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## Common and unique representations in pFC for face and place attractiveness

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### Introduction

Aesthetic evaluations, such as judging beauty and attractiveness, play an important role in our lives, affecting (for example) whom we choose to marry and where we would prefer to live. We can perform aesthetic evaluations on a wide variety of stimuli – a face can be beautiful or ugly, as can a house, room, or landscape. This suggests the possibility that a common evaluative signal might underlie different aesthetic judgments, analogous to the common signal that is believed to underlie different kinds of economic judgments. However, a counterargument is the fact that aesthetic judgments are rarely made across stimulus category (“Is this face more beautiful than this landscape?”). This makes them different from economic judgments, which usually involve comparison across disparate categories of goods, and suggests that a “common currency” for value might not be useful—or calculated—in the aesthetic domain.

Here we test whether human prefrontal cortex computes a common currency for value that is used for aesthetic judgments. Previous studies have shown that fMRI response in ventromedial prefrontal cortex (vmPFC) during economic decision-making corresponds to the “utility” or “subjective value” of a stimulus (Bartra, McGuire, and Kable 2013). This response exhibits some degree of domain-generalizability, insofar as it can be elicited by both money and consumer goods (Chib et al. 2009; Kim et al. 2011; Levy et al. 2011). However, the few studies that have attempted to compare non-economic (e.g. social) to monetary rewards have produced contradictory findings, sometimes showing overlapping activity in vmPFC and sometimes revealing non-overlapping activity or no activity at all in this region (Smith et al. 2010; Lin et al. 2012, Sescousse et al. 2010, Izuma et al. 2008). It remains unclear whether a common evaluative signal exists that could apply to judgments very far removed from economic exchange such as aesthetic judgments.

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To examine this issue, we scanned subjects with functional magnetic resonance imaging (fMRI) while they made attractiveness judgments of faces and places. Our aim was to identify a common neural signal of value that operates across these two very different non-economic stimulus classes. By using faces and places as stimuli, we intended to give our two categories the “best advantage” in terms of possible neural differences. Beautiful faces and beautiful places are associated with distinct reward outcomes: beautiful faces offer the promise of reproductive success and social advancement (see Rhodes 2006 for a review), whereas beautiful landscapes offer the promise of prospect/refuge, physical resources, and rest (Appleton 1975; White et al. 2010; Berman & Kaplan 2008). Faces and places also differ substantially in their visual properties, to the extent that they are processed by distinct regions of visual cortex (Kanwisher et al. 1997; Epstein and Kanwisher 1999). Face and place attractiveness are not typically assigned monetary values (although it is not impossible to assign monetary value to something without a market value - see Smith et al. 2010, Mitchell and Carson 1989). Therefore, a common response for face and place attractiveness is unlikely in the absence of a common currency-type, domain-general evaluative neural signal.

Previous work has shown that activity in vmPFC correlates with face attractiveness (O’Doherty et al. 2003; Ishai 2007; Cloutier et al. 2008), though this is not always the case (Chatterjee et al. 2009). A single study on the neural correlates of indoor place attractiveness showed no activity in vmPFC that correlated with parametric beauty ratings (Vartanian et al. 2013). Consequently, the question of whether face and place attractiveness are represented in the same or different brain regions remains open. To anticipate, our results suggest that there are both category-general and category-specific representations of attractiveness in vmPFC, and a signal specific to face attractiveness in lateral orbitofrontal cortex (latOFC).

## Methods

### Subjects

34 healthy, right-handed volunteers with normal or corrected-to-normal vision were recruited to participate in the fMRI study. All subjects gave written informed consent according to procedures approved by the University of Pennsylvania institutional review board. One subject was excluded due to an incidental finding, two subjects were excluded due to technical issues with their anatomical images, and three subjects were excluded due to excessive motion in the scanner. This left us with 28 subjects whose functional data were analyzed (14 females, mean age 22.5).

### fMRI Acquisition

Scans were performed at the Hospital of the University of Pennsylvania on a 3T Siemens Trio scanner equipped with a Siemens body coil and a 32-channel head coil. High resolution T1-weighted anatomical images were acquired using a 3D MPRAGE pulse sequence (TR = 1620 ms, TE = 3 ms, TI = 950 ms, voxel size = 0.9766 × 0.9766 × 1 mm, matrix size = 192 × 256 × 160). T2\*-weighted images sensitive to blood oxygenation level-dependent (BOLD) contrasts were acquired using a gradient-echo echo-planar pulse sequence (TR = 3000 ms,

TE = 30 ms, voxel size = 3×3×3mm, matrix size = 64 × 64, 46 axial slices). The slices were tilted –30 degrees from the AC-PC plane to reduce signal dropout (Deichmann et al. 2003).

## Stimuli

Stimuli were digitized 400×400 pixel color photographs of 144 places and 144 faces chosen to span a wide range of attractiveness. The places were natural environments with no man-made elements, spanning scene types such as swamps, mountain ranges, beaches, fields, and forests. The face set had equal numbers of males and females, and all faces were Caucasian, upright and forward-facing, with neutral to pleasant expressions, selected from the Glasgow Unfamiliar Face Database (<http://homepages.abdn.ac.uk/m.burton/pages/gfmt/Glasgow%20Face%20Recognition%20Group.html>), Radboud Database (Langner et al. 2010), the Center for Vital Longevity Face Database (Minear & Park 2004), CVL Face Database (Peter Peer, <http://www.lrv.fri.uni-lj.si/facedb.html>), Diana Theater Face Database (courtesy of Dr. Robert Schultz at the Center for Autism Research), and online searches. Face images were extracted from their original background, blurred slightly along the edges, cropped so that hair did not extend below the chin, and resized to span a height of 400 pixels. They were then placed on an abstract colored background created by phase-scrambling a single place image. This ensured that they subtended the same visual angle as the places while retaining a similar background color. A unique scrambling of the background image was used for each face (code used from: <http://visionscience.com/pipermail/visionlist/2007/002181.html>).

These 288 stimuli were chosen from a larger set of 573 face and place images based on pilot testing intended to ensure that they covered a wide range of attractiveness, thus maximizing our ability to see neural activity related to this variability. In these pilot tests, 10 subjects made Likert-scale ratings (1–8) of the visual attractiveness of each place and face. Images were blocked by category (face/place) and subjects used the keyboard to make ratings at their own pace, with instructions to spread their judgments across the whole 1–8 range. Each subjects' ratings were then z-scored across all images and these z-scores were averaged across subjects for each image. The images were then divided into “low”, “average”, and “high” attractiveness bins according to whether they had a z-score below –0.5 (low), between –0.5 and 0.5 (average), or above 0.5 (high). Images were then chosen in equal numbers from these three attractiveness bins to make the final stimulus set.

## Design and Procedure

The fMRI experiment consisted of six 4 min 57 sec scan runs, each of which was divided into two 36-s face blocks, two 36-s place blocks, and two 36-s fixation (or “rest”) blocks in which subjects passively fixated on a central crosshair (Figure 1). Between each block was an additional 9 seconds of passive fixation. 18 seconds of fixation were added at the beginning and end of each run to allow the T2\* signal to reach a steady state and to model the final HRF, respectively. During each face and place block, subjects used a button box to give “low”, “average”, or “high” attractiveness ratings to 12 faces or places, each presented for 1 s followed by a 2 s interstimulus interval (ISI) during which only a crosshair was on the screen. Subjects made their ratings any time within the 3-second trial; button assignment was counterbalanced across subjects. Blocks were ordered such that no block type repeated

twice in a row (including fixation blocks), and the block orders were counterbalanced across runs.

To acclimate subjects to the distribution of attractiveness in the stimulus set, they were asked to rate prior to the scan the attractiveness of 24 faces and 24 places not used in the main experiment on a 1–8 scale. These 48 images were chosen to span the entire range of attractiveness found in the main stimulus set. In addition, immediately after the scan session, subjects were presented with the images from the main experiment again in a random order and asked to rate them on the same 1–8 scale. These post-scan ratings were used in the subsequent fMRI analysis because they provided a finer-grained measure of face and place attractiveness than the high/average/low ratings made in the scanner.

