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The neural representation of social status in the extended face-processing network

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Abstract

Social status is a salient cue that shapes our judgment and memory for other people and ultimately guides our social interactions. Despite the pervasive influence of status on social behavior, how information about the status of others is represented in the brain remains unclear. Here, we tested the hypothesis that social-status information is embedded in our neural representations of other individuals. Participants learned to associate faces with names, job titles that varied in associated status, and explicit markers of reputational status (star ratings). Trained stimuli were presented in an fMRI experiment where participants performed a target detection task orthogonal to the variable of interest. A network of face-selective brain regions extending from the occipital lobe to the orbitofrontal cortex was localized and served as regions of interest. Using multivoxel pattern analysis, we found that face-selective voxels in the lateral orbitofrontal cortex – a region involved in social and nonsocial valuation, could decode faces based on their status. Similar effects were observed with two different status manipulations – one based on stored semantic knowledge (e.g. different careers) and one based on learned reputation (e.g. star ranking). These data suggest that a face-selective region of the lateral orbitofrontal cortex may contribute to the perception of social status, potentially underlying the preferential attention and favorable biases humans display toward high status individuals.

Keywords

dominance; MVPA; face processing; orbitofrontal cortex; social perception

Both humans and non-human primates rapidly assign status information to others based on a host of variables, such as physical size, lineage, financial status, and reputation (Deaner et al., 2005; Moors & Houwer, 2005; Paxton et al., 2011). The automatic tendency to assign status to group members may serve an important function: understanding where one ranks

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relative to others provides essential information regarding social roles and how to behave in social interactions, and facilitates intergroup cooperation and function (Halevy et al., 2011; Savin-Williams, 1979). Social status information may specifically aid in the formation of social hierarchies, a tendency that is highly pervasive across human cultures (Sidanius & Pratto, 1999) and appears spontaneously in both human and primate social groups (Anderson et al., 2001; Berger et al., 1980; Chase et al., 2002; Gould, 2002; Magee & Galinsky, 2008). Humans demonstrate high levels of consistency with status judgments regarding themselves and others (Anderson et al., 2006), suggesting status is both a salient and reliable social cue.

Several behavioral studies have illustrated the salience of status information by showing that people rapidly and automatically follow the gaze of high status, as compared to low status, individuals (Dalmaso et al., 2012; Jones et al., 2010) and to fixate on high status speakers more often and for longer periods of time (Foulsham et al., 2010). Notably, the averted gaze of high-status individuals influences subtle and immediate shifts in attention even when faces are unfamiliar and status is implied via fictional career information (Dalmaso et al., 2012), suggesting reputation alone can bias social attention in favor of high status.

Neuroimaging studies have explored how humans process status information by exploring the neural basis of status judgments. Prior findings have identified status-sensitive neural regions in networks typically involved in rank and magnitude judgments (Chiao et al., 2009), affective and value/reward processing (Kumaran et al., 2012; Ly et al., 2011; Zink et al., 2008), and executive processing (Mason et al., 2014). However, in order for status to be a useful social cue, status information needs to be embedded in the representations of other people. It is presently unclear where in the brain abstract information about an individual's status is represented, and through what mechanism this information is signaled as valuable.

One possibility is that neural regions involved in reward and valuation act alongside those involved in social memory and perception to store information about an individual's status, and to signal this information as motivationally relevant. Prior work in monkeys suggests that viewing high-status group members is fundamentally rewarding (Deaner et al., 2005), and that neurons in the orbitofrontal cortex (OFC) may be particularly sensitive to motivationally salient social information, including status (Azzi et al., 2012). Other researchers have proposed that brain regions involved in value computation and reward processing, including the OFC and ventral striatum, as well as the amygdala, involved in the emotive coding of stimuli, may comprise a neural network important for assigning social value and guiding visual orienting (Klein et al., 2009). While a direct comparison has not been made in humans, there is suggestive evidence that areas known to be involved in reward processing, such as the ventral striatum, are active when humans view or make explicit status judgments about others (Ly et al., 2011; Zink et al., 2008).

A well-studied network of regions in the ventral visual stream are associated with face processing. These regions include the occipital face area (OFA) and fusiform face area (FFA; Haxby et al., 2000; Kanwisher & Yovel, 2006). More anterior regions of this network include a "face patch" in the ventral anterior temporal lobes (ATL; Freiwald & Tsao, 2010; Ku, Tolia et al., 2011; Kriegeskorte et al., 2007; Leopold et al., 2006; Rajimehr et al., 2009;

Tsao et al., 2008;), thought be involved in mnemonic and conceptual aspects of person processing (Von der Heide et al., 2013; Collins & Olson, 2014; Collins et al., 2016). Since some types of status information are conceptual in nature, such as one's income or title, it is plausible the ATL face patches are sensitive to status.

There is also a poorly understood face patch in the orbitofrontal cortex (OFC; Ishai et al., 2005; Roll, 2000; Tsao et al., 2008). The OFC has a general, albeit under-specified role in social behavior (Hornak et al., 2003), as well as social and nonsocial valuation (Lin et al., 2012; Rushworth et al., 2007). Recent findings indicate that face-sensitive patches in the medial OFC are sensitive to faces over and above other rewards, whereas the lateral OFC has a more general reward sensitivity, responding to both food and social rewards (Troiani et al., 2016). Although the function of the OFC face patches is poorly understood, it is possible that this region plays a role in evaluating socially important or rewarding information, like a conspecific's social status (Klein et al., 2008). Indeed, one study in non-human primates reported that neurons in the OFC were sensitive to motivationally salient social information, including status (Azzi et al., 2012).

Although previous studies have implicated various neural networks in status processing (reviewed by Koski et al., 2015), it is presently unclear where knowledge about an individual's status is represented, and how neural networks involved in social knowledge and valuation potentially interact when viewing high or low status individuals. Additionally, it is unclear whether the neural representations of status are exclusively social, or whether they apply to nonsocial valuation as well.

Here we used functional magnetic resonance imaging (fMRI) to examine neural representations of person status, and object status as a nonsocial comparison. Participants were trained to associate status cues with faces and objects across two consecutive days, and they were presented again with the trained stimuli during an fMRI scan on the third day. We perform a multivoxel pattern analysis (MVPA) on the imaging data to test the following hypotheses: (1) Brain regions that store high-level face and object concepts will have status information embedded in the abstract concept and will be able to discriminate high from low status faces and objects respectively; and (2) Brain regions that play a general role in valuation will be able to discriminate high from low status information, regardless of stimulus category.

Materials and Methods

Participants

Twenty participants (12 males) ranging in age from 18 – 29 years ($M = 24.4$; $SD = 2.96$) were recruited from Temple University and the surrounding community. All participants were without history of brain injury or psychiatric illnesses, had normal or corrected color vision, and were right-handed. Only participants with some college education were included in the study to control for the possibility that personal status might influence status perception (e.g., Ly et al., 2011). Two male participants were excluded from subsequent analyses. Both participants displayed problematic motion (> 5 mm displacement) across experimental runs, and one participant additionally had low recall performance ($< 65\%$

accuracy) for trained information. Thus final sample size was 18. This study and its procedures were approved by the Temple University Institutional Review Board (IRB), and all participants gave written informed consent in compliance with the human subject regulations of Temple University prior to the first training session. Participants received monetary compensation for their participation.

Status Training Paradigm

Stimuli and Design—Face stimuli consisted of grey-scale images of 8 male faces, all lacking facial hair and glasses and facing forward. Images were provided by Michael J. Tarr (see <http://www.tarrlab.org/>). Object stimuli consisted of grey-scale images of 8 different restaurant or hospital tools from 4 different object categories. Object images were taken from the Internet. All stimuli were 360 by 360 pixels and displayed on a white background. A null stimulus consisting of a grey background and central fixation cross was also used.

