asset position, or object that could potentially impact on internal physio-

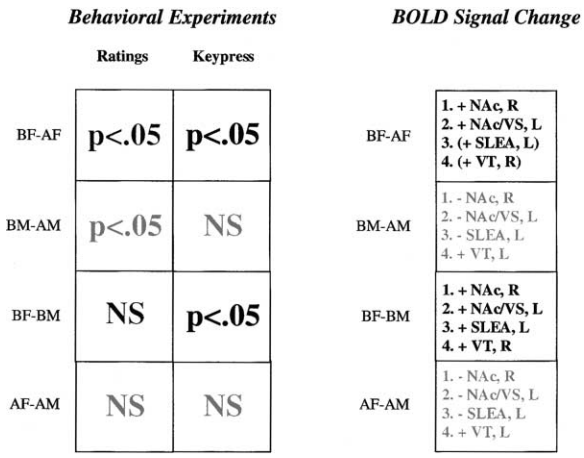

Figure 5. A Summary of the Behavioral and BOLD Signal Results for the Specific Effects of Beauty and Gender

The left table in the figure shows "$p < 0.05$" when the difference in the results from the rating and keypress tasks is statistically significant and shows "NS" when it is not. The table on the right describes the BOLD signal changes in the following reward regions: (1) right NAc (activation clusters listed in row 1 of Table 2), (2) region of the left ventral striatum proximate to the NAc, including the NAc (NAc/VS) (this includes the maxima that was localized in the NAc via the ROI selection procedure for the random effects analysis as ROI A in Table 1A, and the cluster localized over a larger area from the fixed effects analysis that is listed in row 2 of Table 2), (3) left SLEA (this is ROI C in Table 1A that was localized in the SLEA via the ROI selection procedure for the random effects analysis, and the activation clusters listed in row 9 of Table 2 from the fixed effects analysis), and (4) right and left VT (this is ROI B in Table 1A that was localized in the right VT via the ROI selection procedure for the random effects analysis, and the activation clusters in rows 5 and 4 of Table 2 from the fixed effects analysis for the right and left VT, respectively). Activation in brackets were subthreshold per Table 2. In viewing this summary table, it is important to consider the comparisons as tentative, since there is not perfect parallelism between the behavioral data and imaging data (see Discussion). With this in mind, the BOLD signal in the NAc, NAc/ventral striatum (NAc/VS), SLEA, and VT produce positive signal changes when $p < 0.05$ for the keypress task (emphasized with text in bold tone). These regions also alternate signal valence across conditions, while VT activation switches laterality; these observations suggest a need for greater dynamic range in the behavioral tasks to fully determine their correspondence with reward circuitry signal change.

logical signals. Further work is clearly needed to evaluate alliesthesia effects (Cabanac, 1971, 1979) for this category of stimuli. Further behavioral tasks are also needed to evaluate informational features not assessed in the current study. For instance, it is possible that young heterosexual males experience the perception of beautiful males in a more aversive fashion than the perception of average males, as suggested by the correspondence of NAc signal change between beautiful male and average male faces, to NAc signal change between aversive and nonaversive thermal stimuli (Becerra et al., 2001).

Reward Circuitry Activation to Facial Stimuli

One goal of this study was to determine if beautiful faces, or a subgroup thereof, motivated behavior on one hand, while on the other producing reward circuitry activity when passively observed. It is not surprising that men like to watch beautiful women's faces; however, it was not obvious that this class of stimuli would activate the classical reward circuitry that has previously been associated with drug rewards, homeostatic rewards, and monetary rewards, all of which have direct physiological implications or can be readily transformed into goal-objects with physiological effects. This is a critical issue since many literatures outside of neuroscience consider facial attractiveness as a social construct that is not necessarily tied into the function of fundamental reward circuitry (reviewed in Etcoff, 1999).