Experiment trials within blocks were ordered such that the place and face attractiveness regressors used in the subsequent analyses would have maximal power to detect variability in fMRI response. Although these regressors were ultimately based on the attractiveness judgments made by the subjects in the scanner, which could not be known in advance, we were able to obtain a rough estimate of their shape by using the high/average/low attractiveness ratings provided by the pilot subjects. We generated 10,000 random orders of face and place stimuli that fit our experimental design, convolved the corresponding attractiveness ratings with a canonical hemodynamic response function (HRF), and determined the power by calculating the ratio of variance before and after convolution. A “best” sequence of attractiveness levels was chosen (the one with the highest power), and images corresponding to these bins were drawn randomly from the stimulus set to create a unique stimulus sequence for each subject.

### fMRI Data Analysis

Pre-processing and data analysis for individual subjects was performed using the FMRIB Software Library (FSL v.4.1.6) (Jenkinson et al. 2012). Functional images were corrected for differences in slice time acquisition and then de-obliques to correct for the 30 degree tilt slice acquisition. For each run, the first six volumes were removed to account for the fMRI signal not yet reaching steady-state, and data were then motion corrected by spatially realigning each image with the central image in the run, registered to the subject-specific T1-weighted image using 6 degrees of freedom rigid-body transformations, and high-pass filtered to remove temporal frequencies below 0.0074 Hertz.

After preprocessing, we performed both univariate and multivariate pattern analyses on the data, as described below. An overview of the analysis scheme is provided in Figure 2.

### Univariate Analyses

General linear modeling was used to estimate neural activity correlated with subject-specific ratings of face and place attractiveness. Each subjects' post-scan 1–8 ratings were used to create parametric regressors for face and place attractiveness which extended across all six experimental scans. The model also included regressors corresponding to face and place in-scan reaction times (RTs), as our behavioral data revealed that reaction time was significantly negatively correlated with place attractiveness (but not face attractiveness). We did not include quadratic regressors for face and place attractiveness, in contrast to previous

studies (e.g. Winston et al. 2007), because these quadratic regressors were strongly negatively correlated with RT. Finally, categorical regressors were added for face trials, place trials, and instruction screens, and nuisance regressors were added to account for between-scan variability and outliers (outliers calculated with the Gabrieli Lab's Artifact Detection Tools: [http://www.nitrc.org/projects/artifact\\_detect/](http://www.nitrc.org/projects/artifact_detect/)). All regressors, except scan indicators, were convolved with a canonical HRF.

We used this model to perform two sets of analyses. The first was a set of targeted analyses focusing on regions in the frontal lobe that have been previously implicated in the processing of information about stimulus value. The second was a whole-brain random effects analysis intended to find areas responding to face and place attractiveness without any *a priori* hypotheses about where these areas would be. For the targeted frontal lobe analyses, unsmoothed parameter estimates from the contrasts of interest were registered to the cortical surface using surface templates derived from each subject's T1-weighted anatomical image using Freesurfer's segmentation function (recon-all). The data were then averaged across subjects by spherically registering these subject-specific surfaces to the group brain (an average of the subject-specific surfaces, where vertex coordinates are calculated as the average Talairach coordinates of that vertex across subjects). During this registration process the data was smoothed on the group-average surface at 3mm FWHM. Using the unfolded cortical surface for inter-subject registration in this manner reduces the variability when averaging across volumetric data associated with regions containing highly variable cortical folding patterns, which was especially important in this case because orbitofrontal cortex is known to have a high degree of anatomical variability between subjects (Chiavaras & Petrides 2000; Chiavaras et al. 2001). Random-effects analyses were then performed on the contrasts of interest to identify regions within vmPFC and latOFC that responded to face and place attractiveness. Output was cluster-corrected for small-volumes in vmPFC and latOFC and Bonferroni corrected to account for observations across 2 hemispheres (clusters defined at  $p < 0.05$  uncorrected and then permutation corrected to  $p < 0.05$  using Freesurfer's simulation function to estimate the distribution of maximum cluster sizes under the null hypothesis). The medial surface *a priori* small volume was defined using a functional mask for vmPFC (Bartra, McGuire, & Kable 2013) which we translated into surface space. As there is some evidence of category-specific signals in latOFC (e.g. Sescousse et al. 2010), we also used this area as an *a priori* small volume, defined by using the ventral surface of the "lateralorbitofrontal" ROI from Freesurfer's APARC library (taken from the Desikan-Killiany atlas).

We performed a leave-one-subject-out iterative cross-validation analysis (Kriegeskorte et al. 2009, supplementary discussion) on the significant clusters resulting from the targeted frontal lobe analysis to test whether activity within any clusters responding to face attractiveness or place attractiveness responded differentially to face versus place attractiveness. On each iteration, data from a single subject was held out as the test set. Clusters within vmPFC and latOFC responding to face or place attractiveness were then defined based on a group analysis of the  $n-1$  remaining subjects, using the procedures described above. The response in these clusters in the  $n$ th subject was then analyzed, and the procedure repeated. This method gave us an estimate of the response in each cluster to face

and place attractiveness, using independent data sets to define the boundary of the cluster and the strength of the effect.

For the whole-brain analyses, pre-processed data were smoothed with a 5mm FWHM kernel and parameter estimates for regressors of interest were obtained for each voxel for each subject. These were normalized to standard volumetric MNI152 space using linear 12 degree of freedom transformations, resampled to 2×2×2 mm voxels in this standard space, and submitted to group level random effects analyses for contrasts of interest. The true Type 1 error rate for each contrast was calculated from FSL's randomise function using Monte-Carlo simulations that permuted the signs of wholebrain data from individual subjects (10,000 relabelings; method based on Freedman & Lane 1983). The resulting reported voxels are significant at  $p < 0.05$  corrected for multiple comparisons across the whole brain.

We also performed a follow-up analysis which examined response in functional ROIs in visual cortex. Because we did not conduct independent localizer scans for all subjects, these ROIs were defined by using a set of 40 subjects' localizer contrast files (19 which came from our current study). These group-defined "parcels" were created using an algorithmic method which is fully described in Julian et al. (2012) (We diverged from the Julian et al. description in that we chose a more liberal threshold of  $p < 0.001$  for the Face>Objects contrast maps.) Parcels were defined using the contrasts Faces>Objects (fusiform face area, FFA), Scenes>Objects (parahippocampal place area, PPA), Objects>Scrambled Objects (posterior lateral occipital cortex, LOC) Scrambled Objects > Objects (early visual cortex, EVC). For the ROI analysis, we then translated individual subject contrast maps for face and place attractiveness into standard space and extracted parameter estimates for each subject within these group-defined ROIs.

### Pattern Analysis

Our univariate analyses revealed clusters of activity in vmPFC that responded similarly to both face and place attractiveness. To further examine whether there were any differences between the signals for face and place attractiveness in vmPFC, we used a pattern classification analysis to test whether *patterns* of response rather than overall *mean* response within these clusters might reflect category-specific attractiveness information. Using well-established methods (Haxby et al., 2001), we split the data into independent halves (each consisting of 3 of the 6 scan runs), identified activity patterns for face and place attractiveness in each half, and then compared these patterns across halves to establish their reliability and distinguishability. Activity patterns in each half were calculated based on the same general linear model described above, except that the regressors spanned 3 scans instead of 6. The resulting unsmoothed maps were then registered to the group-defined surface-space, which allowed us to perform the classification analysis within the same independently defined, leave-one-subject-out vmPFC clusters that were used in our univariate analysis. Parameter estimates (beta values) were extracted for each subject's 4 independently defined vmPFC clusters, and classification was run iteratively over all possible split halves of the data (10 ways in which 6 scans can be split into two groups of 3). Classification was considered successful if the average Pearson correlation between the face attractiveness patterns (or place attractiveness patterns) in opposite halves of the data

(within-category comparison) was greater than the correlation between face and place attractiveness patterns in opposite halves of the data (cross-category comparison) (Haxby et al. 2001). Raw correlation difference scores on which classification accuracy was based (e.g. face to face – face to place) were also calculated. Both the accuracy and correlation difference scores were then compared to chance (50%) and zero, respectively, to determine if category-specific information was present in any of the vmPFC clusters.