Participants learned to associate 3 pieces of conceptual information with 8 unfamiliar faces and 8 objects: 1) name; 2) category (occupation or object type); and 3) performance ranking (2 or 5 stars). To make object and face information as conceptually similar as possible, two object categories and two occupation categories were selected from two familiar public locations: restaurants and hospitals. Object categories with at least two different, distinct exemplars were selected, and these two exemplars represent the individual object names within each object category. Similarly, different male names were chosen to represent individual faces within each occupation category. Common, distinct male names were selected from the US Social Security list of the top 100 baby names for the 2000s (www.socialsecurity.gov).

Our study design allowed facial-status to be manipulated in two ways: reputation-based status, and career-based status (see Figure 1). Reputation-based status was indicated with a star ranking. Two items (faces or objects) within each object or occupation category was associated during the training phase with a high ranking (5 stars) and two items in each category were associated with a low ranking (2 stars). Star ranking was chosen because it has been used in prior fMRI work assessing status (e.g., Zink et al., 2008) and is intuitive for our sample population given that it is commonly applied to restaurants, hotels, and objects in online reviews. Career-based status was indicated via career titles.

Status Training Procedure: Status training was conducted over 2 days in a laboratory setting, with the first session lasting approximately 45 minutes and the second lasting approximately 30 minutes. The first training session consisted of 3 trial types. During the ‘show trials,’ participants viewed slides containing a face or object image, along with that face or object’s associated information, and were instructed to memorize the names, categories, and status ratings for each image. Each slide was presented 4 times (64 trials total) for 5 seconds in a random order. Next, participants completed ‘category-response trials’ in which they viewed the trained faces and objects one at a time and were instructed to select the category that matched with each from a list presented on screen. Following response, the correct answer was displayed for 2 seconds. Each image was presented twice (32 trials total) in a random order. Finally, during ‘status-response trials,’ participants

viewed each trained image one at a time and were instructed to select the status rating assigned to each (either 2 or 5 stars). Following their response, the correct answer was displayed for 2 seconds. Each image was presented twice in a random order (32 trials total). Participants completed blocks of trials in the following order, two times: show trials (64 total), category-response trials (32 total), show trials (64 total), status-response trials (32 total).

The second training session used the same trial blocks in the same order as the first session. Afterwards, participants completed a free recall test, where a number was presented on the computer screen with one of the 16 trained images. Participants were instructed to write down on a separate sheet of paper all of the information they learned for each image, including name, category, and status information.

Status survey: To identify whether objects and career titles presented in the stimulus set hold some inherent status or value among members of the population sampled, an additional survey was administered to a separate group of college undergraduates ($N = 24$; 8 males), age 19-27 years ($M = 21.67$, $SD = 2.06$). These individuals completed a series of questions asking them to compare all possible pairs of objects within each category and report whether one was better than the other (e.g., “Do you think one of these is better: infrared thermometer, or digital thermometer?”). They were asked to make a similar comparison between all possible pairs of objects categories (thermometer vs. blood pressure gauge, blood pressure gauge vs. mixer, etc) and career categories (pediatrician vs. radiologist, chef vs. bartender, etc.).

fMRI Session—The fMRI session occurred on the third day of study participation, following two days of training sessions. Participants completed an additional recall test immediately before their fMRI session, to ensure they had retained all information learned during training. The recall test consisted of a piece of paper with the 16 trained images, and participants were instructed to write next to each face or object the associated name, category, and status information learned during training.

Functional Localizer: A functional localizer scan occurred prior to the main experiment to localize areas sensitive to faces (specifically, in the occipital face area (OFA), FFA, ATL, OFC) and objects (the lateral occipital complex (LOC)). The LOC is a region of extrastriate cortex involved in object recognition, which extends bilaterally from the lateral occipital lobes into posterior regions of the temporal lobes (Grill-Spector, Kourtzi, & Kanwisher, 2001).

The localizer task was a block design, presenting category blocks of faces (famous and nonfamous), places (famous and nonfamous), objects, and scrambled images. Famous stimuli were included to improve localization of the ATL face patches, based on prior findings showing that the ATL face patches are particularly sensitive to well-known stimuli (e.g., Ross & Olson, 2012; Von der Heide et al., 2013). Objects and faces differed from those in the experimental task, and famous images were previously pilot tested (See Ross & Olson, 2012) to ensure that they are highly familiar within the cohort sampled in the present study.

Images were randomly selected from lists of 89 images per category, and presented one at a time for 400ms (350 ISI) in 8 category blocks consisting of 14 trials each. Participants completed two full localizer runs, each consisting of 5 cycles presenting all 8 category blocks in a fixed randomized order. Each cycle ended with a 1200 ms presentation of a central fixation cross. Two times per block, a randomly selected image was repeated, and participants were instructed to indicate with a button-press each time this occurred. This served to ensure attention was maintained throughout the task.

Main Experiment: Four novel exemplars (i.e., images of the same object that differed from the training image) of each of the 8 objects used during status training were used in the experimental run. This is similar to prior work looking at object representations in the ATLs (see Peelen & Caramazza, 2012) to avoid neural decoding of individual images, rather than object identity. Similarly, 4 novel exemplars of the same 8 male faces used during status training were used in the experimental runs. The faces studied during status training were angled 30 and 45 degrees to the right and left from the viewpoint of the training image to produce novel perceptual images for each identity, similar to previous work assessing neural decoding of face identity (e.g., Collins et al., 2016).

The main experiment was a block design with a target detection task. Stimuli were presented in 16 identity blocks (8 face, 8 object), consisting of 16 trials each. Blocks were presented in a fixed random order, alternating between faces and objects. Within each block, each exemplar image for the relevant identity (face or object) was presented 4 times in a fixed random order for 700ms (425ms ISI), and each block ended with 3000ms presentation of a fixation cross. Participants completed 6 total runs consisting of 16 blocks each. This design was shown to be sufficient in prior MVP analyses in the temporal lobes (e.g., Peelen & Caramazza, 2012).

A target detection task served to ensure attention was maintained throughout the task. Importantly, the detection task was orthogonal to the interests of the study to ensure any observed activations were not due to top-down, task-related effects. Participants were instructed to respond with a button press each time a green dot appeared on an image. Target images appeared 3 times per block, with their exact locations following one of 4 predetermined patterns that varied across trial blocks in a fixed random order (to make the pattern unpredictable).

Data Acquisition—Neuroimaging sessions were conducted at Temple University Hospital on a 3.0 T Siemens Verio scanner using a twelve-channel Siemens head coil. The functional runs were preceded by a high-resolution anatomical scan lasting approximately 10 minutes. The T1-weighted images were acquired using a three-dimensional magnetization-prepared rapid acquisition gradient echo pulse sequence. Imaging parameters consisted of: 144 contiguous slices of 0.9766 mm thickness; repetition time (TR) = 1900 ms; echo time (TE) = 2.94 ms; FOV = 188 x 250 mm; inversion time = 900 ms; voxel size = 1x 0.9766 x 0.9766; matrix size = 188 x 256; flip angle = 90 degrees.

Functional T2*-weighted images sensitive to blood oxygenation level-dependent contrasts were acquired using a gradient-echo echo-planar pulse sequence and automatic shimming.

Imaging parameters consisted of: repetition time (TR) = 3000 ms; echo time (TE) = 20 ms; inversion time = 900 ms; FOV = 240 x 240; voxel size = 3 x 3 x 2.5mm; matrix size = 80 x 80; flip angle = 90 degrees. This pulse sequence was optimized for ATL coverage and sensitivity based on pilot scans performed for this purpose, details of which are reported in Ross and Olson (2010). Sixty-one interleaved axial slices of 2.5 mm thickness were acquired to cover the temporal lobes.

