

COGNITIVE NEUROSCIENCE

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 perceptions of 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 a functional magnetic resonance imaging 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.

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

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 relative to others provides essential information regarding social roles and how to behave in social interactions, and facilitates intergroup cooperation and function (Savine-Williams, 1979; Halevy *et al.*, 2011). 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 (Berger *et al.*, 1980; Anderson *et al.*, 2001; 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.*, 2001), 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 (Jones *et al.*, 2010; Dalmaso *et al.*, 2012) 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 (Zink *et al.*, 2008; Ly *et al.*, 2011; Kumaran *et al.*, 2012) 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

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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 (Zink *et al.*, 2008; Ly *et al.*, 2011).

A well-studied network of regions in the ventral visual stream is 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; Leopold *et al.*, 2006; Kriegeskorte *et al.*, 2007; Tsao *et al.*, 2008a, b; Rajimehr *et al.*, 2009; Freiwald & Tsao, 2010; Ku *et al.*, 2011), thought to be involved in mnemonic and conceptual aspects of person processing (Von Der Heide *et al.*, 2013a,b; Collins & Olson, 2014; Collins *et al.*, 2016). As 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; Rolls, 2000; Ishai *et al.*, 2005; Tsao *et al.*, 2008a,b). The OFC has a general, albeit underspecified role in social behavior (Hornak *et al.*, 2003), as well as social and nonsocial valuation (Rushworth *et al.*, 2007; Lin *et al.*, 2012). 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 (Troianni *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 to 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 gray-scale images of eight 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 gray-scale images of eight different restaurant or hospital tools from four 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 gray background and central fixation cross was also used.

Participants learned to associate three pieces of conceptual information with eight unfamiliar faces and eight objects: (i) name; (ii) category (occupation or object type); and (iii) 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.socialedgegov).

Our study design allowed facial status to be manipulated in two ways: reputation-based status and career-based status (see Fig. 1). Reputation-based status was indicated with a star ranking. Two items (faces or objects) within each object or occupation category were 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 min and the second

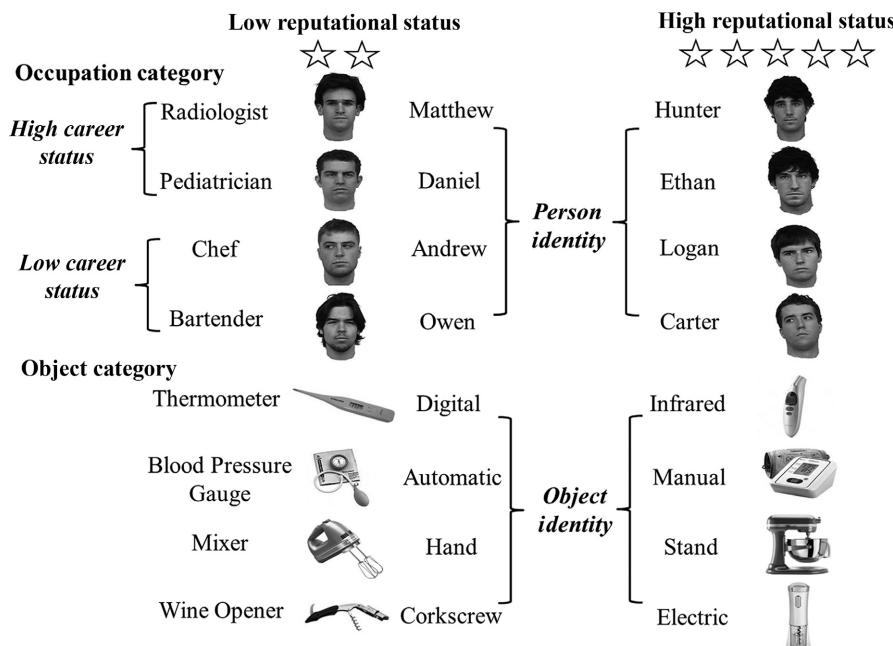


FIG. 1. Example stimuli and status training information. Prior to the functional magnetic resonance imaging task, participants learned to associate identity, category and status information with faces and objects. Social status was manipulated in two ways: reputation-based status indicated with a star ranking and occupation-based status indicated by career title. Object reputational status served as a nonsocial comparison. There were eight social and nonsocial identities across four 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.

lasting approximately 30 min. The first training session consisted of three 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 four times (64 trials total) for 5 s 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 s. 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 s. 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. Afterward, 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 ($N = 24$; eight 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 2 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 *et al.*, 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.*, 2013a,b). 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 this study.