## Results

### Behavioral Results

Within-scan ratings of face and place attractiveness were strongly correlated with post-scan ratings (Pearson's  $r$  averaged across subjects for faces = 0.74,  $t(27)=45.04$ ,  $p<0.0001$  and for places = 0.71,  $t(27)=35.17$ ,  $p<0.0001$ ;  $p$ -values reflect repeated-measures  $t$ -tests on correlation scores), and there was no significant difference between categories regarding the degree of correlation between these within-scan and post-scan ratings (repeated-measures  $t$ -test on the difference between correlation scores:  $t(27)=-1.4$ ,  $p=0.17$ ). Post-scan ratings for face and place attractiveness showed extremely high levels of consistency across subjects (Cronbach's alpha for faces: 0.958; places: 0.956). The within- and between-subjects consistency of attractiveness ratings confirms the validity of using the finer-scale post-scan ratings to analyze the fMRI response.

Subject-specific means of face and place attractiveness ratings were not significantly different, although there was a trend for places to have higher mean ratings than faces ( $t(27)=1.94$ ,  $p=0.06$ ). Figure 3a displays histograms of post-scan face and place attractiveness ratings. Post-scan ratings for places were significantly negatively correlated with in-scan response times (Pearson's  $r$  averaged across subjects =  $-0.24$ , repeated-measures  $t$ -test on correlation scores:  $t(27)=-9.07$ ,  $p<0.0001$ ). In contrast, there was no significant correlation between post-scan face ratings and in-scan response times ( $r=-0.01$ ,  $t(27)=-0.27$ ,  $p=0.79$ ). By plotting response time as a function of attractiveness, visual inspection revealed that rather than a linear function, RT exhibited an inverted-U shaped relationship with both face and place attractiveness, peaking in the center range of attractiveness (Figure 3b). RTs for face judgments were highly symmetrical around the mean, and therefore were not correlated with face attractiveness ratings, whereas RTs for place judgments had an elongated linear slope for the upper half of the attractiveness scale. For each item, we also calculated the mean RT and the standard deviation of rating judgments across subjects. These measures were moderately correlated for both face and place stimuli (Pearson's  $r$  for face stimuli: 0.43, and place stimuli: 0.57). In other words, RTs were slower when there was greater disagreement among subjects about the rating of an image, suggesting that RT may in part reflect the degree to which a subject is uncertain about their rating.

### Activity for face and place attractiveness in frontal cortex

We then turned to the primary question of interest: whether there was overlap between regions responding to face and place attractiveness in the frontal lobes. To answer this, we looked for effects of place and face attractiveness within frontal regions known *a priori* to

exhibit subjective value signals: ventromedial prefrontal cortex (vmPFC) and lateral orbitofrontal cortex (latOFC). We conducted the analyses in surface-space to better account for the large variability in cortical folding patterns along the ventral surface of frontal cortex. We focused on two (non-overlapping) regions.

Our vmPFC ROI was functionally-defined based on Barta and colleagues' meta-analysis of subjective value responses in the brain (Bartra, McGuire, & Kable 2013). Within this ROI, we observed clusters that responded linearly to face attractiveness at  $p < 0.05$  (corrected for small volumes) in both hemispheres ("LvmPFC-face" and "RvmPFC-face"; see Table 1 and Figure 4) and clusters that responded linearly to place attractiveness in both hemispheres ("LvmPFC-place" and "RvmPFC-place"). Visual inspection makes clear that there is a great degree of overlap between the face and place clusters in each hemisphere. The face attractiveness clusters were found in similar locations to activity correlated with face attractiveness in previous studies (e.g. O'Doherty et al. 2003, Ishai et al. 2007; Cloutier et al. 2008) (Figure 4).

To assess whether any of these clusters responded selectively to attractiveness for a single stimulus category, we performed a cross-validation analysis in which we iteratively defined the clusters on  $n-1$  subjects and then extracted parameter estimates for the "left-out" subject. This provides a stringent test of whether a cluster responded to both kinds of attractiveness: although each cluster was defined based on its response to either face or place attractiveness, it was tested for its response to the other category in an independent data set. Repeated-measures t-tests comparing face to place attractiveness revealed that all vmPFC clusters showed a significant response to both face and place attractiveness (LvmPFC-place response to face att.  $t(27)=2.11$ ,  $p=0.04$ , response to place att.  $t(27)=4.09$ ,  $p=0.0004$ ; LvmPFC-face response to face att.  $t(27)=4.19$ ,  $p=0.0003$ , response to place att.  $t(27)=3.70$ ,  $p=0.001$ ; RvmPFC-place response to face att.  $t(27)=3.36$ ,  $p=0.002$ , response to place att.  $t(27)=3.60$ ,  $p=0.001$ ; RvmPFC-face response to face att.  $t(27)=4.17$ ,  $p=0.0003$ , response to place att.  $t(27)=2.18$ ,  $p=0.04$ ; statistics obtained by t-tests comparing extracted mean parameter estimates against zero). Importantly, all clusters were equally sensitive to both face and place attractiveness regardless of how they were initially defined (Face attractiveness > place attractiveness: LvmPFC-face  $t(27)=0.09$ ,  $p=0.93$ , RvmPFC-face  $t(27)=1.04$ ,  $p=0.30$ , LvmPFC-place  $t(27)=-1.39$ ,  $p=0.18$ , RvmPFC-place  $t(27)=-0.34$ ,  $p=0.73$ , all n.s., see Figure 4; all statistics were obtained by repeated-measures t-tests comparing extracted mean parameter estimates across categories.) These results suggest that vmPFC responds similarly to variation in attractiveness for these two categories; that is, clusters in vmPFC sensitive to face attractiveness are also sensitive to place attractiveness, and vice-versa. Note that this is the case even though the overall response in these regions was greater to faces than to places (Faces > places in LvmPFC-face  $t(27)=3.51$ ,  $p=0.002$ , RvmPFC-face  $t(27)=4.52$ ,  $p=0.0001$ ; LvmPFC-place  $t(27)=4.44$ ,  $p=0.0001$ , RvmPFC-place  $t(27)=3.18$ ,  $p=0.004$ ).

Our second region of interest was the lateral orbital-frontal cortex (latOFC). This region has been implicated in subjective value representation of distinct categories of reward (e.g. Sescousse et al. 2010), though value-based response is observed here less frequently than in vmPFC. Our analysis revealed a cluster in the right hemisphere whose response correlated with face attractiveness ( $p < 0.05$  cluster-wise permutation corrected for small-volumes, see

Table 1 and Figure 4). We again used the cross-validation analysis to determine whether the attractiveness response in this cluster was category-specific. A repeated-measures t-test found significantly higher response for face attractiveness compared to place attractiveness ( $t(25)=2.64$ ,  $p=0.01$ ). Indeed, place attractiveness response in the cluster was not significantly different from zero (t-test,  $t(25)=-0.46$ ,  $p=0.65$ ). Of note, the overall response to faces and places did not differ in this region ( $t(25)=0.08$ ,  $p=0.94$ ).