Visual stimuli were presented using a rear-mounted projection system, and stimulus delivery was controlled by E-prime software (Psychology Software Tool, Inc.; Pittsburgh, PA) on a Windows laptop located in the scanner control room. Responses were recorded using a five-button fiber optic response pad system.

Data Analysis—Data preprocessing and univariate analysis of fMRI data were performed using FEAT (fMRI Expert Analysis Tool) version 6.0, part of the software library of the Oxford Centre for Functional MRI of the Brain (fMRIB; www.fmrib.ox.ac.uk/fsl). MVPA analysis was carried out using the Princeton MVPA Toolbox version 0.7.1 running on MATLAB R2012b, and with custom MATLAB software.

Preprocessing: Preprocessing included removal of non-brain tissues using BET, MCFLIRT motion correction, high-pass temporal filtering with a 200 second cutoff, and fieldmap-based correction of EPI data to reduce spatial distortions. The EPI data was registered to each participant's T1-weighted anatomical scan using BBR and normalized to a standard Montreal Neurological institute (MNI-152) template. Functional localizer data was smoothed using a 5mm Gaussian kernel, however MVPA data was not smoothed.

Defining Regions of Interest (ROIs): Preprocessed functional localizer data were submitted to a fixed effects general linear model including each condition of interest. Predictors' time courses were modeled for each experimental block type (faces, places, objects, scrambled images), excluding instructions and fixations, using a double-gamma model of hemodynamic response function. Functional data were z-transformed to normalize the time course.

Functional regions of interest (ROIs) were defined in both face and object sensitive cortex using the functional localizer data, using the uncorrected output from the general linear model with a threshold value of $p = .05$. The Harvard-Oxford Cortical and Subcortical Structural Atlases in FSL were used to restrict our analysis to regions that have previously been implicated in face processing (see Figure S1 for anatomical masks). Contrasting the average activation to faces versus objects + places identified bilateral face-selective regions corresponding to the occipital face area, located in the inferior occipital gyrus, the FFA located on the fusiform gyrus, and ATL face patches located on the ventral surface of the anterior temporal lobes. Face-selective regions were also defined in the left and right lateral OFC and in the medial OFC, using the methods described in Troiani et al., 2016. See Figure S2 for a group map of functionally localized face-selective regions.

Contrasting the average activation to objects versus scrambled images identified object selective regions in bilateral lateral occipital cortex (LOC), a region known to process object

identity (Grill-Spector et al., 2001). As with faces, there is evidence of object-sensitive cortex in both the ATLs and the OFC (e.g., Rolls et al., 2000). Thus, object ROIs were functionally identified in the bilateral ATL, and the medial and lateral OFC as well. Using the method employed by (Anzellotti et al., 2013) final ROIs were defined by centering a 9mm sphere on the voxel of peak value in each face and object selective region. See Table S1 for peak coordinates from the group map of functionally localized face-selective regions.

Following methods used by (Bracci et al., 2014) a lower-level visual control ROI was functionally defined in early visual cortex (EVC; located using the V1/Brodmann area 17 mask in the Juelich Histological Atlas in FSL), by contrasting the average response to all stimulus categories in the localizer task (faces, place, objects, scrambled images) with fixation periods. Since the number of voxels within an ROI may influence MVPA outcomes (e.g., Anzellotti et al., 2013; Eger et al., 2008), the early visual cortex control region was defined in a similar manner as the face and object ROIs, by centering a 9mm sphere in the voxel of peak value.

Final ROIs were examined to ensure each was centered on a discrete cluster of voxels, and there was no overlap. In cases where regions overlapped, ROIs were manually repositioned to center on a discrete cluster of voxels. All participants had activation in bilateral early visual cortex, OFA, and FFA for faces, and bilateral early visual cortex and LOC for objects. Participants varied in ATL, amygdala and OFC activations (see Table S2). Medial OFC was not analyzed by hemisphere, as activation across participants was along the midline of the brain and discrete lateralized ROIs could not be identified with 9mm ROIs.

Additionally, a structural ROI was created for bilateral amygdala and bilateral ventral striatum using the Harvard-Oxford Subcortical Structural Atlas and Oxford-Manova Striatal Connectivity Atlas in FSL, respectively, so that patterns of activation in these regions could be assessed. The average number of voxels for each bilateral (i.e., per hemisphere) amygdala mask was 252 voxels, and for each bilateral ventral striatum mask it was 604. Bilateral functional ROIs contained approximately 389 voxels. For each ROI analysis, only participants who had “face patches” were included.

Temporal Signal to Noise Ratio: Given that the ATL and inferior portions of the frontal lobe are prone to susceptibility artifacts, TNSR maps were examined to ensure adequate signal in these regions. Probability maps were generated across participants using a threshold of 40, which prior work has deemed sufficient to detect BOLD differences between conditions (Murphy et al., 2007). A group TSNR map indicated adequate coverage across participants.

Multivoxel Pattern Analysis (MVPA): Multivoxel pattern analysis (MVPA) was used to examine whether unique multivoxel patterns could accurately discriminate high from low status faces and objects. Separate regressors were created for each condition of interest. Data were z-scored within each run to control for baseline shifts in the magnetic resonant signal, and all regressors were convolved with a standard hemodynamic response function.

Analysis was performed using a Gaussian Naïve Bayes (GNB) classifier. This classifier has been shown to perform well in pattern classification analyses (Mitchell et al, 2004) and is commonly used in MVPA (see Coutanche & Thompson-Schill, 2012). For the main analyses, a 6-fold leave-one-run-out cross validation scheme was employed, where the classifier was trained on five runs of data and tested on the remaining un-trained run. The training and test datasets included some of the same images (i.e., same visual angles of faces and same exemplars of objects), though they were presented at different times and in different orders across runs. This procedure was repeated 6 times, each time using a different test run, and the average classification accuracy was calculated for each ROI and compared to chance using a group-level one-sample *t*-test. See Supplementary data for univariate analyses.

Statistical Tests, MVPA: For face reputational status, regressors were defined for 5-star faces and 2-star faces, collapsing across career title. MVPA was conducted in the functionally defined extended face network, including the bilateral OFA, FFA, ATL, lateral OFC, medial OFC, as well as a control region, EVC, and anatomically defined bilateral amygdala and ventral striatum. For object reputational status, regressors were defined for 5-star objects and 2-star objects, collapsing across object category. MVPA was conducted on functionally defined object selective cortex, as well as bilateral LOC, ATL, lateral OFC, medial OFC and EVC. Classification accuracy within each ROI for high versus low status was calculated and averaged across 6 iterations of cross-validation and compared to chance (.50) in a group level one-sample *t*-test. Because our hypotheses predict greater than chance-level classification, we used a one-tailed *t*-test for these analyses. A Bonferroni corrected *p*-value of .00313 (.05/16) was used to test for significance.

For career status, regressors were defined for pediatricians and bartenders, collapsing across reputational star ranking. As in the face reputational status analyses, MVPA was conducted in functionally defined face-selective cortex, and classification accuracy for high versus low status was calculated and averaged across 6 iterations of cross-validation and compared to chance (.50) in a group level one-sample, one-tailed *t*-test.

Results

Survey Data

Survey data from separate group of college undergraduates ($N = 24$; 8 males), age 19-27 years ($M = 21.67$, $SD = 2.06$) was analyzed to gauge inherent preferences for stimuli used in the main experiment. Data revealed that 100% of respondents identified radiologists and pediatricians as higher status than bartenders, and 83.3% identified radiologists and pediatricians as higher status than chefs. Pediatricians were considered higher status than radiologists (41.7%) more frequently than the reverse (16.7%). Thus, pediatricians and bartenders served as the high status and low status career in the career-based analysis. See Supplementary data for object status responses.