In the random effects analysis of ROI data from the six targeted reward regions, only the NAc met our corrected statistical threshold and produced subsequent pairwise comparisons for contrasts involving signal collected during the observation of beautiful female faces. The NAc, like the fusiform gyrus (GF), was one of the few brain regions to even meet a Bonferroni threshold ($p < 7.1 \times 10^{-6}$) for the general contrast of all face conditions versus baseline used in the ROI-selection procedure (Breiter et al., 1997, 2001). The NAc achieved this despite having counterposed activation for conditions that were nonrewarding versus conditions that were rewarding (see Figure 4). In contrast to the NAc, the fusiform gyrus (GF) evidenced two foci of BOLD signal change in the comparison of all face conditions versus baseline; however, the sex by beauty interaction was not significant for either of these ROIs in the analysis of variance. BOLD signal change in the GF in response to faces has been reported to be affected by alterations in attention (Wojciulik et al., 1998). The absence of significant contrasts between conditions in the GF for this sample of subjects argues that the significant effects observed in the NAc were not strictly due to differences in subject attention to stimuli.

Given the keypress results, the observation of NAc activity in response to beautiful female faces implicates it in the assessment of reward value. Since the classic formulation of a dedicated reward circuitry (Wise et al., 1978; Louilot et al., 1989), the meso-accumbens dopamine pathway has been considered a central component of circuitry processing the reinforcing effects of most goal-objects. Recent work further suggests that the NAc has complex reward functions, including the assessment of reward expectancy (Schultz et al., 1997; Berns et al., 1997; Breiter and Rosen, 1999; Breiter et al., 2001; Schultz and Dickinson, 2000; Knutson et al., 2001). The current work extends the set of categories of stimuli producing NAc activity beyond homeostatic, monetary, and drug rewards, to include rewards with direct social relevance, such as beautiful faces.

Fixed effects analysis of averaged data was further performed to determine if other reward regions produced differential patterns of activation that paralleled the dissociation of effects for the beautiful face conditions in the behavioral studies. Indeed, distinct profiles of signal change were observed for the general contrasts regarding beauty and gender in other reward regions besides the NAc and proximate ventral striatum (i.e., NAc/ventral striatum), namely the SLEA, VT, and GOb. Of these regions, no focus of signal change met our post-hoc corrected statistical threshold for the general effect of gender (Table 2). This appears to be partly due to the counterposing of activations (see Figure 4) in the

specific contrasts of beautiful women versus beautiful men and average women versus average men (Table 2), thus reducing their additive effect for the general effect of gender. In the case of beauty, the general effect largely reflected additive inputs (see Figure 3) between responses for beautiful women versus average women and beautiful men versus average men (Table 2).

Alongside the observations in the NAc, NAc/ventral striatum, and VT, the post-hoc observations of signal change in the GOb and SLEA is consistent with extensive animal experimentation. GOb neurons in the rat (Schoenbaum et al., 1999) and monkey (Rolls, 1999; Schultz and Dickinson, 2000) fire during the anticipation and experience of positive and negative outcomes. Furthermore, the responses of GOb neurons may represent relative reward preferences (Schultz and Dickinson, 2000). This latter observation has particular relevance to the current data showing GOb activation for subtractions involving beautiful female faces compared to other face conditions. The presence of GOb activity in the average female versus average male subtraction may also be similarly interpreted if one assumes the behavioral tasks did not have enough dynamic range to distinguish a preference for average females over average males. Alternately, the GOb activation associated with this contrast could reflect the assessment of conflict between options connected to the stimuli, as has been shown to be important for choices between gambling positions (Bechara et al., 1998).

Neurons in the SLEA are activated by rewarding brain stimulation in the rat (Arvanitogiannis et al., 1996, 2000; Flores et al., 1997; Nakahara et al., 1999; Shizgal, 1997). Furthermore, lesions of the SLEA reduce the rewarding effect of stimulation to the medial forebrain bundle (Arvanitogiannis et al., 1996), reduce cocaine self-administration (Robledo and Koob, 1993), and disrupt operant performance for sucrose pellets in rats (Brown et al., 1996). Data from other human studies also suggests that the SLEA, GOb, and VT may respond to nonrewarding stimuli: transient activation in these regions has been reported following painful thermal stimulation (Becerra et al., 2001).