### Distributed category-specific encoding in vmPFC

Our univariate analyses revealed that clusters in vmPFC that have significant mean response to one category of attractiveness also have a significant mean response to the other category, and that the strength of these responses are not significantly different from each other. While these results are in line with the “common currency” hypothesis for evaluative signals in vmPFC, it remains possible that these brain regions contain separate but intermixed valuation mechanisms for faces and places, which were not discriminable when responses were averaged over all voxel in the cluster. For example, Kahnt et al. (2010) showed that high and low rewards could be classified during reward anticipation, even though there was no significant difference in mean response between the two conditions. We tested for a similar possibility by measuring vertex-wise activation patterns for face and place attractiveness in separate halves of the data within each vmPFC cluster and examining whether we could classify face vs. place attractiveness across the split. Classification accuracy for the right hemisphere cluster defined by place attractiveness (RvmPFC-place) was above chance (accuracy = 58%,  $t(27)=2.63$ ,  $p=0.014$ ; see Figure 5). Accuracy in this cluster was similar for both categories, though within-place accuracy was just above the threshold for significance (face-face vs. face-place = 58%,  $t(27)=2.5$ ,  $p=0.02$ ; place-place vs. face-place = 58%,  $t(27)=2.0$ ,  $p=0.055$ ). RvmPFC-face also showed a trend toward significant classification (accuracy = 55.8%,  $t(27)=1.9$ ,  $p=0.068$ ) though neither individual category was significant on its own (face-face vs. face-place = 55.9%,  $t(27)=1.66$ ,  $p=0.11$ ; face-face vs. face-place = 55.7%,  $t(27)=1.55$ ,  $p=0.13$ ). Given the fact that RvmPFC-face overlaps to a large degree with RvmPFC-place (see Figure 4) but it also extends further anterior, these results suggest that the locus of category-specific information is centered within the RvmPFC-place. Accuracy was not significant for LvmPFC-place (accuracy = 50.3%,  $t(27)=0.1$ ,  $p=0.92$ ) or LvmPFC-face (accuracy = 46.1%,  $t(27)=-1.33$ ,  $p=0.20$ ). We also examined the raw correlation scores themselves (upon which the accuracy measures were made) by calculating the difference scores between within- and cross-category Pearson correlations. These difference scores were significantly different from zero only within the same RvmPFC-place cluster that showed significant place vs. face attractiveness classification (face/face – face/place difference score=0.08,  $t(27)=2.08$ ,  $p=0.05$ ; place/place – face/place difference score=0.08,  $t(27)=2.25$ ,  $p=0.03$ ).

To observe the focal point of pattern classification without using predefined clusters, we also performed a searchlight analysis, meaning that, for every vertex on the cortical surface, we centered a 7mm radius disc around that vertex and performed the same classification analysis. Within the vmPFC, peak correlation scores for both face and place attractiveness (face-face vs. face-place; place-place vs. face-place) were located close to the RvmPFC-place cluster but slightly more posterior (peak coordinates for face-face vs. face-place: 5.6,

19.4, -7.6; peak coordinates for place-place vs. face-place: 5.7, 17.3, -7.9. Analysis and coordinates are derived from fsaverage/MNI305 space). These searchlight results reinforce the finding that it is a ventral and posterior portion of vmPFC that contains category-specific information; the univariate-derived cluster appears to be picking up on the more anterior portion of this region.

### Whole brain analysis

We next looked for regions whose response correlated with face attractiveness and place attractiveness outside of our *a priori* regions in frontal cortex. We observed bilateral response in fusiform gyrus that was positively correlated with face attractiveness, as well as a response in right intraparietal sulcus (See Table 2). In contrast, no attractiveness-related activity for places survived wholebrain corrections, though we observed sub-threshold activity in posterior cingulate, ventral striatum, vmPFC, and in the region of parahippocampus gyrus/collateral sulcus/hippocampus ( $p < 0.001$  uncorrected). In a direct contrast of face attractiveness vs. place attractiveness, no voxels survived wholebrain corrections.

To explore whether the areas that responded to face and place attractiveness overlapped with face- and place-selective visual regions that have been previously identified in occipitotemporal cortex, we conducted an ROI analysis using independently defined ROIs for fusiform face area (FFA), parahippocampal place area (PPA), a posterior object-selective region (LOC), and early visual cortex (EVC). Somewhat surprisingly, face attractiveness was positively correlated with activity in all higher level regions (right FFA:  $t(27)=2.9$ ,  $p=0.007$ , left FFA:  $t(27)=2.2$ ,  $p=0.037$ ; right PPA:  $t(27)=3.8$ ,  $p=0.0008$ , left PPA:  $t(27)=2.5$ ,  $p=0.017$ ; right LOC:  $t(27)=3.37$ ,  $p=0.002$ , left LOC:  $t(27)=3.05$ ,  $p=0.005$ ) while place attractiveness only showed positively correlated activity within right LOC ( $t(27)=2.1$ ,  $p=0.04$ ). Correlations between place attractiveness and fMRI response were nonsignificant for right FFA ( $t(27)=0.8$ ,  $p=0.41$ ), left FFA ( $t(27)=0.7$ ,  $p=0.46$ ), right PPA ( $t(27)=0.35$ ,  $p=0.73$ ), and left PPA ( $t(27)=0.00$ ,  $p=0.997$ ). Neither face nor place attractiveness was significantly correlated with activity in EVC. Figure 6 shows the location of the functional ROIs and activity related to face and place attractiveness in visual regions.

Finally, for completeness, we compared categorical differences in activity between face and place trials (irrespective of attractiveness). We observed significantly greater response during place compared to face trials in regions previously reported to respond preferentially to places and scenes (bilateral PPA, RSC, OPA/TOS). Conversely, we observed significantly greater response during face compared to place trials in visual regions previously reported to respond preferentially to faces (bilateral FFA, OFA), and also in posterior cingulate, bilateral amygdala, vmPFC, and, surprisingly, a region of right latOFC. (Table 2 reports the MNI coordinates of all significant clusters for this comparison.) Because we had also observed activation in right latOFC for face attractiveness, we sought to determine whether the right latOFC region defined by our face > place contrast also responded to face attractiveness. We defined this region as an ROI, thresholded at  $t > 3.5$  on the group map, and extracted the betas values from each subjects' response to face attractiveness. Unexpectedly, this region's response was not significantly correlated with

face attractiveness ( $t(27) = -0.75$ ,  $p = 0.46$ ). Figure 7 shows an overlay of both the face > place map and the face attractiveness map, demonstrating that the face > place peak response is located on the posterior orbital gyrus, whereas peak activity for face attractiveness is more medially located within the sulcus.

## Discussion

Attractive faces and attractive places promise very different rewards to a person, and comparisons are not often made between these rewards. Despite this, our results demonstrate that the vmPFC exhibits both category-general and category-specific responses to attractiveness. Clusters sensitive to face attractiveness in vmPFC were also sensitive to place attractiveness; however, a multivertex pattern analysis found that place and face attractiveness were distinguishable in one of these clusters, which was located in the posterior and ventral portion in the right hemisphere. These results suggest that some parts of vmPFC might encode category-general reward signals even when the stimuli are not exchangeable goods, while other parts might retain information about category-specific rewards. In right lateral orbitofrontal cortex (latOFC) we observed two distinct face-specific regions: one sensitive to the categorical difference between faces and places but insensitive to face attractiveness, and one sensitive to face (but not place) attractiveness but insensitive to categorical differences. As we found only face attractiveness and not place attractiveness signals in latOFC, this region may be more involved in basic reward processing that is specific to some but not all stimulus categories.

### Common response to face and place attractiveness in vmPFC

In vmPFC, we identified clusters that were sensitive to face attractiveness and clusters that were sensitive to place attractiveness, and these face and place clusters were highly overlapping. Further analysis revealed a common response to face and place attractiveness: clusters in vmPFC identified based on their response to face attractiveness responded equally strongly to place attractiveness, while clusters identified based on their response to place attractiveness responded equally strongly to face attractiveness.

These findings are consistent with a recent meta-analysis that demonstrated a region of vmPFC that encodes a common evaluative signal in studies where two or more categories were directly compared (Levy and Glimcher 2012). Although most of the studies in the meta-analysis involved economic and consumer goods, a few compared various social rewards to monetary rewards. Smith et al. (2010) showed overlapping activity in vmPFC for face attractiveness and monetary value when subjects passively viewed intermixed images of faces and money. Lin et al. (2012) showed overlapping activity in vmPFC between monetary value and another type of social reward, pictures of smiling or angry people (paired with audio of emotionally matched words). Our results extend these findings by showing that even in the case where both judgments are entirely outside the economic domain, in the realm of aesthetics, an overlapping evaluative signal exists in vmPFC.

Indeed, previous findings in the neuroaesthetics literature have suggested that vmPFC is generally involved in aesthetic evaluations (Ishizu and Zeki 2013; Brown et al. 2011). For example, Ishizu and Zeki (2011) found overlapping response in vmPFC for beautiful

paintings and music, demonstrating that a common evaluative mechanism in vmPFC is recruited by stimuli of different modalities (visual, auditory). However, it is possible that their subjects evaluated all of the items within the same conceptual/reward framework of “artwork” because the items were presented as such. Our current results demonstrate an important extension to the results of Ishizu and Zeki, therefore, because faces and places in our study were not described as artwork, but rather as distinct natural categories. Furthermore, they did not explore the possibility of separable distributed responses to visual and auditory artwork, whereas our pattern analysis revealed distinct face and place attractiveness patterns in at least one region that showed equal mean response between categories.

