

## Distinct and overlapping fusiform activation to faces and food

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### ABSTRACT

The fusiform cortex is a part of the ventral visual stream and is typically associated with face processing. Indeed, a subregion of the fusiform has been named the “fusiform face area” or FFA, based on its robust response to faces relative to other objects. In a separate literature, appetizing food has also been shown to activate bilateral fusiform cortex, yet no study to date has directly compared face and food responses within the same paradigm. Here, we use functional magnetic resonance imaging (fMRI) to compare face and food responses in ventral visual cortex and other regions that are typically associated with face processing. We present evidence that a region of the left fusiform cortex (typically associated with face processing) actually responds equally to faces and food. We go on to describe the similarities and differences in location of face- and food-responses in the fusiform, the relationship of fusiform activation to body mass index (BMI), and resting state connectivity of face- and food-selective fusiform. Results are interpreted within a model in which motivational relevance or value influence fusiform response.

### Introduction

The fusiform face area (FFA) is a functionally defined region within ventral visual cortex associated with a preferential response to faces (Kanwisher et al., 1997; McCarthy et al., 1997; Puce et al., 1996; Sergent et al., 1992). The original ‘face specificity’ hypothesis by Kanwisher et al. (1997) proposed that the FFA is activated by faces because face perception is accomplished using dedicated and specialized neural machinery that is not shared with other cognitive functions. This hypothesis followed from neuropsychological and behavioral research indicating that humans have distinct processes dedicated to facial recognition relative to other objects (Farah et al., 1998; Gauthier and Tarr, 2002; McCarthy et al., 1997; Moscovitch et al., 1997; Valentine, 1991) and evidence that neurons in the visual cortex of non-human primates respond preferentially to faces (Gross et al., 1972). Although we now recognize that a network of regions contribute to human’s variety of face processing abilities (Haxby et al., 2000, 2002), the FFA is generally thought to encode the spatial relationship among face features in order to extract the configural or holistic representation that is important for accurate face perception (Liu et al., 2009; Schiltz et al., 2010; Yovel and Kanwisher, 2004).

Another hypothesis suggests that the FFA may be an area that is important for processing object categories such as faces because they require visual expertise and fine-grained discrimination between

exemplars (Gauthier et al., 1999). Original evidence for the ‘expertise hypothesis’ comes from studies in which individuals develop expertise through visual training on a novel object category and subsequently show FFA activation to trained objects following training (Gauthier et al., 1999; Xu, 2005). Additional evidence for the role of expertise in fusiform activation comes from fMRI studies that examine subjects that have visual expertise in unique domains (bird watchers and car experts). These individuals also activate the fusiform when viewing items of their relevant expertise category (Bilalić et al., 2016; Gauthier et al., 2000; Xu, 2005). Similar to faces, these objects of expertise require attention to fine-grained details in order to discriminate between exemplars. Thus, within the ‘expertise hypothesis’ framework, activation to faces stems from a more general role of the fusiform in processing objects that must be frequently individuated from others with a common form (Gauthier et al., 1999).

Neuroimaging research from the visual processing of food cues has shown that pictures of food consistently activate bilateral fusiform (for review and meta-analysis, see Van der Laan et al., 2011), but this field is not traditionally referenced in studies of face processing. Importantly, previous studies found that the relative value of the food (high fat vs. low fat) influences fusiform response in healthy weight adults (Frank et al., 2010; Siep et al., 2009; Uher et al., 2006) and being overweight is associated with increased response in the fusiform to food cues (Frankort et al., 2012; Nummenmaa et al., 2012). Thus, this separate literature on

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food cues also suggests that food images activate the fusiform and that the relative value of the food influences the response in this region.