The patterns of signal change observed in reward regions with the random effects and the fixed effects analyses suggest some potential parallels with the behavioral tasks (Figures 1C, 2, and 5). Such comparisons must be considered tentative since there is not perfect parallelism between the behavioral data and imaging data in that the imaging data has a broader scale of measurement and thus greater sensitivity (suggesting a need for greater sensitivity of measurement in future behavioral tasks). Signal change from some of the ROIs (e.g., ROIs A–D from Table 1A and Figure 2) used in the random effects analysis suggest a qualitative similarity to a subset of results from the keypress procedure (i.e., the beautiful female, average female, and beautiful male conditions) (Figure 1C). The results of the fixed effects analysis support this observation, in that clusters of activation in the right NAc (row 1 of Table 2), left NAc/ventral striatum (row 2 of Table 2), left SLEA (row 9 of Table 2), and right VT (row 5 of Table 2) produce positive signal changes for comparisons between conditions that are significant for the keypress task (Figure 5). These results support the observations of the random effects analysis in that three of these clusters overlap ROIs in the NAc(A), VT(B), and SLEA(C) used in the random effects analysis (Table 1A and Figure 2). If one looks at all of the contrasts for the specific effects of beauty and gender, one notes that the BOLD signal in the NAc, NAc/ventral striatum, and SLEA alternate signal valence across conditions, while VT activation switches laterality (Table 2 and Figure 5). Suggestions that these activations follow the outcomes of the keypress task are not warranted, though, since there is a potential discrepancy between BOLD signal produced in the NAc, SLEA, and VT (e.g., ROIs A–C in Figure 2) during the average male condition and the keypress results for that experimental condition (Figure 1C). Behavioral work to characterize responses to the average male faces may be helpful in this regard. Furthermore, future studies with more sensitive behavioral experiments might consider use of the same subjects for both behavioral and imaging tasks to allow quantitative evaluation via multivariate analysis of these observations.

The keypress task indicated a significant difference between categories of faces when one of the categories was that of the beautiful female faces (which was the only condition to be positively reinforcing). The other three categories of faces were actively suppressed (thus indicating that they were mildly aversive). The presence of positive and negative NAc signals for contrasts involving reinforcing rewards versus contrasts involving nonrewards (i.e., aversive outcomes) has an intriguing parallel to data indicating positive BOLD signal changes to rewards (such as cocaine and morphine; Breiter et al., 1997, 2000), and the report of negative BOLD signal changes to painful stimuli (Becerra et al., 2001). Given that the changes in signal observed for rewarding and nonrewarding outcomes is dependent on expectancy conditions (Breiter et al., 2001), such differences in signal valence in the NAc and other reward regions may not be absolute but represent a relative ordering of signal associated with the experimental conditions.

General Circuitry of Reward and Its Activity during Aesthetic Assessment

A similar set of brain reward regions appears to respond in common to very distinct categories of reward. At the spatial scale offered by current neuroimaging methodology, at least five brain regions (plus or minus the hypothalamus, and the ventral striatum proximate to the NAc) have been implicated in the perceptual assessment of rewarding stimuli. In particular, the NAc, SLEA, amygdala, GOb, and VT have all been implicated in expectancy functions (Breiter et al., 2001) and to various degrees in the processing of positive and negative outcomes. In human neuroimaging studies, stimuli leading to significant signal changes in these regions have included drugs such as cocaine, nicotine, amphetamine, and morphine, pleasant or aversive tastants, pleasant tactile stimuli, and monetary rewards (Berns et al., 2001; Breiter et al., 1996b, 1997, 1998, 2000, 2001; Breiter and Rosen, 1999; Delgado et al., 2000; Drevets et al., 2001; Elliott et al., 2000; Francis et al., 1999; Knutson et al., 2000, 2001; O'Doherty et al., 2001; Rogers et al., 1999; Small et al., 2001; Stein et al., 1998; Thut et al., 1997; Zald et al., 1998). Such congruence of findings between

brain regions producing responses at the spatial scale of cubic millimeters of tissue and reward stimuli that induce activity in these brain regions supports the thesis of a common generalized circuitry that processes reward information across category and dissects discrete features of such stimuli for the planning of behavior (Breiter and Rosen, 1999; Breiter et al., 2001). Future studies face the challenge of dissecting the relative contributions of these distributed brain regions to the assessment of reward and aversion, and the organization of behavior around these assessments.