Images were randomly selected from lists of 89 images per category and presented one at a time for 400 ms (350 ISI) in eight category blocks consisting of 14 trials each. Participants completed two full localizer runs, each consisting of five cycles presenting all eight category blocks in a fixed randomized order. Each cycle ended with a 12000 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 eight 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, four novel exemplars of the same eight male faces used during status training were used in the experimental runs. The faces studied during status training were angled 30° and 45° 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 (eight faces, eight objects), 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 four times in a fixed random order for 700 ms (425 ms ISI), and each block ended with 3000 ms presentation of a fixation cross. Participants completed six 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 three times per block, with their exact locations following one of four 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 min. 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 × 250 mm; inversion time = 900 ms; voxel size = 1 × 0.9766 × 0.9766; matrix size = 188 × 256; flip angle = 90°.

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 × 240; voxel size = 3 × 3 × 2.5 mm; matrix size = 80 × 80; flip angle = 90°. 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 & 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 (fMRI; 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-s cutoff and fieldmap-based correction of EPI data to reduce spatial distortions. The EPI data were 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 were smoothed using a 5-mm Gaussian kernel; however, MVPA data were not smoothed.

Defining regions of interest

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 $P = 0.05$. 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 Fig. S1 for anatomical masks). Contrasting the average activation to faces vs. 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 Fig. S2 for a group map of functionally localized face-selective regions.

Contrasting the average activation to objects vs. 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, 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 9-mm 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. As the number of voxels within an ROI may influence MVPA outcomes (e.g., Eger *et al.*, 2008; Anzellotti *et al.*, 2013), the early visual cortex control region was defined in a similar manner as the face and object ROIs, by centering a 9-mm 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 9-mm ROIs.

Additionally, a structural ROI was created for bilateral amygdala and bilateral ventral striatum using the Harvard-Oxford Subcortical Structural Atlas and Oxford-Imanova 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, TSNR 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

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 sixfold leave-one-run-out cross-validation scheme was employed, where the classifier was trained on five runs of data and tested on the remaining untrained run. The training and test data sets included some of the same images (i.e., same visual angles of faces and same exemplars of objects), although they were presented at different times and in different orders across runs. This procedure was repeated six 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 Appendix S1 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 vs. low status was calculated and averaged across six iterations of cross-validation and compared to chance (0.50) 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 0.00313 (0.05/16) 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 vs. low status was calculated and averaged across six iterations of cross-validation and compared to chance (0.50) in a group-level one-sample, one-tailed *t*-test.

Results

Survey data

Survey data from separate group of college undergraduates ($N = 24$; eight males), age 19–27 years ($M = 21.67$, $SD = 2.06$) were 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 Appendix S1 for object status responses.

Behavioral results

Participants were quite accurate at recollecting information about trained people and objects immediately following training ($M = 0.98$, $SD = 0.05$) and immediately prior to scanning

($M = 0.97$, $SD = 0.04$). Recall accuracy did not differ across information types. Likewise, participants were highly accurate at detecting targets across both functional localizer runs ($M = 0.97$, $SD = 0.03$) and all six experimental runs ($M = 0.98$, $SD = 0.04$) 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.

Reputational status

We first assessed whether unique multivoxel patterns could accurately classify high from low rated faces, based on the trained star ranking associated with each individual (depicted in Fig. 2). Classification accuracy for face reputational status was significantly above chance in the left lateral face-selective OFC ($t(15) = 3.46$, $P = 0.004$, $M = 0.65$, $SD = 0.16$) face-selective ROI. 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 (two-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: $t(14) = 0.98$, $P = 0.34$; right: $t(15) = 1.80$, $P = 0.09$) or ATL (left: $t(16) = -0.30$, $P = 0.77$; right: $t(15) = 1.70$, $P = 0.11$).

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 Fig. 2).