### Category-specific attractiveness coding in vmPFC

Our pattern classification analysis revealed that a subregion in right vmPFC (RvmPFC-place) contains separable distributed response patterns to face and place attractiveness, even while showing similar mean response. In contrast, the other three vmPFC clusters, which also showed significant mean response to both place and face attractiveness did not display evidence of category-specific encoding, suggesting that category information in vmPFC may be restricted to a posterior and ventral subregion (see Figure 4) (though null results in the other clusters cannot be used to ultimately reject the category-specificity hypothesis in those clusters).

While our classification rates were not especially high, they were significantly greater than chance. Moreover, our results provide an intriguing parallel with results from a recent study by McNamee, Rangel, and O’Doherty (2013) who also used pattern classification to demonstrate category-specific encoding for food and trinket value in ventral vmPFC. They also demonstrated that dorsal regions of vmPFC showed both mean and distributed response patterns indicative of category-general encoding, a result that is consistent with our observation of overlapping mean activity for face and place attractiveness in vmPFC clusters which did not exhibit category-specific responses in the classification analysis. Thus, our results provide independent support for the claim that vmPFC contains category-specific as well as category-general reward information, and furthermore, we show that these components exist for non-economic rewards.

### Face-specific activity in right latOFC

We observed two separate regions in right latOFC that contained face-specific responses, one that exhibited a categorical preference for faces over places and one whose response scaled with face but not place attractiveness.

The previous literature on face attractiveness has not shown consistent results in latOFC. Two studies have found activity that positively correlated with face attractiveness in latOFC (left latOFC: Winston et. al 2007; right latOFC: Tsukiura & Cabeza 2011). In contrast, in a passive viewing task, Liang, Zebrowitz, & Zhang (2010) showed activity negatively correlated with face attractiveness in bilateral latOFC, though this study included disfigured faces, possibly causing an emotional/saliency signal to override a positive attractiveness response. O’Doherty et al. (2003) reported activity negatively correlated with attractiveness

in right latOFC, but in their study, subjects were making gender judgments rather than attractiveness judgments. When combined with these previous results, the current data suggest that positive latOFC activity for face attractiveness may only arise when subjects are explicitly evaluating face attractiveness.

At least two other studies have reported a similar region of right latOFC that showed greater activation for faces than places (Rajimehr, Young, & Tootell 2009; Von Der Heide, Skipper, & Olson 2013). Interestingly, both groups used methods to reduce noise in this frontal region (surface-based group registration and a tilted acquisition, respectively). It is worth noting that this latOFC region should be distinguished from the commonly observed face-selective region in the lateral inferior frontal cortex, a more dorsal region that is involved in social attention (see Nummenmaa and Calder 2008 for a meta-analysis).

No human neuroimaging study to our knowledge has shown a disjunction between regions exhibiting face-specific categorical response and regions exhibiting face-specific attractiveness response in latOFC. Our finding of this functional dissociation provides an important link to findings from the macaque, where multiple kinds of face-specific responses have been observed in orbitofrontal cortex (O Scalaidhe et al. 1997; Rolls et al. 2006; Tsao et al. 2008; Watson & Platt 2012). Using fMRI, Tsao et al. showed that, in macaque OFC, a patch on the orbital surface (lateral orbital sulcus) responded more strongly to faces with emotional expressions than to neutral faces, whereas a more lateral face-specific patch (inferior convexity) showed a categorical face response that did not vary with facial emotions. These anatomical locations are congruent with our own results: the categorical face patch was located on the posterior/lateral gyrus, and the face attractiveness patch was found in the lateral orbital sulcus. While these similarities are suggestive of possible functional homologues, more research is needed to test the robustness and clarify the roles of these regions in humans, especially since the emotion-patch in macaques responded to both positive and negative faces, whereas we were only able to test for linear responses to positive faces.

It is notable that we did not observe place-specific activity in latOFC. Places, unlike faces, may not act as a “basic” reward category in the same way as faces and food. The calculation of place beauty might instead be highly reliant on a dynamic process of integrating “component parts,” such as spatial envelope or contrast/lighting, which may be associated with rewards only over time. Barron et al. have shown evidence that online construction of novel reward categories happens in vmPFC and hippocampus (2013). In line with this theory, place attractiveness was found in our data to correlate with activity in vmPFC and at sub-threshold levels in the hippocampal region.

### Visual region differences

Consistent with previous findings (Chatterjee et al. 2009), we observed activity correlated with face attractiveness across a large area of visual cortex, including face-responsive (FFA) and object-responsive (LOC) regions. Importantly, this activity was not simply due to time-on-task, as RTs instead showed non-linear patterns of response to attractiveness. Chatterjee et al. theorized that response to face attractiveness in the FFA reflects processing of face beauty per se, while response in LOC reflects processing of visual aesthetics regardless of

the category. They hypothesized that place beauty might activate place-specific mechanisms in the PPA in addition to general visual aesthetic mechanisms in LOC. While we did observe activity in right LOC correlating with place attractiveness, consistent with this prediction, we did not observe attractiveness-related activity in PPA for places. Rather, we observed an unexpected response to face attractiveness in this region.

Why might there be a weaker signal in visual cortex for place attractiveness? As discussed above, it may be the case that faces signify more immediate/basic rewards, and attractive faces may therefore recruit visual cortex as a part of an automatic approach response, whereas places would not. It could also be the case that we saw less activity for place attractiveness because the places spanned a greater variety of environment types (e.g. forests, beaches, deserts, fields) than did faces (males, females). For example, a recent study using a narrower range of place stimuli (indoor built environments) showed that place beauty was correlated with activity in the middle occipital gyrus, although there was no correlated activity within the ventral visual cortices (Vartanian et al. 2013). One study has reported greater activity in PPA for preferred scenes versus non-preferred scenes (Yue, Vessel, & Biederman 2007), but it is important to note that this study markedly differs from our own in both task and stimuli, in that subjects were asked to make ratings based on the content of the scenes, many of which were not places but images containing highly salient foreground objects, people, and animals. While we did observe response to place attractiveness in the parahippocampal/hippocampal region anterior to the PPA, this did not survive the stringent threshold for significance in the whole-brain analysis. Taken as a whole with these previous findings, our data suggest that there are regions in visual cortex that respond reliably to face attractiveness, but response to place attractiveness may depend on the nuances of the judgment task or the stimulus set.

## Conclusions

Our data demonstrate a bridge between aesthetic and economic neural signals, in that a functionally similar evaluative mechanism in vmPFC is recruited for these disparate types of judgments. We expect that further research will continue to illuminate our understanding of this mechanism as well as the unique neural representations underlying specific reward categories.