Together with the contrasting results of the rating and keypress procedures, our fMRI results suggest a hypothesis that aesthetic evaluation may be separate from reward assessment; although both might follow a common early step in valuation of potential goal-objects (i.e., of their reward intensity) (Breiter and Rosen, 1999). Initial inspection of results from the fixed effects analysis suggests that the VT, SLEA, and GOb may be associated with the general effect of beauty. Of these regions, one focus in the SLEA (Table 2, #A8), in particular, is unique to the general effect and cannot be accounted for by the subsequent specific effects. Such an interpretation would be supported by the fact that the SLEA and VT share connections through the medial forebrain bundle, which is an important site of brain stimulation reward effects (Olds and Milner, 1954) and has been theorized to be important for assessment of reward intensity (Shizgal, 1999). VT dopamine neurons have also been interpreted to respond to salient sensory events, regardless of their relationship to reward (Breiter et al., 2001; Horvitz, 2000).

Arguing against a common basis for aesthetic and reward assessments, though, is the observation that of the two behavioral tasks, only the keypress procedure produced responses that paralleled to some degree responses in reward regions such as the NAc, SLEA, and VT (Figures 1C, 2, and 5). No reward region responded in a similar fashion to the outcomes of the rating procedure. These results are consistent with predictions of the incentive salience or Bindra/Toates model described by Berridge and colleagues (Berridge, 1996, 2000), which discusses "wanting," but not "liking," in terms of meso-accumbens dopaminergic function (Wyvell and Berridge, 2000).

A longstanding debate in aesthetics concerns the question of whether perception of beauty can be "disinterested," or separate from desire (Kant, reprinted 1960). The post-hoc analysis of our data did not show completely separated patterns of activation in reward regions for aesthetic assessments and reward assessments, but instead demonstrated a set of regions that resembled aspects of the keypress results alone. This suggests that beautiful faces produce a valuation signal (potentially involving the SLEA), which is processed in different brain regions for reward functions and aesthetic judgements in young heterosexual male subjects. Given that it may be particularly difficult to dissociate rewarding from aesthetic effects with faces, future studies with non-face stimuli and nonbiological categories of goal-objects may help determine if these effects are dissociable.

Limitations

A number of limitations apply to this fMRI study (see Breiter et al., 1996a, 1996c, 1997, 2001). These issues include the limited signal-to-noise ratios of BOLD signals recorded from small subcortical structures, spatial resolution after data analysis, and magnetic susceptibility.

Particular to this study, it is important to note that participants in all three experiments were young heterosexual males. Recent evidence suggests that women's facial preferences may change across the menstrual cycle. Penton-Voak et al. (1999) have found that women in the follicular phase of the menstrual cycle are more attentive to phenotypic markers indicating immunocompetence and therefore prefer stereotypically "masculine" faces more than they do at other times of their cycle. Given the more complex results of human female preferences, we decided to conduct this initial investigation with male subjects only. Thus, these results should not be generalized to women, nor to individuals with a different sexual orientation.

Finally, it is possible that the difference between the two behavioral tasks was not caused by a difference between aesthetic evaluations and motivation but rather was a result of scaling changes in the ratings task. It is possible that when using ratings as the response measure, our subjects rated males relative to other males and females relative to other females (Ariely and Loewenstein, 2000). The keypress method does not suffer from this changing scale problem because effort is a scale that is constant across all images presented. Further work is needed in order to better understand if the rating task results are a response language artifact or a real effect.