Behavioral Results

Participants were quite accurate at recollecting information about trained people and objects immediately following training ($M = .98$, $SD = .05$) and immediately prior to scanning ($M = .97$, $SD = .04$). Recall accuracy did not differ across information types. Likewise, participants were highly accurate at detecting targets across both functional localizer runs ($M = .97$, $SD = .03$) and all six experimental runs ($M = .98$, $SD = .04$) indicating attention to stimuli was maintained across the experiment.

MVPA Results

Analyses addressed the hypotheses that face and object selective cortex involved in conceptual knowledge and valuation discriminate high from low status faces and objects. Detailed statistics for MVPA analyses are listed in Table 1.

Next, we examined whether multivoxel patterns could accurately classify high from low rated objects, based on the trained star ranking associated with each item. The analysis was similar to that performed for face reputational status but was performed on a tailored set of ROIs that included functionally defined object selective cortex, lateral occipital cortex, was included as an ROI (see Figure 2). Classification accuracy for object reputational status was greater than chance in left LOC ($t(17) = 4.20$, $p < .001$; $M = .66$, $SD = .16$). Classification accuracy failed to reach significance in all other ROIs after correcting for multiple comparisons (see Table 1 for uncorrected p -values). Paired t -tests (2-tailed, p -value corrected for multiple comparisons) showed that classification accuracy in the right LOFC was significantly higher than in right EVC ($t(17) = 3.47$, $p = .003$). No other effects were significant after correcting for multiple comparisons (left IOFC: $t(16) = -.74$, $p = .47$; left ATL: $t(17) = -.26$, $p = .80$; right ATL: $t(17) = 2.25$, $p = .04$).

Career Status—Career status was defined based on status ratings obtained in the Status Survey, which identified pediatricians as the highest status career and bartenders as the lowest status career. Analyses assessed whether multivoxel patterns could accurately classify high from low status faces, based on the status of the trained career title associated with each individual (see Figure 3).

Similar to the results for reputational status, classification accuracy was again greater than chance in the left lateral OFC ($t(17) = 4.32$, $p < .001$, $M = .71$, $SD = .18$) face-selective ROI. Using our stringent correction for multiple comparisons, classification accuracy failed to reach significance in all other ROIs. Paired t -tests (2-tailed, p -value corrected for multiple comparisons) found no significant difference between classification accuracy in early visual areas and classification accuracy in lateral OFC (left: $t(14) = 1.37$, $p = .19$; right: $t(15) = 1.80$, $p = .09$) or ATL (left: $t(16) = -.05$, $p = .96$; right: $t(15) = 2.13$, $p = .05$).

Finally, we examined classification of reputational (star ranking) status for doctors only, given that these career titles were rated as higher status overall than restaurant careers by survey respondents. These analyses aimed to reduce any confounding effects of pre-existing status rankings associated with restaurant workers compared to doctors, which might interfere with the trained reputational status rankings. Regressors were defined for 5-star

doctors (pediatricians and radiologists) and 2-star doctors. Figure 3 depicts findings. Again, classification accuracy was greater than chance in the left lateral OFC ($t(17) = 3.27, p = .003; M = .70, SD = .21$). Paired t -tests (2-tailed, p -value corrected for multiple comparisons) found no significant difference between classification accuracy in early visual areas and classification accuracy in lateral OFC (left: $t(14) = 1.07, p = .30$; right: $t(15) = 1.59, p = .13$) or ATL (left: $t(16) = -.14, p = .89$; right: $t(15) = 2.44, p = .03$).

Generalization Tests—Is reputational status represented as an abstract construct independent of the social or nonsocial nature of the stimulus? If voxel patterns classify reputational status across social categories (i.e., above-chance classification of object status in face ROIs), this suggests that voxels are decoding status as a general concept, and not just lower level visual features of a stimulus. To test this, the classifier was trained on face reputational status and tested on object reputational status. Analyses were focused within the face-selective ATL and face-selective lateral OFC ROIs, given that prior analyses found that these regions were the ones most sensitive to status. One-sample, one-tailed t -tests were conducted comparing classification accuracy to chance (.50), using a Bonferroni corrected p -value of .0125 (.05/4) to test for significance (Figure 4). Classification accuracy was significantly above chance in the left lateral OFC (left: $t(14) = 2.98, p = .005, M = .63, SD = .17$), as well as the left ATL ($t(16) = 2.94, p = .005, M = .59, SD = .13$). Right lateral OFC and Right ATL classification accuracy was not significant using a corrected p -value (right OFC: $t(15) = 2.16, p = .02, M = .57, SD = .13$; right ATL: $t(16) = 1.82, p = .04, M = .57, SD = .15$).

One possible confound in the generalization analysis is that the original ROIs were large (9 mm) and potentially contained object-selective voxels. To address this possibility, face-selective ROIs in the ATL and lateral OFC were modified by subtracting the object selective voxels identified using the functional localizer data. Note that the number of voxels subtracted from the original ROIs varied (ATL overlapping voxels: $M = 83.58, SD = 71.09$; lateral OFC overlapping voxels: $M = 114.75, SD = 82.08$). The original test for object reputational status was repeated in the modified face-selective ROIs. As in the previous analysis, classification accuracy was significantly above chance in the (modified) left lateral OFC ($t(14) = 3.37, p = .003$) and approached significance in the right lateral OFC ($t(15) = 2.29, p = .019$), however classification of object reputational status in the ATL was not above chance after correcting for multiple comparisons (left: $t(16) = 1.85, p = .042$; right: $t(14) = 1.90, p = .038$).

In sum, reputational status appears to be represented as an abstract construct in the lateral OFC; the same voxels that decode face status also decode object status.

Exploratory Analyses

Using an uncorrected p -value of .05, we ran correlations to explore whether classification accuracy in the left lateral OFC for facial status was related to classification accuracy in other ROIs. We chose to focus on this region since it was the only area where classification accuracy for facial status survived correction for multiple comparisons across all analyses. Classification accuracy for reputational status in left lateral OFC was positively correlated

with classification accuracy in right OFA ($r = .54$, $p = .04$, $N = 15$), and classification accuracy for career status in left lateral OFC was positively correlated with classification right lateral OFC ($r = .57$, $p = .040$, $N = 13$), and negatively correlated with left ATL ($r = -.57$, $p = .05$, $N = 15$) and left FFA ($r = -.53$, $p = .04$, $N = 15$). No other significant correlations were observed between classification accuracy for facial status in the left lateral OFC and other ROIs (see Table S3 for all correlation coefficients). These results suggest that the coordinated activity of face-selective regions in the right and left lateral OFC may contribute to the accurate representation of the social status of other individuals.

Searchlight Analysis—In addition to MVPA analyses focused within functionally defined ROIs, we conducted a whole-brain searchlight analysis using the Princeton MVPA Toolbox. Given that results for ROI tests were fairly consistent across analyses, including generalization tests, the searchlight focused on face reputational status and tested whether multivoxel patterns outside of the extended face-network ROIs classified generalizable social status rank. Using the same face reputational status regressors and cross-validation method described for the main MVPA analysis, the searchlight moved a 9mm sphere ROI across voxels within a whole-brain mask (excluding the cerebellum). Classification accuracy was averaged across the 6 cross-validation iterations performed per subject, then averaged across subjects to create a group classification map. Chance level classification accuracy (.5) was subtracted from the group map, and the resulting classification map was compared to 0 with a non-parametric (5000 permutations) one-sample t-test using FSL's Randomise function. The resulting statistical map was corrected for multiple comparisons using a voxelwise threshold of $p < 0.01$, family-wise error (FWE) corrected.