Classification accuracy for object reputational status was greater than chance in left LOC ($t(17) = 4.20$, $P < 0.001$; $M = 0.66$, $SD = 0.16$). 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 (two-tailed, P -value corrected for multiple comparisons) showed that classification accuracy in the right LOFC was significantly higher than in right EVC ($t(17) = 3.47$, $P = 0.003$). No other effects were significant after correcting for multiple comparisons (left IOFC: $t(16) = -0.74$, $P = 0.47$; left ATL: $t(17) = -0.26$, $P = 0.80$; right ATL: $t(17) = 2.25$, $P = 0.04$).

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 Fig. 3).

Similar to the results for reputational status, classification accuracy was again greater than chance in the left lateral OFC ($t(17) = 4.32$, $P < 0.001$, $M = 0.71$, $SD = 0.18$) 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: $t(14) = 1.37$, $P = 0.19$; right: $t(15) = 1.80$, $P = 0.09$) or ATL (left: $t(16) = -0.05$, $P = 0.96$; right: $t(15) = 2.13$, $P = 0.05$).

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

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
Left Hemisphere				
EVC	$t(17) = 2.76$, $P = 0.007$	$t(17) = 2.55$, $P = 0.011$	$t(17) = 3.13$, $P = 0.003^{**}$	$t(17) = 1.81$, $P = 0.044$
LOC	–	–	–	$t(17) = 4.20$, $P < 0.001^{**}$
OFA	$t(17) = 2.19$, $P = 0.022$	$t(17) = 2.88$, $P = 0.005$	$t(17) = 2.64$, $P = 0.009$	–
FFA	$t(17) = 1.05$, $P = 0.155$	$t(17) = 1.51$, $P = 0.075$	$t(17) = 0.46$, $P = 0.326$	–
ATL	$t(16) = 2.65$, $P = 0.009$	$t(16) = 2.46$, $P = 0.013$	$t(16) = 3.03$, $P = 0.004$	$t(17) = 1.94$, $P = 0.035$
Amyg	$t(10) = -1.57$, $P = 0.074$	$t(10) = 2.51$, $P = 0.016$	$t(10) = -0.75$, $P = 0.235$	$t(16) = 0.97$, $P = 0.173$
VS	$t(17) = -0.13$, $P = 0.451$	$t(17) = 2.07$, $P = 0.027$	$t(17) = -0.85$, $P = 0.205$	$t(17) = -0.15$, $P = 0.442$
mOFC	$t(14) = 0.72$, $P = 0.243$	$t(14) = 1.53$, $P = 0.074$	$t(14) = 0.99$, $P = 0.170$	$t(16) = 1.81$, $P = 0.044$
IOFC	$t(14) = 3.46$, $P = 0.002^{**}$	$t(14) = 4.58$, $P < 0.001^{**}$	$t(14) = 3.59$, $P = 0.002^{**}$	$t(17) = 1.94$, $P = 0.036$
Right Hemisphere				
EVC	$t(17) = 0.67$, $P = 0.255$	$t(17) = 0.67$, $P = 0.256$	$t(17) = 1.03$, $P = 0.160$	$t(17) = -0.32$, $P = 0.377$
LOC	–	–	–	$t(17) = -0.27$, $P = 0.400$
OFA	$t(17) = 1.85$, $P = 0.041$	$t(17) = 1.88$, $P = 0.039$	$t(17) = 1.89$, $P = 0.038$	–
FFA	$t(17) = 1.74$, $P = 0.050$	$t(17) = 0.19$, $P = 0.428$	$t(17) = 0.88$, $P = 0.194$	–
ATL	$t(15) = 2.29$, $P = 0.019$	$t(15) = 2.42$, $P = 0.015$	$t(15) = 2.35$, $P = 0.017$	$t(17) = 2.97$, $P = 0.005$
Amyg	$t(13) = -0.29$, $P = 0.390$	$t(13) = 1.86$, $P = 0.043$	$t(13) = -0.24$, $P = 0.408$	$t(15) = 1.65$, $P = 0.060$
VS	$t(17) = -1.48$, $P = 0.079$	$t(17) = 2.19$, $P = 0.022$	$t(17) = -0.12$, $P = 0.454$	$t(17) = -0.12$, $P = 0.454$
mOFC	$t(14) = 0.57$, $P = 0.290$	$t(14) = 1.62$, $P = 0.065$	$t(14) = 1.68$, $P = 0.058$	$t(16) = 1.43$, $P = 0.086$
IOFC	$t(15) = 2.04$, $P = 0.030$	$t(15) = 2.40$, $P = 0.015$	$t(15) = 1.90$, $P = 0.039$	$t(17) = 2.90$, $P = 0.005$

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; IOFC, lateral orbitofrontal cortex. T -values, degrees of freedom and P -values are listed. Significant tests (Bonferroni-corrected P -value of 0.00313) are indicated with asterisk (**).