Conclusion

This study sought to determine if social stimuli distinct from money, namely categories of faces segregated by gender and attractiveness, had different reward values, and in turn induced reward circuitry activity when observed. The keypress procedure demonstrated that a social stimulus that was not linked to any post experiment asset or reward, had a distinct valuation that could be objectively quantified. fMRI of subjects passively viewing these faces demonstrated a significant effect by analysis of variance across individual subjects in the NAc, particularly in response to the beautiful female faces. By the post-hoc analysis, no one region responded in a similar fashion to the rating study alone, but a number of reward regions produced signal change with approximate similarity to the keypress data. These results suggest that aesthetic judgement may not be mediated by reward systems.

The observations of this study build upon prior neuroimaging work with multiple categories of reward stimuli to argue that, at the spatial resolution of current imaging techniques, an extended set of deep gray matter and paralimbic regions serves as a generalized circuitry to process goal-related stimuli. In a previous study using monetary reward and a game of chance, our group observed this extended set of reward regions to display differential activation to expectancy conditions and to the monetary gains and losses embedded in them

(Breiter et al., 2001). The segregation of expectancy and outcome responses demonstrated that reward/motivation systems could be dissected into their constituent functional subsystems, but left open the issue of their involvement in valuation processes. The current study suggests that the same set of regions implicated in the processing of expectancies and outcomes, may also be involved with valuation functions. A challenge for future work is to determine the varied contributions of this distributed set of reward regions to the processes of expectancy, valuation, and their combination for motivation.

Studies are further warranted to address issues raised by the design and focus of the current work. For instance, there is the issue that differences in the gender or sexual orientation of the volunteers used for this study might lead to different behavioral and imaging results. The signals from reward regions in response to average male faces did not resemble the results of the two behavioral tasks, suggesting the need for assessing other subjective dimensions. Another question arises about whether the results produced by beautiful faces generalize to those produced by bodies, or nonanimate stimuli. Lastly, there is the issue of what brain regions might process information regarding "aesthetic" beauty (i.e., follow the pattern of the rating task results), as opposed to processing information regarding "desirable" beauty. In pursuing these issues regarding brain function, it is possible we may begin to approach an understanding of Ruskin's concept of the "sublime" (reprinted 1997) with regard to the grandeur imbedded in the function of motivation.

Experimental Procedure

Subjects

All subjects in the three experiments gave informed consent to participate in these procedures following the rules of the Subcommittee on Human Studies at the Massachusetts General Hospital, the Institutional Review Board at the Massachusetts Institute of Technology, and the Institutional Review Board at Harvard University.

Behavioral Tasks

A group of eight male subjects, ages 21–35 years (mean 24.0, SD 4.4), all heterosexual and right-handed by self-report, participated in the rating study, and were paid $15. A separate group of fifteen male subjects between the ages of 21 and 25 years (mean 23.0, SD 2.3), also all heterosexual and right-handed by self-report, participated in the "keypress" study and were paid $14 for their participation.

Neuroimaging

Ten male volunteers, who had not participated in the behavioral tasks, volunteered for the fMRI experiment. All subjects were medically, neurologically, and psychologically normal by self-report and physician-directed medical review of systems. All subjects were right-handed and heterosexual by self-report. fMRI data collected from three participants had significant signal spiking, along with uncorrectable motion, and could not be analyzed; data from one participant was excluded due to noncompliance with instructions. The six remaining participants were aged 21–28 (mean 25.2, SD 2.5).

Stimuli

Two sets of 40 nonfamous human faces [digitized at 600 dpi in 8-bit grayscale, spatially downsampled, and cropped to fit in an oval "window" sized 310–350 pixels wide by 470 pixels high using Photoshop 4.0 software (Adobe Systems)] classified as "beautiful" and "average" (according to pilot test results) (see Figure 1A), were selected from print media. Each set consisted of 20 male and 20 female faces.

Experimental Design

Behavioral Tasks

Rating Procedure. The rating task measured the attractiveness of the female and male faces for the experimental subjects. Subjects viewed the 80 faces three times each, on each occasion rating each face's "attractiveness" on a scale of 1–7, with 1 representing "very unattractive" and 7 representing "very attractive." Faces were organized in blocks by gender, and the order of gender was counterbalanced across subjects. Within each block (by gender), the 40 beautiful and average faces were always presented in a new randomly generated order.