The fusiform is part of a more complex network of brain regions important for face processing. These include core regions, thought to process aspects of the visual appearance of faces (FFA, occipital face area, OFA; lateral occipital sulcus, LOS; and superior temporal sulcus, STS) and extended regions involved in emotional processing (amygdala, AMY; insula, INS; nucleus accumbens, NACC; orbitofrontal cortex, OFC), motor simulation (frontal eye fields, FEF; inferior parietal sulcus, IPS; inferior frontal gyrus, IFG), and person knowledge (medial prefrontal cortex; anterior temporal lobe, ATL; and precuneus) (Haxby et al., 2000; Ishai et al., 2005). Interestingly, many of these regions are also activated in response to food images, including the OFC, amygdala, and nucleus accumbens, and scale with the increased energy density of the food and/or weight status (Pursey et al., 2014). The connectivity between these nodes when viewing faces versus food is of interest, particularly the potential interaction between regions important for the visual processing (FFA, OFA, STS, ATL) and those involved in processing the rewarding aspects (AMY, INS, OFC, NACC) of face and food stimuli.

In the present study, we examined neural responses to faces and food within the region typically described as the FFA. To our knowledge, no study has been conducted that directly compares response to pictures of faces versus food within the fusiform. After completing our first analysis (1) using a priori masks from an independent study of face processing (Julian et al., 2012) to assess overall differences between face and food activation, we go on to (2) describe the location and overlap of fusiform face- and food-nodes across subjects using several analysis methods, and (3) examine the relationship between individual differences in BMI and category-specific fusiform response. Finally, we (4) explore the connectivity profile of face- and food-networks at rest.

## Materials and methods

### Participants

Forty-nine healthy adults are described in the analyses in this paper. Forty-eight healthy adults (24 females; mean age 22) were included in the group analysis. This cohort includes a secondary analysis of 20 subjects scanned at Temple University Medical Center (and included in a manuscript identifying orbitofrontal cortex activation in Troiani et al., 2016), and 28 that were scanned at the Autism & Developmental Medicine Institute of Geisinger Medical Center. We combined these two cohorts in order to achieve greater power and include scanner/cohort as a covariate in all analyses. Because head coil was also different between the two sites, we additionally confirmed that tSNR in the fusiform was comparable across sites and include individual fusiform tSNR as a covariate in ROI analyses; see Image Acquisition section for further details. Ages ranged from 19 to 31 years old ( $22.3 \pm 3.1$  years). Education levels ranged from 13 to 18 years of education ( $16.0 \pm 1.4$  years). We also recruited one additional subject following initial group analyses and initial manuscript review in order to assess test-retest reliability of the fusiform response to food. This individual was within the same average age and education level of the population in the group analysis. None of the subjects had a history of self-reported neurological or psychiatric disorders. Informed consent was obtained according to the guidelines of the Institutional Review Board of Temple University and/or Geisinger Medical Center. Participants received monetary compensation for participation in the experiment.

This analysis is a segment of a larger study that collected a broad neuroimaging battery, in-person phenotyping, and online questionnaires. Our main interest and hypothesis surrounded BMI. We include here any other metrics that were assessed in both cohorts in order to provide a more complete description of the cohort phenotype and allow for comparisons to new cohorts in any potential replications of this finding.

### Phenotype metrics

(1) **Body mass index (BMI)** is a measure that reflects the ratio of metric weight to height. These values were self-reported during an in-person testing session and then converted to BMI using an online calculator ([https://www.nhlbi.nih.gov/health/educational/lose\\_wt/BMI/bmicalc.htm](https://www.nhlbi.nih.gov/health/educational/lose_wt/BMI/bmicalc.htm)). The average BMI for the cohort was  $24.3 \pm 3.9$ , with a range from 17.8 to 35.4. Of those in the cohort, 13 met the criteria for being overweight (BMI ranging from 25 to 29.9) and 5 met the criteria for being obese (BMI greater than 30). Average BMI of males in the cohort was 25.4 and average BMI of females was 23.1. These values are consistent with average BMI in the US population (mean BMI of US females ages 20–29 is 27.5 and males of the same age range is 26.8; for more information on anthropometric reference data, see Fryar et al., 2012) (see Table 1).