Searchlight results were consistent with ROI analyses, and showed above chance classification of reputational status of faces in the lateral OFC and other regions of the temporal lobes (see Figure 5).

Discussion

Humans and nonhuman primates organize social groups in a hierarchical manner stratified by social status. Higher status individuals reap numerous rewards from their position in society and greater control of resources, including superior nutrition and longer lives. Lower status individuals tend to defer to those of higher status and unconsciously bias their attention toward them, perhaps because there is something inherently valuable in rapidly identifying and attending to high status individuals (reviewed by Koski et al., 2015). Recent neuroimaging evidence using univariate analyses has begun to build a picture of the neural circuitry that underlies status perception, implicating regions of the parietal lobe involved in numerical ordering (Chiao et al., 2009; Wang et al., 2017), as well as affective processing and reward, such as the ventral striatum, orbitofrontal cortex, and amygdala (Klein et al., 2009; Ly et al., 2011; Zink et al., 2008).

However status goes beyond rank orders and affective responses: it is deeply embedded in our conceptual representations of different individuals. People's titles, manner of dress, even their physiognomy, are imbued with cues about power and status. The present study

examined whether status information is embedded in person representations and at which level in the person-processing neural hierarchy this information is represented.

The results showed that reputational status, defined by a star ranking system, was decoded by multivoxel patterns in face-sensitive cortex located bilaterally in the lateral orbitofrontal cortex. Neural representations of career status were also examined, though this information was not trained since most adults have pre-existing knowledge about the relative status of various careers. This was also represented in the lateral OFC. We additionally showed that reputational status for individuals within the same career category (e.g. doctors) was also represented by MVPs within the left lateral OFC ROI. Across all of the aforementioned analyses, classification accuracy for the status of facial stimuli was also above chance in face-selective regions of the bilateral ATLs, though these effects failed to survive conservative corrections for multiple comparisons. In contrast, classic early face perception regions - the OFA and the FFA - did not decode reputational status. Likewise, regions known to be sensitive to reward and affect - the ventral striatum and the amygdala - did not decode reputational status.

Social Sensitivity in the OFC

Over 30 years ago Thorpe and colleagues (1983) reported that neurons in the macaque OFC were preferentially sensitive to faces. This was later confirmed by other investigators (Booth & Rolls, 1998; Rolls, 2000; Rolls et al., 1999) who additionally noted that the response profiles of these neurons had subtle differences from those in classic visual areas: they responded better to real faces than pictures of faces and they responded with relatively longer latencies (Rolls & Baylis, 1986). Rolls speculated that the function of these face neurons was primarily for social learning since specific faces might be associated with valenced information, such as a previous altercation, that could act as a reinforcer (2000). Social status is an evolutionarily preserved reinforcer. Both humans and monkeys place a tremendous premium on social status information, forgoing other rewards and engaging in battles to display or obtain desired status.

The present finding that social status was consistently decoded by lateral OFC neurons is consistent with a large literature on reward and the OFC. Several studies have shown that there is overlapping activity in the OFC to rewarding stimuli from different modalities such as juice, money, or sexually-relevant stimuli (Chib et al., 2009; Kim et al., 2011; Levy & Glimcher, 2012). Likewise, the present results support prior work suggesting a “common currency” response in the OFC (Chib et al., 2009; Kim, et al., 2011; Levy & Glimcher, 2012) in that the same voxels decoded social status and object status.

Laterality

Classification accuracy was slightly higher in the left lateral OFC than in the right lateral OFC for social status specifically. This was unexpected, given that left hemispheric regions like the ATL tend to be most sensitive to verbal information (e.g., Patterson et al., 2007) and our stimuli were pictures. However, these findings are less surprising if the semantic nature of the status cues is considered. Interestingly, reputational status was represented bilaterally in the OFC whereas occupational status was represented only in the left hemisphere.

Reputational status was linked to visual cues (number of stars), whereas occupational status was more abstract and thus more likely linked to its semantic representation. It is possible that if more primitive, visual status cues were used, such as body size or facial dominance, classification would be more right lateralized.

Social vs. Non-social social status

The present study included objects with varied status ratings as a non-social control condition. Classification accuracy for the reputational status, or star-ranking, of objects was significantly above chance only in object-sensitive cortex (LOC). Analyses were also performed to examine whether face-sensitive regions in the ATL and OFC classified reputational status across stimulus categories. The classifier was trained on person reputational status and tested on objects, and results revealed above-chance classification in the left ATL and left lateral OFC. Results from this analysis suggest overlap in the regions that decode reputational status for objects and people. However when object selective voxels were removed from face-selective ROIs, object classification dropped to chance in the ATLs but remained significant in the OFC. Thus, despite responding more to faces than objects in the functional localizer, the lateral OFC face patch appears to be sensitive to the reputational status, or star-ranking, of both social and non-social stimuli.

Early Visual Classification

Our findings unexpectedly showed above-chance classification accuracy in early visual areas – left EVC and left OFA – for social status. These early visual regions were included in the design as perceptual controls, since classifiers have a tendency to be sensitive to perceptual features of images and may over fit the data (Periera et al., 2009). Thus, it is possible that effects found in the ATLs and OFC are being driven by perceptual attributes associated with status categories.

We think that this is unlikely for several reasons. First, great care was taken to reduce the likelihood of visual-level differences between status categories. All facial stimuli were arbitrarily paired to status categories, and reputational and career status individuals were crossed such that half of the high reputational status faces were low career status, and vice versa. Yet we found above chance classification for status when categorizing by either reputational or career status. We were also careful to categorize faces such that no status group was more similar in appearance than the others, and the fMRI task included a variety of image exemplars to reduce perceptual-level classification. Second, if effects were being driven primarily by visual attributes of the facial stimuli, we would expect higher classification accuracy for status in EVC than in OFC, which was not the case. Classification in EVC did not survive correction for multiple comparisons in the ROI-based analysis, and a wholebrain searchlight revealed greater regions of sensitivity to facial status in the OFC.

Finally, further research is needed to fully understand the relationship between EVC activation and activation in higher-order neural regions. It is possible that the sensitivity of EVC to facial status is being driven by top-down feedback from higher-order areas (Bar et al., 2006). Feedback from the OFC to EVC could plausibly rely on a large white matter tract called the inferior frontal occipital fasciculus (IFOF), which has been implicated in face

processing and semantic memory (Wang et al., under review). Other research suggests EVC activation may be associated with attention to the stimulus (Serences, 2008; Vuilleumier, 2005), or EVC may code stimulus value (Persichetti et al., 2015). Indeed, our univariate analysis found higher activations in early visual cortex to high status faces, suggesting that the MVPA response in EVC may have been driven by differential attention to or value associated with the high-status stimuli rather than something about representational content. It is possible that, as part of this feedback loop, OFC is also sensitive to salience and the present findings reflect increased attention to status. However, OFC may be sensitive to value specifically (Kahnt et al., 2014), or there may be a functional dissociation among subregions, whereby lateral OFC is implicated in value and medial OFC in salience (Rothkirch et al., 2012). Thus, it is likely that status effects found in the present study in lateral OFC (and NOT in medial OFC) are due to value rather than salience, although future research should continue to disentangle the relative roles of OFC subregions in social and nonsocial valuation and salience.

Limitations

One limitation of the present study is inherent to any study that uses an ROI approach: it is unclear to what extent regions beyond the functional ROIs tested here comprise a “social status network.” For instance, The ATLS and OFC may be more sensitive to social status based on career titles and other valued social cues, but regions involved in magnitude processing (e.g., IPS; see Chiao et al., 2009) may be more sensitive to rank-based status cues. Additionally, the posterior superior temporal sulcus (STS) is implicated in certain kinds of status processing, particularly when status cues are exhibited through body posture (e.g., Mason et al., 2015).