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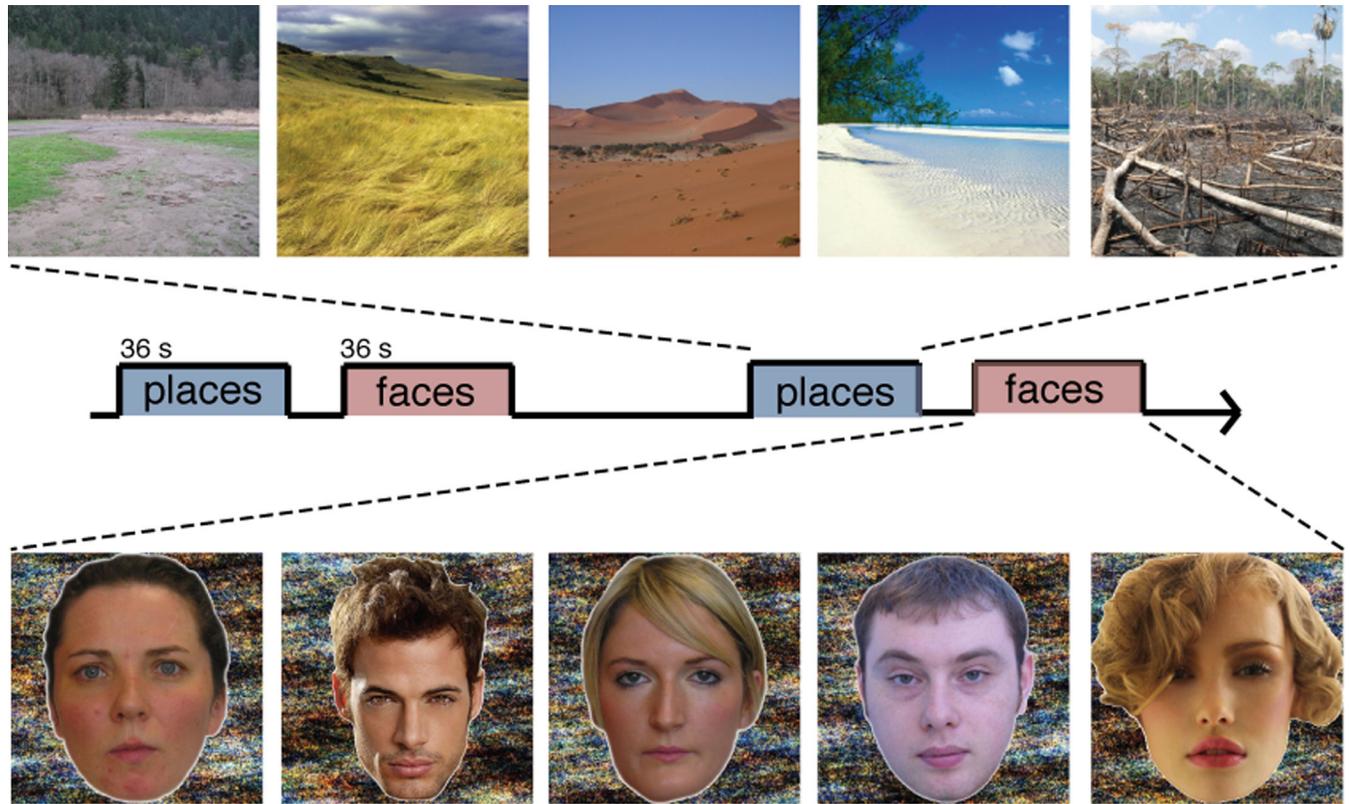
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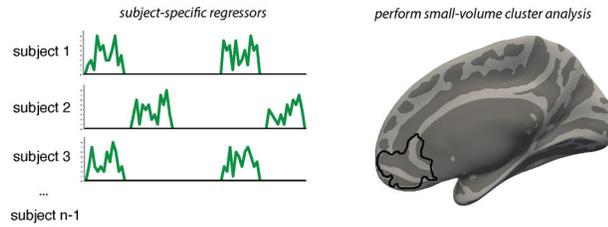
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**Figure 1.**

Places and faces were presented to subjects in blocks of 12 images. Two 36s fixation blocks were also included in each scan run. Each face appeared for 1 second with a 2 second ISI. Subjects made coarse attractiveness ratings for each image in the scanner (“low”, “medium”, “high” attractiveness), and then rated the images again outside of the scanner using a Likert scale, 1–8. The post-rated images were presented to subjects in one randomized block of faces and one randomized block of places (order counterbalanced across subjects).

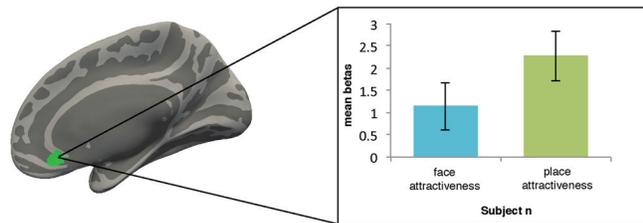
**Step 1: Look for effects of place attractiveness in vmPFC using n-1 subjects**



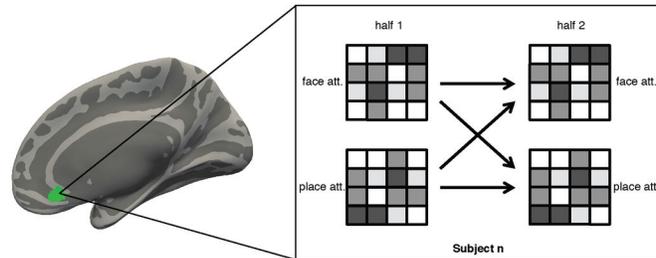
**Step 2: Use the resulting cluster from the group analysis to define an ROI**



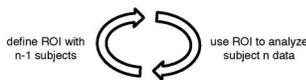
**Step 3: Use ROI to extract mean face and place attractiveness from left-out subject (subject n)**