BMI calculated based on self-reported height and weight tends to underestimate true BMI (Merrill and Richardson, 2009). Therefore, we corrected self-reported height and weight using corrective factors and methods derived from population estimates and outlined in Mozumdar and Liguori (2016). Briefly, corrected height and weight is calculated using the regression equation: Measured Height = Intercept + b1 X Self-reported Height + b2; where b1 = regression coefficient for self-reported height and b2 = regression coefficient for age group. An identical equation using self-reported weight and relevant tables was also followed, with each considering appropriate sex and race-specific corrective factors outlined in Table 2 of Mozumdar and Liguori (2016). Corrected values resulted in average BMI for the cohort of  $24.9 \pm 4.12$ , with a range from 18.7 to 38.6. Using these corrected values, 15 met criteria for being overweight and 4 met the criteria for being obese. Corrected average BMI of males in the cohort was 25.8 and average BMI of females was 24.1. Thus, corrected BMI values result in more individuals being characterized as overweight.

(2) **The Broad Autism Phenotype Questionnaire (BAPQ; Hurley et al., 2007)** was collected from all subjects as a measure of subclinical autism traits. Originally created to identify subclinical traits in parents of children with autism spectrum disorder, the BAP has since been used as a quantitative measure of identifying subclinical traits within a normally distributed population (Troiani et al., 2016). BAP Total scores ranged from 2 to 3.8 in this population, with a mean of 2.7. Using normative cutoff scores based on a large community sample (Sasson et al., 2013) male cutoff 3.47; female cutoff 3.19), four individuals scored above these cutoff values (2 males, 2 females).

(3) **The Cambridge Face Memory Test (CFMT; Duchaine and Nakayama, 2006)** was completed by all participants. The CFMT is a freely available, 72-item assessment that measures face processing abilities with respect to face memory. Although face processing abilities are largely attributed to fusiform activation, a specific link between fusiform size and face memory was made only recently (Elbich and Scherf, 2017).

**Table 1**

Table indicating total number of subjects with left- and right-hemisphere face and food patches. Average location of peak voxel in left and right-hemisphere for Face > All and Food > All, with significance reflecting differences in spatial location of face and food peaks in a given plane.

	Left	Right		
Total N	48			
# of Subjects with Face Patches	48		48	
# of Subjects with Food Patches	43		32	
	x	y	z	
Average peak location: Face > All	62	37	27	26
Average peak location: Food > All	61	34	29	30
Significant difference between Face & Food peak locations	NS	*	***	***
				NS **

(\* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ; NS = Not Significant).

CFMT total scores ranged from 56.9% to 97.2%, with a mean of 79.52 ( $\pm SD = 11.6$ ). Mean score for females was 78.56 ( $\pm SD = 11.9$ ), and mean score for males was 80.44 ( $\pm SD = 11.6$ ).

### Image acquisition

MRI scanning was conducted at Temple University Hospital, Philadelphia, PA and the Geisinger Autism & Developmental Medicine Institute, Lewisburg, PA. Scanning at Temple University was conducted on a 3.0 T Siemens Verio scanner (Erlangen, Germany) using a Siemens twelve-channel phased-array head coil. High-resolution anatomical images (T1-weighted 3D MPRAGE) were also collected for each participant with the following parameters: 160 axial slices, 1 mm slice thickness, TR = 1900 ms, TE = 2.93 ms, inversion time = 900 ms, flip angle = 9°, FOV = 256 mm. Scanning at Geisinger was conducted on a 3.0 T Siemens Magnetom Trio scanner (Erlangen, Germany) using a Siemens thirty-two-channel phased-array head coil. High-resolution anatomical images (T1-weighted 3D MPRAGE) were also collected for each participant with the following parameters: 192 semi-axial slices, 0.8 mm slice thickness, TR = 1900 ms, TE = 2.99 ms, inversion time = 900 ms, flip angle = 9°, FOV = 250 mm<sup>2</sup>, resolution = 0.8 mm<sup>2</sup>.

Functional data for the experimental task consisted of one 8-min run of whole-brain T2\* weighted BOLD echoplanar images (EPI) with 142 vol (61 oblique axial slices, 2.5 mm slice thickness, voxel size = 3 × 3 × 2.5 mm; matrix size = 80 × 80; TR = 3000 ms, TE = 20 ms, flip angle = 90°, GRAPPA = 2). In the Geisinger cohort, we also collected 120 vol of resting state data immediately following the task-based experiment using identical EPI sequence parameters. We reduced signal dropout in regions near air interfaces (orbitofrontal cortex, anterior temporal lobes) by tilting slice acquisition –30° from the AC-PC plane (Deichmann et al., 2003).