Keypress Procedure. The keypress task examined the reward value of average and beautiful faces. Subjects were told that they would be exposed to a series of pictures that if not interfered with, would change every eight seconds. However, if they wanted a picture to disappear faster, they could alternate pressing the "z" and "x" keys, whereas if they wanted a picture to stay longer on the screen, they could alternate pressing the "n" and "m" keys. The dependent measures of interest were the amount of work in units of key press that subjects exerted in response to the different categories of stimuli, and their resulting viewing durations.

Each pair of keypresses increased or decreased the total viewing time according to the following formula:

$$\text{NewTotalTime} = \text{OldTotalTime} + (\text{ExtremeTime} - \text{OldTotalTime})/K,$$

where ExtremeTime was 0 s for keypresses reducing the viewing time, ExtremeTime was 16 s for keypresses increasing the viewing time, and K was a scaling constant set to 40. If the elapsed time for the picture surpassed the total time determined by keypressing, the picture was removed and the next trial began. A "slider" was displayed left of each picture indicating total viewing time at any moment, and changing with every keypress (Ariely et al., 2001). This procedure was controlled by Authorware (Macromedia).

Subjects were informed that the task would last 40 min and that this length was independent of their behavior during the task, as was their overall payment of $14.

Neuroimaging

Subject Instructions Prior to Scanning. Subjects were told that they would see rapid presentations of faces intermixed with fixation points, that sometimes the faces would change, and that they were to focus on the fixation points while getting an overall sense of the faces. One to two minutes prior to imaging, subjects viewed a separate set of average faces with neutral expressions for image focusing and centering.

Functional Imaging. Subjects were scanned on an Instascan device (3 T General Electric Signa, modified by Advanced NMR Systems) using a head coil, bite-bar, and standard protocol (Breiter et al., 2001). This protocol included: (1) a sagittal localizer scan [conventional T1-weighted spoiled gradient refocused gradient echo (SPGR) sequence; through-plane resolution = 2.8 mm; 60 slices] to orient, for subsequent scans, 16 contiguous axial oblique 7 mm slices along the AC-PC line, (2) an automated shimming routine with second order shims to optimize magnetic field homogeneity (mean FWHM = 26.6Hz, SD 2.6), (3) an SPGR T1-weighted flow-compensated scan (resolution = 1.6 mm × 1.6 mm × 7 mm), (4) a T1-weighted echo planar inversion recovery sequence (TI = 1200 ms, in-plane resolution = 1.6 mm), and (5) a gradient echo, T2*-weighted functional sequence (TR = 2000 ms, TE = 30 ms; flip = 60∼; FOV = 40 × 20 cm; in-plane resolution = 3.125 mm; 110 images per slice; disdaq = 4).

Experimental Paradigm. Each experimental run included five 28 s baseline epochs interleaved with four 20 s face epochs (e.g., block design). To minimize attentional modulation of gaze (Breiter et al., 1996a), face stimuli were presented in a tachistoscopic fashion for 200 ms (face, or empty oval with a fixation point for baseline), followed by a blank screen for 3800 ms. During each run, either male or female faces were presented, with alternating epochs of average and beautiful faces. Epochs of average and beautiful faces were

counterbalanced within run, with an *A*B*B*A* or *B*A*A*B* order (A = average, B = beautiful, * = fixation point baseline). The gender of the faces shown and block sequence was counterbalanced across the eight runs administered to each subject. This resulted in each face being viewed twice. A break of approximately 2–4 min was taken between runs.

Subject Debriefing. After functional imaging, subjects filled out a questionnaire about what they had seen and thought, and completed the Beck Anxiety and Depression Inventories (BAI: mean 2.2, SD 1.7, range 0–4 out of 63; BDI: mean 3.7, SD 3.8, range 0–12 out of 63). Three of the six subjects spontaneously reported noticing that the faces differed in attractiveness.

Data Analysis

Transformation of fMRI BOLD Data before Statistical Mapping

Motion Correction and Talairach Transformation. These procedures followed those detailed elsewhere (Breiter et al., 2001).