**Step 4: Use ROI to perform pattern analysis from independent halves of left-out subject data**

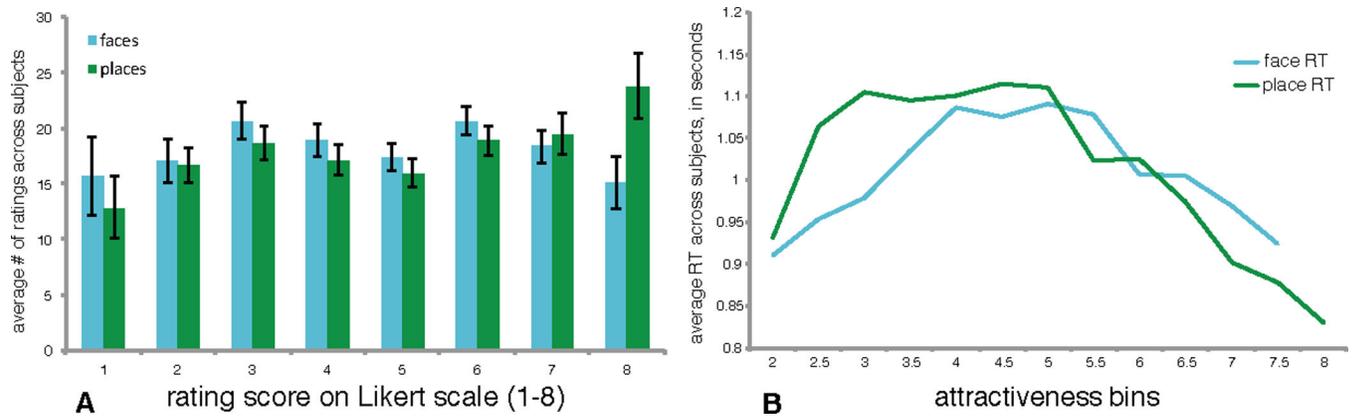


**Step 5: Iterate steps 1-4, each with a different subject left out.**

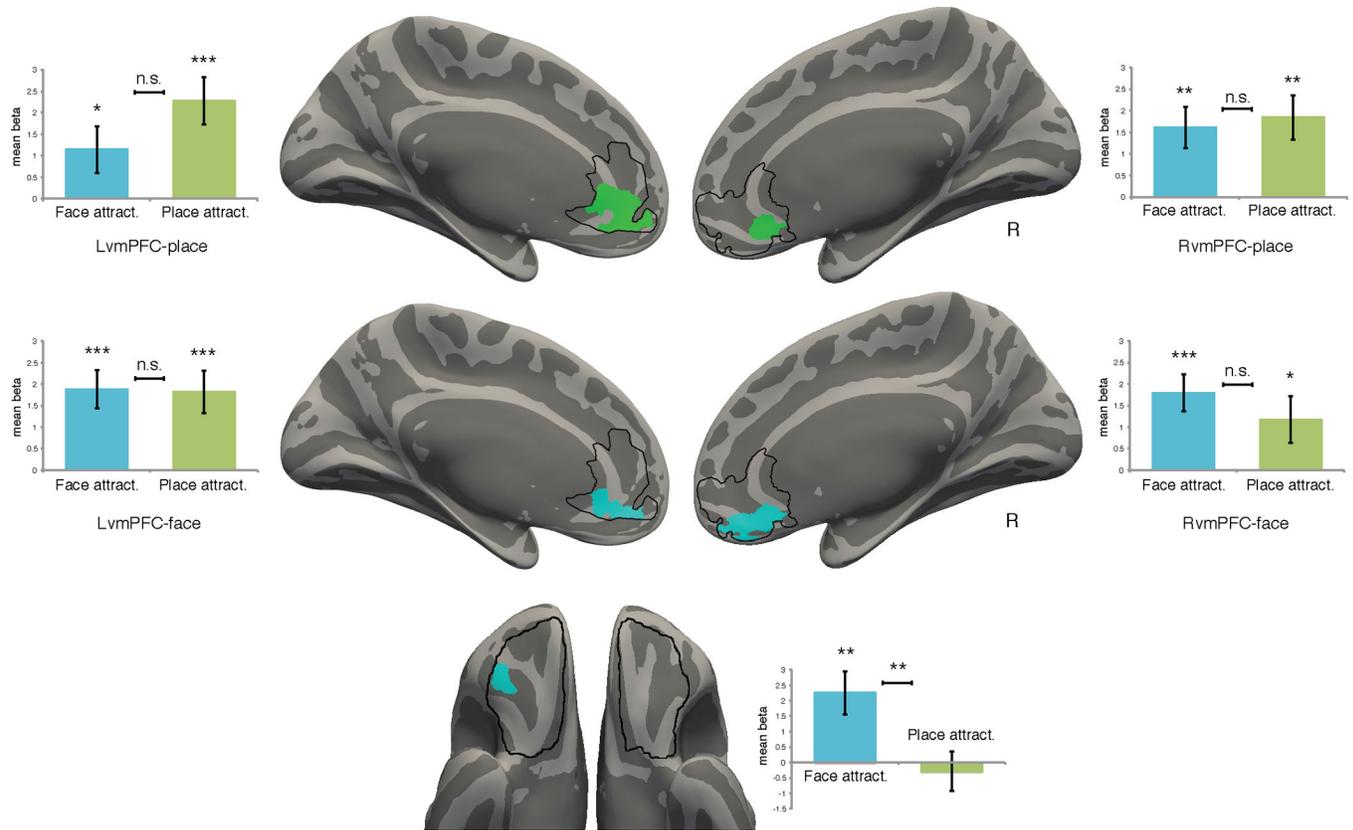


**Step 6: Average results from step 3 to obtain the univariate results, and average results from step 4 to obtain the multivariate results.**

**Figure 2.** Diagram illustrating the steps by which univariate and multivariate analyses were conducted.

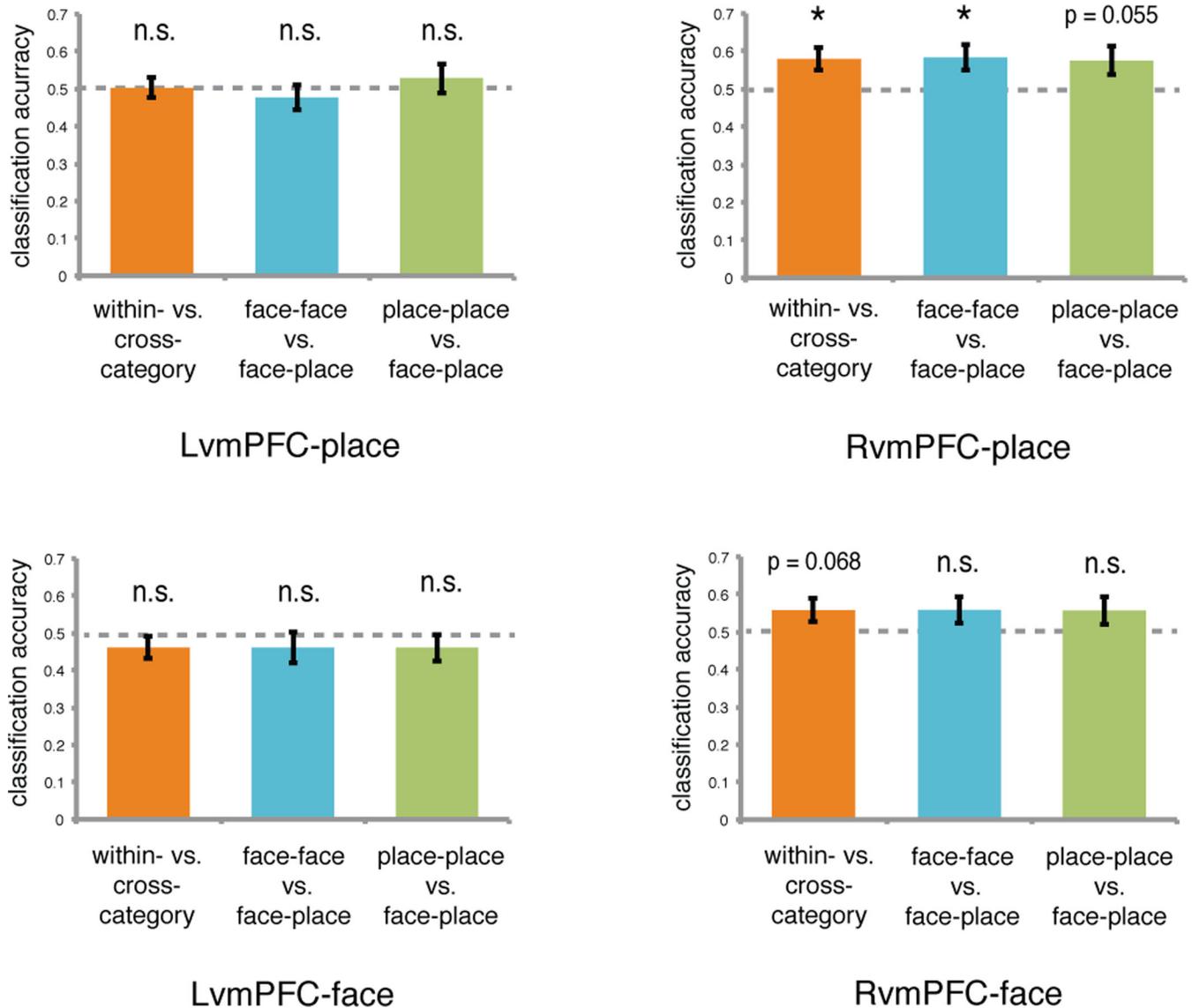
**Figure 3.**

(A) Average of subject-specific histograms of post-scan attractiveness ratings. Error bars measure the standard error across subjects. (B) Response time plotted as a function of average attractiveness. Both face and place attractiveness exhibit an inverted-U shaped function, with the longest response times for mid-range images.



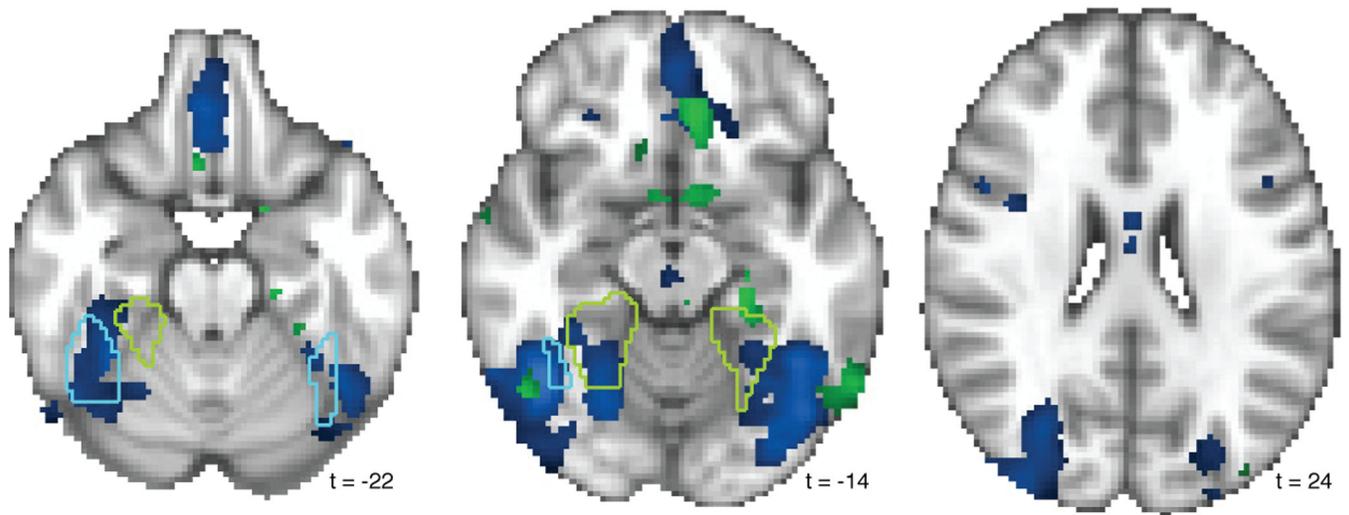
**Figure 4.**

Cross-subject validation results for univariate cluster-corrected group analysis. Clusters responding to face attractiveness (blue) and place attractiveness (green) are shown on the cortical surface. Bar graphs show mean parameter estimates for face and place attractiveness within these clusters. These parameter values were extracted using a leave-one-subject-out cross-validation procedure so that data used to define the clusters were independent of data used to estimate the size of the effects and response patterns. The black outlines on the medial surface indicate boundaries of vmPFC while black outlines on the orbital (i.e. ventral) surface indicate boundaries of latOFC. All vmPFC clusters show significant response to both face and place attractiveness. The face attractiveness cluster in right latOFC only responds to face attractiveness.