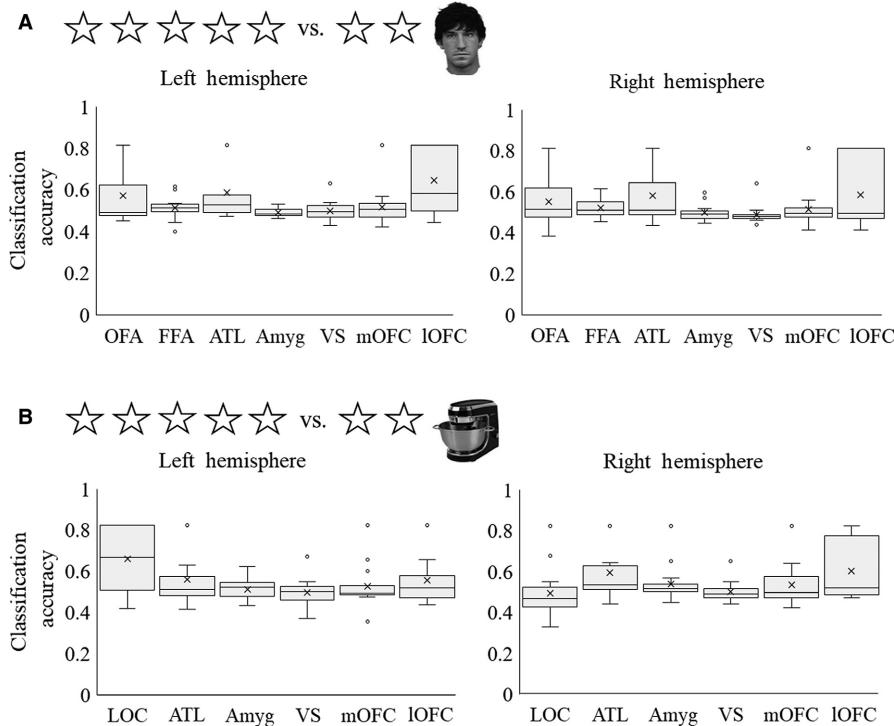


FIG. 2. Classification accuracy for reputational status. (A) Classification accuracy for face reputational status in face-selective regions of interests (ROIs). (B) Classification accuracy for object s reputational status in object-selective ROIs. Boxplots display ROI classification accuracy by hemisphere, 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 0.50. 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.

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 ($t(17) = 3.27, P = 0.003; M = 0.70, SD = 0.21$). Paired t -tests (two-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: $t(14) = 1.07, P = 0.30$; right: $t(15) = 1.59, P = 0.13$) or ATL (left: $t(16) = -0.14, P = 0.89$; right: $t(15) = 2.44, P = 0.03$).

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 (0.50), using a Bonferroni corrected P -value of 0.0125 (0.05/4) to test for significance (Fig. 4). Classification accuracy was significantly above chance in the left lateral OFC (left: $t(14) = 2.98, P = 0.005, M = 0.63, SD = 0.17$), as well as the left ATL ($t(16) = 2.94, P = 0.005, M = 0.59, SD = 0.13$). Right lateral OFC and right ATL

classification accuracy were not significant using a corrected P -value (right OFC: $t(15) = 2.16, P = 0.02, M = 0.57, SD = 0.13$; right ATL: $t(16) = 1.82, P = 0.04, M = 0.57, SD = 0.15$).

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 ($t(14) = 3.37, P = 0.003$) and approached significance in the right lateral OFC ($t(15) = 2.29, P = 0.019$); however, classification of object reputational status in the ATL was not above chance after correcting for multiple comparisons (left: $t(16) = 1.85, P = 0.042$; right: $t(14) = 1.90, P = 0.038$).