Absolute movement across participants in the experimental task averaged 0.21 mm ( $\pm 0.14$  mm). For the resting state task, movement across participants was 0.19 mm ( $\pm 0.14$  mm). No participants moved more than 3 mm in any run from either the main experimental task or the resting state task.

The temporal signal to noise ratio (tSNR) for each participant was computed using the first run of the experimental task, by dividing the mean of the time series by the residual error SD after pre-processing. Average tSNR for each participant for the left and right fusiform regions were assessed using the masks described below (in section, *Group Analysis: Region of interest based on atlas-derived masks*) and derived from Julian et al. (2012). We confirmed that there were no significant differences in our ability to detect signal in the fusiform in either cohort. Average tSNR in the left fusiform was 174 ( $\pm 27$ ) and 164 ( $\pm 42$ ) for the Temple and Geisinger cohort, respectively, while average tSNR in the right fusiform was 159 ( $\pm 21$ ) and 158 ( $\pm 38$ ). There were no statistically significant differences between the tSNR between scanner cohorts in the left ( $t(46) = 0.91$ ,  $p = .369$ , N.S.) or right fusiform ( $t(46) = 0.059$ ,  $p = .953$ , N.S.).

### Experiment task and stimuli: face/food task

We used a modified face localizer task described in Troiani et al. (2016). Briefly, images of attractive faces, appetizing food, scenes, and clocks were presented in a block design. Images appeared for 750 ms, separated by a 250 ms interstimulus blank screen. Images were arranged into randomized superblocks with two blocks of each category with stimulus category order randomized along with rest trials over the course of 142 image acquisitions (426 s), with a total of 8 superblocks. Participants responded to image repeats that appeared within each block, and responses were monitored in order to ensure participants were awake and paying attention to the images. The task consisted of 320 images (80 faces images, 80 scene images, 80 food images, and 80 clock images) making the run 7.1 min long. Although the original dataset from Temple

University included 4 runs of the experimental task, only the first run was included in this analysis, in order to match subjects from both sites on number of runs. Please see Supplementary Fig. 1 for a task schematic.

Image stimuli were full color, 400 × 400 pixels. All images were collected via Google image search and individually rated by an independent set of 20 raters. Images were rated using a 9-point likert scale [(Like Extremely (9), Like Very Much (8), Like Moderately (7), Like Slightly (6), Neither Like nor Dislike (5), Dislike Slightly (4), Dislike Moderately (3), Dislike Very Much (2), Dislike Extremely (1)]. Mean values ( $\pm$ standard deviation) for each category were Faces [6.2 (0.94)]; Food [6.8 (1.1)]; Places [5.8 (1.1)]; Clocks [4.9 (1.1)]. Intraclass correlation coefficients (ICC) showed moderate to strong agreement between raters (ICC = 0.67).

### Experiment task and stimuli: resting state

The resting state task consisted of one centrally presented white plus sign on a black background. Participants were asked to keep their eyes open and fixated on the plus sign for the duration of the 6-min scan.

### Data analysis

#### Pre-processing & modeling of task-based experiment

Images were first converted from dicom to nifti format using MRI-Convert (<http://lcn1.uoregon.edu/downloads/mriconvert>) and pre-processing of the images was then completed using the FMRIB Software Library (FSL, [www.fmrib.ox.ac.uk/fsl/](http://www.fmrib.ox.ac.uk/fsl/)). Preprocessing steps included stripping non-brain material using the Brain Extraction Tool (BET) and motion correction, B0 unwarping, and slice time correction with FSL FEAT (fMRI Expert Analysis Tool) version 5.0.8. Images were normalized to 2 mm space via FLIRT and smoothed using a 5 mm Gaussian kernel. Four categorical regressors indicated whether the stimulus for each block was a face, place, food, or clock. Categorical regressors were boxcar functions at stimulus onset convolved with a double gamma function. Six estimated motion parameters were also included as nuisance regressors. Parameter estimate maps for each individual were then transformed into standardized t-statistic maps for each contrast (Faces, Places, Food, & Clocks). These were then transformed into MNI standard space and used in (1) Region of Interest Analyses based on atlas-derived masks and (2) Whole Brain Analyses, described in additional detail below.