The absence of a well-defined status network underscores the fact that status is a socially ubiquitous trait that is also extremely fluid, depending on the particulars of the task and context. For instance, Bill Gates might be deferred to by business leaders and politicians due to his great wealth, however in contexts where physicality dominates, say in an athletic competition or in a bar room brawl, his status would be vastly different. The present analysis focuses specifically on the ventral face-processing network in perceiving faces associated with semantic status cues, and we suggest that the OFC is involved in status tasks in which the socially rewarding aspects of stimuli are made salient. Future research should examine how regions outside of face-specific ROIs decode different types of status information.

An additional limitation is that the present analysis did not account for potentially important individual differences in participants, such as gender and relative social status. For instance, our stimuli were male faces, and masculine faces may be more likely to be perceived as high status (Jones et al., 2010; Quist et al., 2011). Additionally, gender may affect facial perception and associated neural regions (e.g., Freeman et al., 2010). Relative status can also influence status perception. Ly and colleagues showed that a person’s social status modulates activity in their reward regions when viewing individuals with a status that is higher or lower than theirs (Ly et al., 2011), and dominant men may be less sensitive to facial status (Watkins et al., 2010). Finally, how much one values social interactions may

further modulate activity in regions sensitive to value (Smith et al., 2013; Troiani et al., 2016).

Conclusions

The present findings suggest that a face-selective region of the lateral orbitofrontal cortex (OFC) may play a critical role in the representation of social status in humans. Notably, the present study highlights the involvement of a value-sensitive region of the extended face processing network – rather than regions involved in face recognition – in discriminating high from low status individuals. To some extent, regions involved in social semantic knowledge may also contribute to status perception. These results identify a potential mechanism through which value is incorporated into neural representations of people, and suggest that these representations are triggered even during the passive viewing of individuals. Further, the present experimental task did not prompt participants to attend to status or any status-relevant information, and thus results are unlikely to be due to increased attention toward status cues. Future research should explore whether face selective OFC is implicated in the perception of other valuable social traits as well, and whether involvement of OFC in person perception correlates with biased attention and behavior.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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Abbreviations

ATL	anterior temporal lobe
EVC	early visual cortex
FFA	fusiform face area
LOC	lateral occipital cortex
LOFC	lateral orbitofrontal cortex
MVPA	multivoxel pattern analysis
OFA	occipital face area
ROI	region of interest
VS	ventral striatum.

References

- Anderson C, John OP, Keltner D, Kring AM. Who attains social status? Effects of personality and physical attractiveness in social groups. *J Pers.* 2001; 81:116–132.
- Anzellotti S, Fairhall SL, Caramazza A. Decoding representations of face identity that are tolerant to rotation. *Cereb Cortex.* 2014; 24:1988–1995. [PubMed: 23463339]
- Azzi JCB, Sirigu A, Duhamel J. Modulation of value representation by social context in the primate orbitofrontal cortex. *PNAS.* 2012; 109:2126–2131. [PubMed: 22308343]
- Bar M, Kassam KS, Ghuman AS, Boshyan J, Schmid AM, Dale AM, Hamalainen MS, Marinkovic K, Schacter DL, Rosen BR, Halgren E. Top-down facilitation of visual recognition. *PNAS.* 2006; 103:449–454. [PubMed: 16407167]
- Booth MC, Rolls ET. View-invariant representations of familiar objects by neurons in the inferior temporal visual cortex. *Cereb Cortex.* 1998; 8:510–523. [PubMed: 9758214]
- Bracci S, Cavina-Pratesi C, Ietswaart M, Caramazza A, Peelen MV. Closely overlapping responses to tools and hands in left lateral occipitotemporal cortex. *J Neurophysiol.* 2014; 107:1443–1456.
- Chase ID, Tovey C, Spangler-Martin D, Manfredonia M. Individual differences versus social dynamics in the formation of animal dominance hierarchies. *PNAS.* 2002; 99:5744–5749. [PubMed: 11960030]
- Chib VS, Rangel A, Shimojo S, O'Doherty JP. Evidence for a common representation of decision values for dissimilar goods in human ventromedial prefrontal cortex. *J Neurosci.* 2009; 29:12315–12320. [PubMed: 19793990]
- Chiao JY, Harada T, Oby ER, Li Z, Parrish T, Bridge DJ. Neural representations of social status hierarchy in human inferior parietal cortex. *Neuropsychologia.* 2009; 47:354–363. [PubMed: 18992759]
- Collins JA, Olson IR. Beyond the FFA: The role of the ventral anterior temporal lobes in face processing. *Neuropsychologia.* 2014; 61:65–79. [PubMed: 24937188]
- Collins JA, Koski JE, Olson IR. More than meets the eye: The merging of perceptual and conceptual knowledge in the anterior temporal face area. *Front Hum Neurosci.* 2016; 10
- Coutanche MN, Thompson-Schill SL. The advantage of brief fMRI acquisition runs for multi-voxel pattern detection across runs. *NeuroImage.* 2012; 61:1113–1119. [PubMed: 22498658]
- Dalmaso M, Pavan G, Castelli L, Galfano G. Social status gates social attention in humans. *Biology.* 2012; 8:450–452.
- Deaner RO, Khera AV, Platt ML. Monkeys pay per view: adaptive valuation of social images by rhesus macaques. *Curr Biol.* 2005; 15:543–548. [PubMed: 15797023]
- Eger E, Ashburner J, Haynes JD, Dolan RJ, Rees G. fMRI activity patterns in human LOC carry information about object exemplars within category. *J Cognitive Neurosci.* 2008; 20:356–370.
- Foulsham T, Cheng JT, Tracy JL, Henrich J, Kingstone A. Gaze allocation in a dynamic situation: effects of social status and speaking. *Cognition.* 2010; 117:319–331. [PubMed: 20965502]
- Freeman JB, Rule NO, Adams RB Jr, Ambady N. The neural basis of categorical face perception: graded representations of face gender in fusiform and orbitofrontal cortices. *Cereb Cortex.* 2009; 20:1314–1322. [PubMed: 19767310]
- Freiwald WA, Tsao DY. Viewpoint generalization within the macaque face-processing system. *Science.* 2010; 330:845–851. [PubMed: 21051642]
- Gould RV. The origins of status hierarchies: a formal theory and empirical test. *Am J Psychol.* 2002; 107:1143–1178.
- Grill-Spector K, Kourtzi Z, Kanwisher N. The lateral occipital complex and its role in object recognition. *Vision Res.* 2001; 41:1409–1422. [PubMed: 11322983]
- Haxby JV, Hoffman EA, Gobbini MI. The distributed human neural system for face perception. *Trends Cogn Sci.* 2000; 4:223–233. [PubMed: 10827445]
- Haxby JV, Hoffman EA, Gobbini MI. Human neural systems for face recognition and social communication. *Trends Cogn Sci.* 2002; 51:59–67.