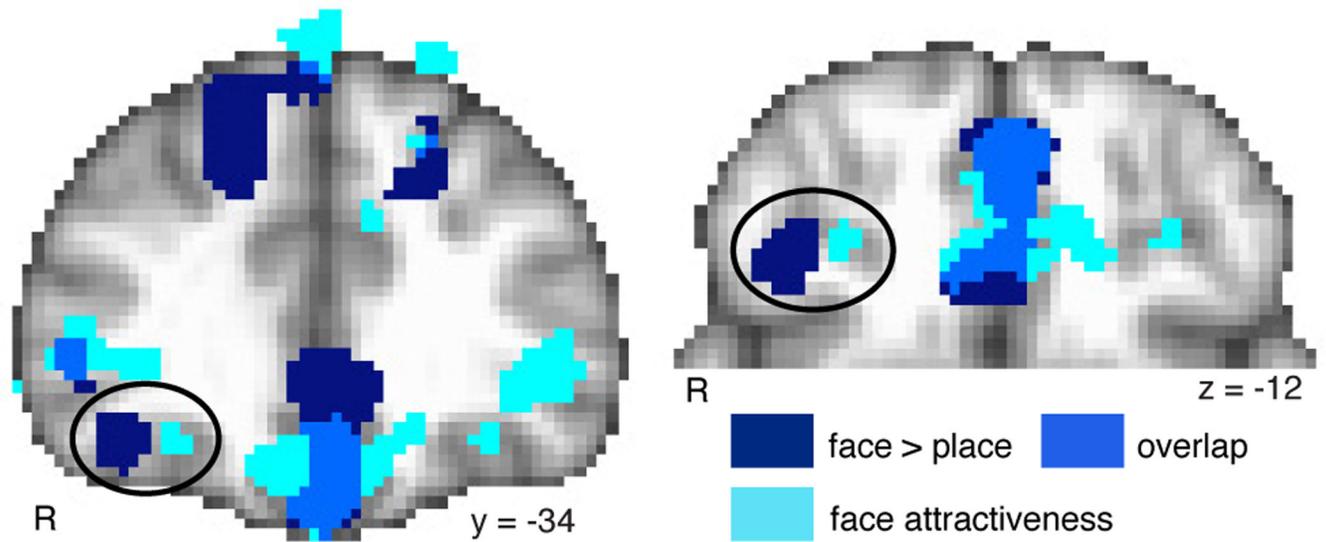


**Figure 5.**

Multivertex pattern analysis of responses to face and place attractiveness in vmPFC. Bar graphs show classification accuracy when comparing response patterns across independent halves of the data. Accuracy (orange bars) was determined by comparing pattern similarity for attractiveness within a category to pattern similarity for attractiveness across categories. The breakdown by category (face-face vs. face-place and place-place vs. face-place) is also shown (blue and green bars). Only one cluster (RvmPFC-place) shows greater classification accuracy for same vs. different attractiveness categories, though RvmPFC-face also shows a trend towards significance.



**Figure 6.** Wholebrain maps for face (blue) and place (green) attractiveness displayed at  $p < .0005$ , uncorrected. The FFA is outlined in light blue, and the PPA is outlined in light green. Note that at this more liberal threshold, vmPFC and ventral striatal activity is visible for place attractiveness, though these regions did not survive volumetric wholebrain corrections.



**Figure 7.** Relationship between face category effect and face attractiveness effect in PFC. The face > place effect (dark blue) was thresholded at  $t > 4.0$ , whereas the face attractiveness effect (light blue) was thresholded at  $t > 2.0$ . Both contrasts were binarized, and the overlapping activity is displayed in pale blue. Peak response for the categorical effect is located lateral to peak response for face attractiveness in right OFC (circled).

**Table 1**

Summary table of significant clusters of response for face or place attractiveness within the vmPFC and latOFC regions of interest (contrast shown in italics). Coordinates and vertex indices for peak values within the clusters are reported in fsaverage space (rather than our group-averaged space) for interpretability across studies. Cluster-wise p-values are permutation corrected for multiple comparisons within the vmPFC or latOFC and additionally Bonferroni corrected to account for observations across 2 hemispheres.

		mm <sup>2</sup>	x	y	z	max vertex	cluster-wise p
<i>face attractiveness</i>							
vmPFC	L	267.97	-11.8	40.2	-6.5	141127	0.016
vmPFC	R	407.91	9.1	30.3	-12.9	25109	0.000
latOFC	R	131.09	32.0	33.8	-7.7	93044	0.044
<i>place attractiveness</i>							
vmPFC	L	588.35	-5.6	33.3	-0.2	83126	0.002
vmPFC	R	145.59	9.2	30.7	-10.0	57203	0.032

Coordinates, voxel count, and peak t-values for significant clusters of voxels. Wholebrain maps for each contrast were thresholded at  $p < 0.05$ , permutation corrected for multiple comparisons. Coordinates are reported in MNI152 space.

**Table 2**

		voxel count	X	Y	Z	Max t
<i>face &gt; place</i>						
fusiform gyrus	R	1135	42	-74	-12	11.03
fusiform face area (FFA)	R	*	42	-52	-18	9.8
occipital face area (OFA)	R	*	42	-74	-12	11.03
cingulate sulcus	medial	960	2	52	18	9.43
amygdala	L	921	-20	-8	-16	11.03
	R	710	20	-8	-14	11.7
anterior cingulate gyrus	medial	603	2	28	-12	7.63
posterior cingulate gyrus	medial	404	4	-52	20	8.62
inferior occipital gyrus	L	341	-42	-82	-16	9.62
inferior frontal sulcus	R	251	48	8	20	7.06
middle temporal gyrus	R	127	58	-4	-26	7.46
cerebellum	L	67	-32	-82	-38	6.36
superior frontal gyrus	R	66	20	38	50	6.7
supramarginal gyrus	L	51	-58	-64	26	5.98
	R	37	56	-60	24	7.19
fusiform gyrus (FFA)	L	46	-40	-50	-24	6.93
posterior orbital gyrus		27	38	32	-16	6.04
<i>place &gt; face</i>						
temporal-occipital cortex	L	4415	-26	-50	-10	21.4
	R	4372	28	-48	-12	15.3
parahippocampal gyrus/collateral sulcus (PPA)	L	*	-26	-50	-10	21.37
	R	*	28	-48	-12	15.26
retrosplenial complex (RSC)	L	*	-14	-56	10	10.01
	R	*	14	-52	8	10.35
middle occipital gyrus (occipital place area)	L	*	-34	-84	18	11.89
	R	*	34	-86	18	12.06
lingual gyrus	R	142	8	-98	-6	7.52

		voxel count	X	Y	Z	Max t
cingulate sulcus	R	81	4	-44	50	8.19
	L	66	-10	-36	44	6.55
cerebellum	L	25	-14	-46	-52	6.67
	R	17	16	-46	-52	6.3
<i>face attractiveness</i>						
intraparietal sulcus (posterior)	R	15	30	-80	24	6.38
fusiform gyrus	L	9	-42	-54	-16	6.09
intraparietal sulcus (anterior)	R	4	22	-54	-14	5.8
	R	4	30	-72	24	5.83

\* peaks are part of a larger cluster