Signal Normalization and Filtering. For all eight runs, fMRI data in the Talairach domain were intensity scaled on a voxel-by-voxel basis to a standard value of 1000 and detrended. The mean signal intensity for each voxel over all runs was removed on a time point by time point basis.

Concatenating and Averaging across Subjects. Pairs of identical 110-time point runs of Talairach-transformed functional data were averaged within each subject (i.e., given four types of runs—female faces: *A*B*B*A*, female faces: *B*A*A*B*, male faces: *A*B*B*A*, male faces: *B*A*A*B*). The resulting four average runs were concatenated within each subject. These 440 time point sequences were then averaged across subjects, as were individual structural images.

Statistical Mapping, ROI-Based Analysis

Statistical Mapping of General Effects as ROIs. Individual data was evaluated to confirm the presence of a normal signal distribution. Then, a t statistic map was created from the data averaged across subjects, using time point ($n = 440$) as the random factor, and contrasting all time points during face events versus all time points during fixation point events.

Within this map, clusters of activation that had maxima (i.e., minimum p value) in one of the six targeted reward regions were identified using a cluster-growing algorithm (Bush et al., 1996), and selected as ROIs for analyses of variance with subject ($n = 6$) as the random factor (i.e., "random effects" analysis). In order to maintain an overall $\alpha < 0.05$, this algorithm specifically localized activations that met a corrected p value threshold of $p < 0.0083$ for the number of hypothesized brain regions interrogated ($0.05/6 = 0.0083$). See Breiter et al. (2001) for specific cluster constraints.

Hypothesis Testing of Individual Data: ANOVAs and Paired Contrasts. ROIs in targeted reward regions were then used to sample signal (as percentage signal change) from each of the eight runs in each subject. Separate, repeated-measures analyses of variance for each ROI were computed, with Gender (male or female) and Attractiveness (beautiful or average) as the dependent measures. The result of primary interest in the ANOVA was the gender $\times$ attractiveness interaction. Given that ANOVAs were carried out for six different ROIs in hypothesized reward regions, we used a more stringent α level ($p < 0.0083$). In cases that met the criterion α level, the pair-wise contrasts were computed (Table 1).

Statistical Mapping, Post-Hoc Voxel-by-Voxel Parametric Analysis on Averaged Data

A post-hoc analysis on the averaged data was undertaken on a voxel-by-voxel basis to check for potential activations missed in the ROI-based analysis (see "Data from Neuroimaging" in Results). Parametric statistical maps (using voxel-by-voxel t tests) were generated on data that had been averaged by the four types of runs across subject and concatenated. Prior to concatenation, functional data were intensity scaled (i.e., normalized to the first run). General contrasts were computed for all beautiful face conditions versus all average face conditions (i.e., general effect of beauty) and for all female faces versus all male faces (i.e., general effect for gender). The four specific contrasts following off of these general effects are listed in Table 2.

Clusters of positive and negative signal change were identified for each contrast in the six targeted regions. In order to maintain an overall $\alpha < 0.05$, activation clusters had to meet a corrected p value threshold (Breiter et al., 1996a, 1996c, 2001) for the volume of tissue (30.97cc) sampled in the six a priori regions (i.e., $p < 0.05/453$ voxels, or $p < 1.1 \times 10^{-4}$) (Makris et al., 1999).

Anatomic Localization

Statistical maps of group-averaged data were superimposed over high-resolution conventional T_1-weighted images that had been transformed into the Talairach domain and averaged. Primary anatomic localization of activation foci was based on the Talairach coordinates (Talairach and Tournoux, 1988) of the maximum voxel from each activation cluster, with secondary confirmation of this via inspection of the juxtaposition of statistical maps with structural scans. Localization followed the region of interest conventions described previously (Breiter et al., 1997) for the NAc, SLEA, amygdala, hypothalamus, VT, and GOb (BA 11/47) (Breiter et al., 2001), and the ventral striatum proximate to the NAc (Drevets et al., 2001). All clusters of activation were checked against the functional image data using an objective method to ascertain that they did not overlap any areas of susceptibility artifact (Breiter et al., 1997, 2001).

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