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 0.05, 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 because it was the only area where classification accuracy for facial status survived correction for multiple

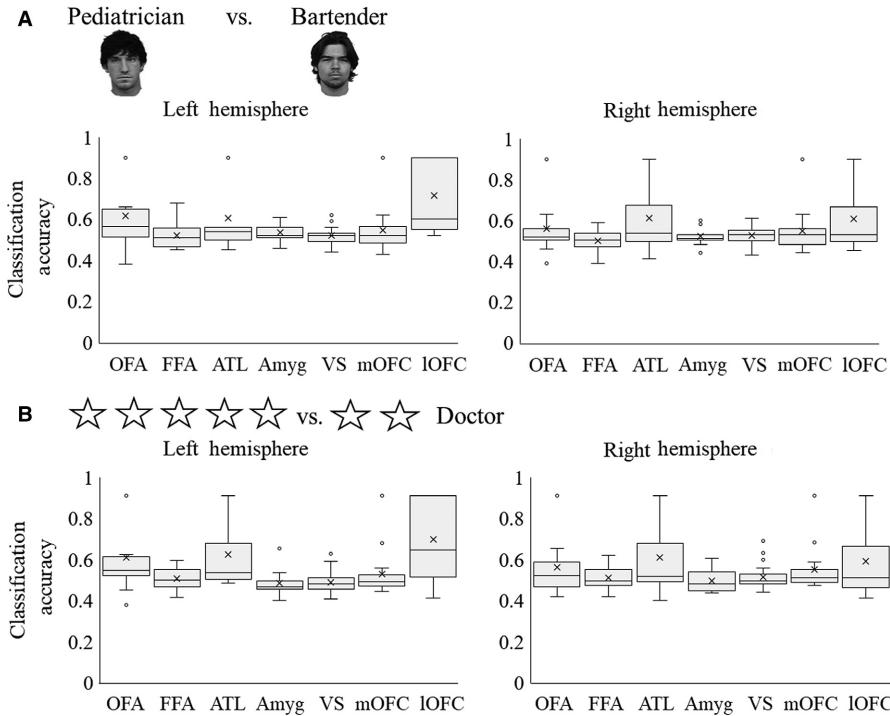


FIG. 3. Classification accuracy for (A) career status and (B) doctor reputational status in face-selective regions of interests (ROIs) as well as regions important in reward and value. Boxplots display ROI classification accuracy by hemisphere, including minimum, 1st quartile, median, 3rd quartile and maximum (inclusive of median) values from the sample. The 'x' represents the group mean. Chance classification is at 0.50. 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.

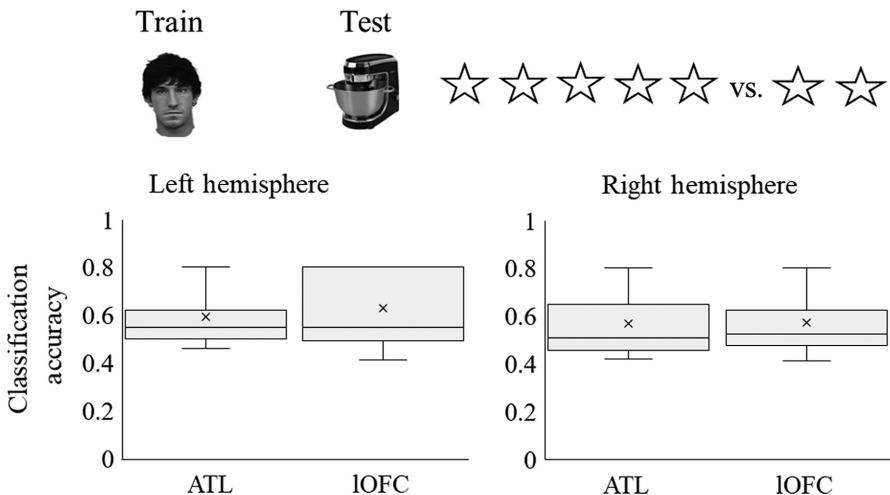


FIG. 4. Classification accuracy for the generalization test: The classifier was trained on reputational status of face stimuli, but tested on reputational status of object stimuli. Boxplots display regions of interest (ROI) classification accuracy by hemisphere, including minimum, 1st quartile, median, 3rd quartile and maximum (inclusive of median) values from the sample. The 'x' represents the group mean. Chance classification is at 0.50. ATL, anterior temporal lobes; IOFC, lateral orbitofrontal cortex.