#### Group analysis: region of interest based on atlas-derived masks

We performed a region of interest (ROI) analysis using regional definitions from an independent data set created by the Kanwisher Lab (Julian et al., 2012). These ROIs were created from a group analysis of thirty-five subjects' overlapping activation to faces relative to places. While our primary focus in this study was the fusiform, we also included other regions that are involved in social information processing in supplementary analyses, in order to demonstrate that our task reliably evokes face-selective responses in other regions implicated in face processing. These included bilateral occipital face area (OFA) and the bilateral superior temporal sulcus (STS), also included in the set of ROIs identified in Julian et al. (2012).

For ROI analyses, masks derived from an independent, published analysis (described above) were used to extract the average standardized response estimates (i.e. t-values) from each regressor (Faces, Food, Places, & Clocks) for each subject. These values were exported to SPSS and effects were measured using a repeated-measures ANOVA with follow-up t-tests, when appropriate. In all analyses, we included whether the subject was from the Temple or Geisinger cohort as a covariate, in order to minimize the impact of any differences between the two groups. We control for family wise error using Bonferroni correction (10 comparisons = critical p value of 0.05/10 = 0.005).

### *Subject-specific analysis: characterization and localization of face-selective responses in the fusiform face area*

Because atlas-based ROI analyses average over all voxels within a given region, we also conducted a subject-specific analysis in order to isolate and further describe individual differences in the location of voxel-wise peak activation to faces and food. Subject-specific analysis was limited anatomically to the region of the fusiform gyrus between the collateral sulcus and the temporo-occipital sulcus.

We first inspected the whole-brain maps for each individual subject, in order to document whether face- and food-selective nodes in the FFA could be detected on an individual level. To do this, each subject's statistical maps for the contrast of Faces > All Other Categories and Food > All Other Categories was viewed at a t score threshold of 2.0 in FSLview. "Patches" were defined for a subject if they had at least five contiguous voxels activated in the chosen contrast while applying the threshold rule of  $t = 2.0$ . This relatively liberal threshold was defined a priori based on previous work identifying subject-specific nodes in the ventral visual cortex (Collins et al., 2016; Troiani et al., 2016, 2012; Tsao et al., 2006). This threshold also allowed us to maximize the number of subjects with 'patches'.

### *Test-retest of individual subject*

In order to confirm that the location of these regions is consistent across time, we scanned an individual subject at two time points, one week apart. Both scans took place at Geisinger. Identical scanning paradigms were used with the subject in order to confirm test-retest reliability of face- and food-activation within the fusiform. This subject was not one of the original Geisinger participants and was not included in the group analysis. Scanning parameters were identical, except we used a longer localizer battery (4 runs of the localizer task). This subject did not move more than 3 mm in any run for either timepoint. Absolute movement for this subject averaged 0.1 mm ( $\pm 0.01$  mm) across runs at Timepoint 1 and 0.02 ( $\pm 0.00$  mm) across runs at Timepoint 2. Data was modeled and analyzed using identical preprocessing and modeling steps described above. In order to emphasize the specificity and similarity of the face- and food-selective nodes across time points, a very high threshold was applied to these images ( $t$ -value  $> 6.0$ ). We present these results in order to establish the reliability of isolating these nodes within an individual across time, since this type of subject-specific analysis is commonly used in the face-processing literature.

### *Whole brain analysis*

In addition to extracting ROIs for our a priori analysis described above, we also completed a group-wise random effects analysis to identify regions showing reliable activation across the group. This analysis was implemented using standard methods within FSL. Individual contrasts from each subject were included in a higher-level group analysis run in FSL FEAT. One-sample t-tests were run for each contrast with scanner site included as a between-subjects variable. Voxel-wise analyses were corrected for multiple comparisons using non-parametric permutation testing (5000 permutations) with the randomize function of FSL. Threshold-Free Cluster Enhancement (TFCE) (Smith and Nichols, 2009) was used and the significance threshold was set to  $p < 0.05$ , corrected for multiple comparisons.