- Hornak J, Bramham J, Rolls ET, Morris RG, Doherty JO, Bullock PR, Polkey CE. Changes in emotion after circumscribed surgical lesions of the orbitofrontal and cingulate cortices. *Brain*. 2003; 26:1691–1712.
- Ishai A, Schmidt CF, Boesiger P. Face perception is mediated by a distributed cortical network. *Brain Res Bull*. 2005; 67:87–93. [PubMed: 16140166]
- Jones BC, DeBruine LM, Main JC, Little AC, Welling LL, Feinberg DR, Tiddeman BP. Facial cues of dominance modulate the short-term gaze-cuing effect in human observers. *P Roy Soc B-Biol Sci*. 2010; 277:617–624.
- Kahnt T, Park SQ, Haynes JD, Tobler PN. Disentangling neural representations of value and salience in the human brain. *PNAS*. 2014; 111:5000–5005. [PubMed: 24639493]
- Kanwisher N, Yovel G. The fusiform face area: a cortical region specialized for the perception of faces. *Philos T Roy Soc B*. 2006; 361:2109–2128.
- Kim H, Shimojo S, O'Doherty JP. Overlapping responses for the expectation of juice and money rewards in human ventromedial prefrontal cortex. *Cereb Cortex*. 2011; 21:769–776. [PubMed: 20732900]
- Klein JT, Deaner RO, Platt ML. Neural correlates of social target value in macaque parietal cortex. *Curr Biol*. 2008; 18:419–424. [PubMed: 18356054]
- Klein JT, Shepherd SV, Platt ML. Social attention and the brain minireview. *Curr Biol*. 2009; 19:R958–R962. [PubMed: 19889376]
- Koski JE, Xie H, Olson IR. Understanding social hierarchies: the neural and psychological foundations of status perception. *Soc Neurosci*. 2015; 10:527–550. [PubMed: 25697184]
- Kriegeskorte N, Formisano E, Sorger B, Goebel R. Individual faces elicit distinct response patterns in human anterior temporal cortex. *PNAS*. 2007; 104:20600–20605. [PubMed: 18077383]
- Ku SP, Tolias AS, Logothetis NK, Goense J. fMRI of the face-processing network in the ventral temporal lobe of awake and anesthetized macaques. *Neuron*. 2011; 70:352–362. [PubMed: 21521619]
- Kumaran D, Melo HL, Duzel E. The emergence and representation of knowledge about social and nonsocial hierarchies. *Neuron*. 2012; 76:653–666. [PubMed: 23141075]
- Leopold DA, Bondar IV, Giese MA. Norm-based face encoding by single neurons in the monkey inferotemporal cortex. *Nature*. 2006; 442:572–575. [PubMed: 16862123]
- Levy DJ, Glimcher PW. The root of all value: a neural common currency for choice. *Curr Opin Neurobiol*. 2012; 22:1027–1038. [PubMed: 22766486]
- Lin A, Adolphs R, Rangel A. Social and monetary reward learning engage overlapping neural substrates. *Imaging*. 2012; 7:274–281.
- Ly M, Haynes MR, Barter JW, Weinberger DR, Zink CF. Subjective socioeconomic status predicts human ventral striatal responses to social status information. *Curr Biol*. 2011; 21:794–797. [PubMed: 21530264]
- Magee JC, Galinsky AD. Social hierarchy: the self-reinforcing nature of power and status. *Acad Manag Ann*. 2008; 2:351–398.
- Mason M, Magee JC, Fiske ST. Neural substrates of social status inference: roles of medial prefrontal cortex and superior temporal sulcus. *J Cognitive Neurosci*. 2014; 26:1131–1140.
- Moors A, Houwer JD. Automatic processing of dominance and submissiveness. *Exp Psychol*. 2005; 52:296–302. [PubMed: 16302538]
- Murphy K, Bodurka J, Bandettini PA. How long to scan? The relationship between fMRI temporal signal to noise ratio and necessary scan duration. *Neuroimage*. 2007; 34:565–574. [PubMed: 17126038]
- O'Doherty J, Kringelbach ML, Rolls ET, Hornak J, Andrews C. Abstract reward and punishment representations in the human orbitofrontal cortex. *Nat Neurosci*. 2001; 4:95–102. [PubMed: 11135651]
- Paxton R, Basile BM, Hampton RR. Rhesus monkeys (*Macaca mulatta*) rapidly learn to select dominant individuals in videos of artificial social interactions between unfamiliar conspecifics. *J Comp Psychol*. 2011; 124:395–401.

- Patterson K, Nestor PJ, Rogers TT. Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat Rev Neurosci.* 2007; 8:976–987. [PubMed: 18026167]
- Peelen MV, Caramazza A. Conceptual object representations in human anterior temporal cortex. *J Neurosci.* 2012; 32:15728–15736. [PubMed: 23136412]
- Persichetti AS, Aguirre GK, Thompson-Schill SL. Value is in the eye of the beholder: early visual cortex codes monetary value of objects during a diverted attention task. *J Cognitive Neurosci.* 2015; 27:893–901.
- Pereira F, Mitchell T, Botvinick M. Machine learning classifiers and fMRI: a tutorial overview. *Neuroimage.* 2009; 45:S199–S209. [PubMed: 19070668]
- Quist MC, Watkins CD, Smith FG, DeBruine LM, Jones BC. Facial masculinity is a cue to women's dominance. *Pers Indiv Differ.* 2011; 50:1089–1093.
- Rajimehr R, Young JC, Tootell RB. An anterior temporal face patch in human cortex, predicted by macaque maps. *PNAS.* 2009; 106:1995–2000. [PubMed: 19179278]
- Rolls ET. Functions of the primate temporal lobe cortical visual areas in invariant visual object and face recognition. *Neuron.* 2000; 27:205–218. [PubMed: 10985342]
- Rolls ET, Baylis GC. Size and contrast have only small effects on the responses to faces of neurons in the cortex of the superior temporal sulcus of the monkey. *Exp Brain Res.* 1986; 65:38–48. [PubMed: 3803509]
- Rolls ET, Critchley HD, Browning AS, Hernadi I, Lenard L. Responses to the sensory properties of fat of neurons in the primate orbitofrontal cortex. *J Neurosci.* 1999; 19:1532–1540. [PubMed: 9952429]
- Ross LA, Olson IR. What's unique about unique entities? An fMRI investigation of the semantics of famous faces and landmarks. *Cereb Cortex.* 2012; 22:2005–2015. [PubMed: 22021913]
- Ross LA, Olson IR. Social cognition and the anterior temporal lobes. *Neuroimage.* 2010; 49:3452–3462. [PubMed: 19931397]
- Rothkirch M, Schmack K, Schlagenhauf F, Sterzer P. Implicit motivational value and salience are processed in distinct areas of orbitofrontal cortex. *Neuroimage.* 2012; 62:1717–1725. [PubMed: 22728149]
- Rushworth MFS, Behrens TEJ, Rudebeck PH, Walton ME. Contrasting roles for cingulate and orbitofrontal cortex in decisions and social behaviour. *Trends in Cogn Sci.* 2007; 11:168–176. [PubMed: 17337237]
- Schoenbaum G, Takahashi Y, Liu T, McDannald M. Does the orbitofrontal cortex signal value? *Ann NY Acad Sci.* 2011; 1239:87–99. [PubMed: 22145878]
- Serences JT. Value-based modulations in human visual cortex. *Neuron.* 2008; 60:1169–1181. [PubMed: 19109919]
- Sidanius J, Pratto F. *Social Dominance: An Intergroup Theory of Social Hierarchy and Oppression.* Cambridge University Press; Cambridge: 1999.
- Smith DV, Clithero JA, Boltuck SE, Huettel SA. Functional connectivity with ventromedial prefrontal cortex reflects subjective value for social rewards. *Soc Cogn Affect Neur.* 2013; 9:2017–2025.
- Skipper LM, Ross LA, Olson IR. Sensory and semantic category subdivisions within the anterior temporal lobes. *Neuropsychologia.* 2011; 49:3419–3429. [PubMed: 21889520]
- Thorpe SJ, Rolls ET, Maddison S. The orbitofrontal cortex: neuronal activity in the behaving monkey. *Exp Brain Res.* 1983; 49:93–115. [PubMed: 6861938]
- Troiani V, Dougherty CC, Michael AM, Olson IR. Characterization of Face-selective patches in orbitofrontal cortex. *Front Hum Neurosci.* 2016; 10
- Tsao DY, Schweers N, Moeller S, Freiwald WA. Patches of face-selective cortex in the macaque frontal lobe. *Nat Neurosci.* 2008; 11:877–879. [PubMed: 18622399]
- Tsao DY, Moeller S, Freiwald WA. Comparing face patch systems in macaques and humans. *PNAS.* 2008; 105:19514–19519. [PubMed: 19033466]
- Von Der Heide RJ, Skipper LM, Olson IR. Anterior temporal face patches: a meta-analysis and empirical study. *Front Hum Neurosci.* 2013; 7