comparisons across all analyses. Classification accuracy for reputational status in left lateral OFC was positively correlated with classification accuracy in right OFA ($r = 0.54$, $P = 0.04$, $N = 15$), and classification accuracy for career status in left lateral OFC was positively correlated with classification right lateral OFC ($r = 0.57$, $P = 0.040$, $N = 13$) and negatively correlated with left ATL ($r = -0.57$, $P = 0.05$, $N = 15$) and left FFA ($r = -0.53$, $P = 0.04$, $N = 15$). 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 9-mm sphere ROI across voxels within a whole-brain mask (excluding the cerebellum). Classification accuracy was averaged across the six cross-validation iterations performed per subject, then averaged across subjects to create a group classification map. Chance-level classification accuracy (0.5) was subtracted from the group map, and the resulting classification map was compared to 0 with a nonparametric (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 Fig. 5).

Discussion

Humans and non-human 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 (Zink *et al.*, 2008; Klein *et al.*, 2009; Ly *et al.*, 2011).

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, although this information was not trained because 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, although 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 *et al.* (1983) reported that neurons in the macaque OFC were preferentially sensitive to faces. This was later confirmed by other investigators (Booth & Rolls, 1998; Rolls *et al.*, 1999; Rolls, 2000) 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 because 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

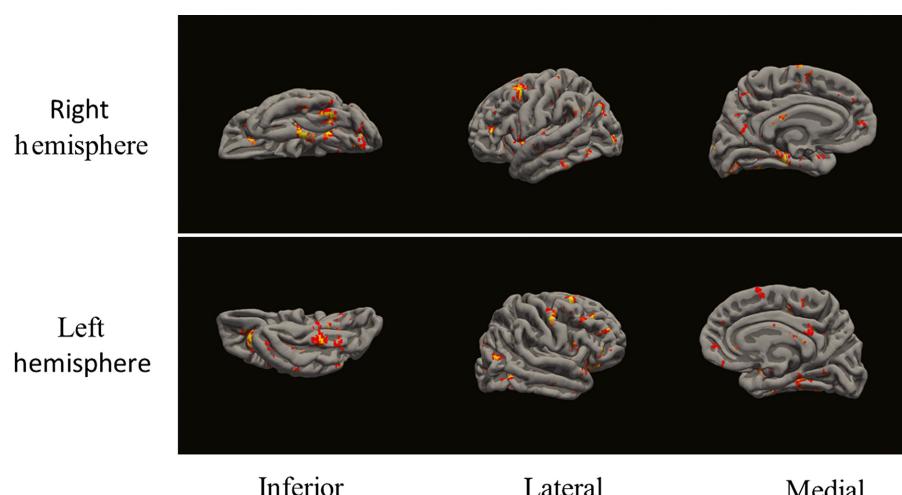


FIG. 5. Searchlight results. Multivoxel pattern analysis whole-brain searchlight analysis using 9-mm spheres showed above chance (0.5) classification of face reputational status in orbitofrontal cortex (OFC) as well as other brain regions. Lateral OFC regions of above-chance classification are circled in white. [Color figure can be viewed at wileyonlinelibrary.com].

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, because classifiers have a tendency to be sensitive to perceptual features of images and may over fit the data (Pereira *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 whole-brain 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 (Vuilleumier, 2005; Serences, 2008), 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 sub-regions 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.*, 2014).

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.*, 2009). 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.

Supporting Information

Additional supporting information can be found in the online version of this article:

Table S1. Peak activation in face sensitive neural regions from group-level analysis of functional localizer data.

Table S2. Face sensitive neural regions across the final sample of 18 participants, by regions and hemisphere.

Table S3. Correlations between left lateral OFC and other functional ROIs for reputational and career social status.

Fig. S1. Masks used for creating functional regions of interest.

Fig. S2. Group map ($N = 18$) of face selective neural regions obtained from functional localizer analysis contrasting faces > places and objects.

Appendix S1. Results from status survey and univariate analyses.

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Conflict of interest

The authors declare no competing financial interests.

Author contributions

All authors contributed to the design of the study. J. Koski programmed the task, collected and analyzed data and wrote the first

draft of the manuscript. J. Collins assisted with MVPA. All authors offered comments on the manuscript and approved the final version.

Data accessibility

Data and materials are not currently available online due to ongoing analyses but will be accessible in the future.

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.

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