In order to identify regions that are selective for both faces and food, we also created 'face/food union maps'. These maps are created by thresholding the individual contrasts of Faces > Places & Clocks and Food > Places & Clocks for each participant ( $p < 0.05$ ). A binary map that reflects voxels that are significantly activated for both of these contrasts is then brought up to a second-level analysis. We refer to these maps as "union maps", as they represent the union of voxels that activate more to Faces and Food than control objects. These individual, binary maps were then summed across subjects, such that the output is a probability map, in which values reflect the number of subjects that activate a given voxel for both contrasts. Importantly, this analysis is different than modeling Faces & Food > Places & Clocks, which could be driven by very strong

activation to either Faces or Food. Critically, the union map reflects voxels that are not statistically biased towards either faces or food. This same procedure was also completed to create group-level probability maps for the contrasts of Faces > All Other Objects and Food > All Other Objects.

### *Correlation with individual differences in BMI*

Average t-values were extracted from a fusiform mask for the contrast of Faces > Food in order to assess the relationship between category-specific activation within the fusiform and BMI. This mask was derived from the group-level probability map described above. A threshold was applied to the probability map, such that only voxels were included in which greater than 50 percent of subjects selectively activated for faces and food. Partial correlations with the t-values for each subject as a dependent variable and their BMI as an independent variable were completed in SPSS, including scanner site (cohort) as a covariate.

### *Resting state preprocessing & analysis*

Data were brain extracted, motion corrected, slice-time corrected, spatially smoothed (5 mm FWHM), undistorted, z-normalized, and co-registered to each participant's T1-weighted anatomical scan and subsequently sampled to the 2 mm MNI-152 template. Face- and food-nodes were identified by individually locating peaks showing greater activity for faces greater than all other objects and food greater than all other objects from the face/food localizer, respectively. Spheres of 9 mm radius were generated, centered on the voxel with the highest activation within each peak. 9 mm spheres were used based on estimated smoothness of the data, followed from previous work (Zhu et al., 2011). These were then used as seed regions for the resting state analysis.

Although our subjects were quite still, we minimized the impact of motion by modeling the 6 motion parameters identified for each subject as nuisance regressors. Average signal time course from lateral ventricles and white matter were estimated prior to spatial smoothing and specified as nuisance regressors. A bandpass filter was then applied to remove high-frequency fluctuations or noise associated with non gray-matter tissue from the resting state data (Carp, 2013; Jo et al., 2013; Power et al., 2013).

Given that face- and food-nodes are relatively close in proximity based on their activation within a task, we used these nodes to explore whether they are interconnected with unique networks at rest. Face- and food-peaks from the subject-specific analysis were used to create 9 mm spheres for each individual (Please see *Supplementary Fig. 2* to view representative subject's face and food seed ROIs displayed in standard space.). These ROIs were then used to identify regions of connectivity (CONN toolbox, <https://www.nitrc.org/projects/conn>) across the whole brain, in which the output represents the covariation between face- and food-specific peaks and every other voxel in an individual's brain. We then extracted average correlation values between these seed regions and nodes of interest, based on regional definitions using previously described masks from Julian et al. (2012) (superior temporal sulcus (STS), anterior temporal lobe (ATL), and occipital face area (OFA)). We also included the orbitofrontal cortex (OFC), insula (INS), amygdala (AMY), and nucleus accumbens (NACC) from the Harvard-Oxford cortical and subcortical atlases (Desikan et al., 2006), due to their role in processing reward. In order to facilitate comparisons of face and food connectivity, we limited analysis to those individuals who had both face and food peaks ( $N = 25$  on the left and  $N = 15$  on the right). We assessed whether correlation values were significantly different from zero using a t-test and control for family wise error using Bonferroni correction (28 comparisons = critical p value of  $0.05/28 = 0.002$ ).