- Von Der Heide RJ, Skipper LM, Klobusicky E, Olson IR. Dissecting the uncinate fasciculus: disorders, controversies and a hypothesis. *Brain*. 2013; 136:1692–1707. [PubMed: 23649697]
- Vuilleumier P. How brains beware: neural mechanisms of emotional attention. *Trends Cogn Sci*. 2005; 9:585–594. [PubMed: 16289871]
- Wang Y, Collins JA, Koski JE, Nugiel T, Metoki A, Olson IR. A dynamic neural architecture for social knowledge retrieval. *PNAS*. 2017; 114:E3305–E3314. [PubMed: 28289200]
- Watkins CD, Jones BC, DeBruine LM. Individual differences in dominance perception: dominant men are less sensitive to facial cues of male dominance. *Pers Indiv Differ*. 2010; 49:967–971.
- Zink CF, Tong Y, Chen Q, Bassett DS, Stein JL. Know your place: neural processing of social hierarchy in humans. *Neuron*. 2008; 58:273–283. [PubMed: 18439411]

Figure 1. Example stimuli and status training information. Prior to the fMRI task, participants learned to associate identity, category, and status information with faces and objects. Social status was manipulated in 2 ways: reputation-based status indicated with a star ranking, and occupation-based status indicated by career title. Object reputational status served as a nonsocial comparison. There were 8 social and nonsocial identities across 4 categories, half of which were high and half low reputational status. During the main experiment, participants viewed identity blocks, with different exemplars per identity presented across trials, and performed an orthogonal target detection task.

Figure 2.

Classification accuracy for reputational status. (a) Classification accuracy for face reputational status in face-selective ROIs. (b) Classification accuracy for object s reputational status in object-selective ROIs. Boxplots display ROI classification accuracy by hemisphere, including minimum, 1st quartile, median, 3rd quartile, and maximum (inclusive of median) values from the sample. The “x” represents the group mean. Chance classification is at .50. OFA = occipital face area; FFA = fusiform face area; ATL = anterior temporal lobes; Amyg = amygdala; VS = ventral striatum; mOFC = medial orbitofrontal cortex; IOFC = lateral orbitofrontal cortex; LOC = lateral occipital cortex.

Figure 3.

Classification accuracy for (a) career status, and (b) doctor reputational status in face-selective ROIs as well as regions important in reward and value. Boxplots display ROI classification accuracy by hemisphere, including minimum, 1st quartile, median, 3rd quartile, and maximum (inclusive of median) values from the sample. The “x” represents the group mean. Chance classification is at .50. OFA = occipital face area; FFA = fusiform face area; ATL = anterior temporal lobes; Amyg = amygdala; VS = ventral striatum; mOFC = medial orbitofrontal cortex; IOFC = lateral orbitofrontal cortex; LOC = lateral occipital cortex.

Figure 4.

Classification accuracy for the generalization test: the classifier was trained on reputational status of face stimuli, but tested on reputational status of object stimuli. Boxplots display ROI classification accuracy by hemisphere, including minimum, 1st quartile, median, 3rd quartile, and maximum (inclusive of median) values from the sample. The “x” represents the group mean. Chance classification is at .50. ATL = anterior temporal lobes; IOFC = lateral orbitofrontal cortex.

Figure 5. Searchlight results. MVPA wholebrain searchlight analysis using 9mm spheres showed above chance (.5) classification of face reputational status in OFC as well as other brain regions. Lateral OFC regions of above chance classification are circled in white.

Table 1

Statistical effects for MVPA analyses of various forms of status: social reputation, person career, the reputation within a career category (doctors), and object reputation.

	Social Status		Object Status	
	Reputation	Career	Doctor Reputation	Reputation
<i>Left Hemisphere</i>				
EVC	$t(17)=2.76, p=.007$	$t(17)=2.55, p=.011$	$t(17)=3.13, p=.003^{**}$	$t(17)=1.81, p=.044$
LOC	–	–	–	$t(17)=4.20, p<.001^{**}$
OFA	$t(17)=2.19, p=.022$	$t(17)=2.88, p=.005$	$t(17)=2.64, p=.009$	–
FFA	$t(17)=1.05, p=.155$	$t(17)=1.51, p=.075$	$t(17)=.46, p=.326$	–
ATL	$t(16)=2.65, p=.009$	$t(16)=2.46, p=.013$	$t(16)=3.03, p=.004$	$t(17)=1.94, p=.035$
Amyg	$t(10)=-1.57, p=.074$	$t(10)=2.51, p=.016$	$t(10)=-.75, p=.235$	$t(16)=.97, p=.173$
VS	$t(17)=-.13, p=.451$	$t(17)=2.07, p=.027$	$t(17)=-.85, p=.205$	$t(17)=-.15, p=.442$
mOFC	$t(14)=.72, p=.243$	$t(14)=1.53, p=.074$	$t(14)=.99, p=.170$	$t(16)=1.81, p=.044$
lOFC	$t(14)=3.46, p=.002^{**}$	$t(14)=4.58, p<.001^{**}$	$t(14)=3.59, p=.002^{**}$	$t(17)=1.94, p=.036$
<i>Right Hemisphere</i>				
EVC	$t(17)=.67, p=.255$	$t(17)=.67, p=.256$	$t(17)=1.03, p=.160$	$t(17)=-.32, p=.377$
LOC	–	–	–	$t(17)=-.27, p=.400$
OFA	$t(17)=1.85, p=.041$	$t(17)=1.88, p=.039$	$t(17)=1.89, p=.038$	–
FFA	$t(17)=1.74, p=.050$	$t(17)=.19, p=.428$	$t(17)=.88, p=.194$	–
ATL	$t(15)=2.29, p=.019$	$t(15)=2.42, p=.015$	$t(15)=2.35, p=.017$	$t(17)=2.97, p=.005$
Amyg	$t(13)=-.29, p=.390$	$t(13)=1.86, p=.043$	$t(13)=-.24, p=.408$	$t(15)=1.65, p=.060$
VS	$t(17)=-1.48, p=.079$	$t(17)=2.19, p=.022$	$t(17)=-.12, p=.454$	$t(17)=-.12, p=.454$
mOFC	$t(14)=.57, p=.290$	$t(14)=1.62, p=.065$	$t(14)=1.68, p=.058$	$t(16)=1.43, p=.086$
lOFC	$t(15)=2.04, p=.030$	$t(15)=2.40, p=.015$	$t(15)=1.90, p=.039$	$t(17)=2.90, p=.005$

T-values, degrees of freedom, and p-values are listed. Significant tests (Bonferroni corrected p -value of .00313) are indicated with asterisk (*).

EVC= early visual cortex; LOC = lateral occipital cortex; OFA = occipital face area; FFA = fusiform face area; ATL= anterior temporal lobe; Amyg = amygdala; VS = ventral striatum; mOFC = medial orbitofrontal cortex; lOFC = lateral orbitofrontal cortex.