## **Results**

### *Question 1: Is activation to faces and food within the FFA significant?*

We first assessed whether there was a significant effect of condition in

left and right FFA ROIs. This was accomplished using a repeated-measures ANOVA with condition (Faces, Food, Places, and Clocks) as the independent variable, BOLD response as the dependent variable, and scanner site (cohort) as a between-subject's variable. Please note, we use the term "FFA" here, because the specific ROIs from an independent group were generated using a contrast to identify face-selectivity (Julian et al., 2012). In left FFA, there was a significant effect of condition ( $F(1, 3) = 4.27, p = 0.006$ ) but no condition by cohort interaction ( $F(1, 3) = 0.722, p = 0.541, n. s.$ ). This effect was similar on the right (condition: ( $F(1,3) = 7.36, p < 0.001$ ); condition by cohort interaction ( $(F(1, 3) = 5.69, p = 0.805, n. s.$ )). Significance in follow-up t tests were corrected for multiple comparisons using Bonferroni correction (10 comparisons = critical p value of  $0.05/10 = 0.005$ ), thus significance is reported as p values less than 0.005. The right FFA showed greater activation for faces relative to any other object (Faces > Food,  $t(47) = 3.04, p = 0.004$ ; Faces > Places,  $t(47) = 4.00, p < 0.001$ ; Faces > Clocks,  $t(47) = 3.82, p < 0.001$ ), indicating that right FFA is face selective. Food activation in the right FFA was not significant (Food > Places,  $t(47) = 1.149, p = 0.256, n. s.$ ; Food > Clocks,  $t(47) = 1.003, p = 0.321, n. s.$ ). Within the left FFA, food showed greater activation than places while faces did not (Food > Places  $t(47) = 3.047, p = 0.004$ ; Faces > Places,  $t(47) = 2.70, p = 0.01, n. s.$ ). Food and face activation was not significantly greater than Clock activation (Food > Clocks,  $t(47) = 2.32, p = 0.025, n. s.$ ; Faces > Clocks,  $t(47) = 1.93, p = 0.06, n. s.$ ). Importantly, there was no difference between Faces and Food in the left FFA (Faces > Food,  $t(47) = -0.154, p = 0.879, n. s.$ ). These results are visualized in Fig. 1. For comparisons sake, we include the results of other face-selective ROIs (bilateral STS and OFA) in the Supplementary Results and Supplementary Fig. 3.

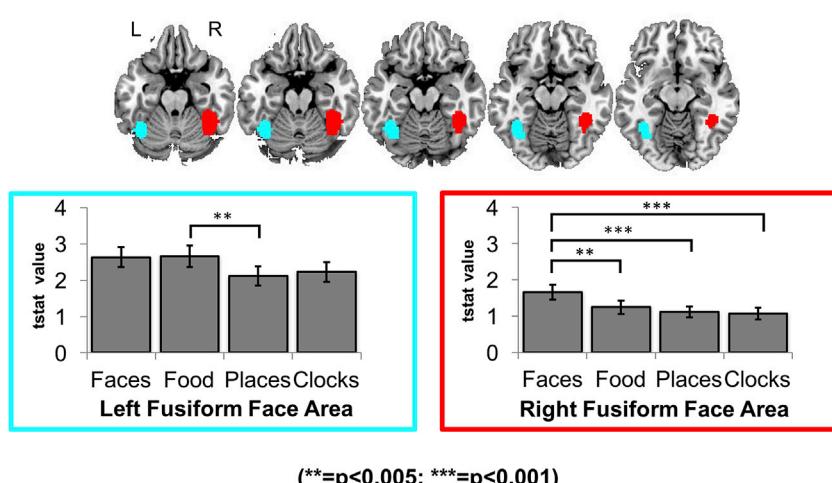
**Question 2: In what percentage of Participant's can face and food-selective activation be identified and where is this activation located?**

In order to illustrate the location and quantify the number of individuals with face and food selective patches, we next identified the peak location of activity for the contrasts of Faces > All Other Objects and Food > All Other Objects within the region classically defined as the FFA in each of the 48 subjects (methods outlined in the subject-specific methods section). Activation to faces was consistently found across subjects, as all 48 (100%) of subjects had bilateral activation to faces that could be identified individually. Food-specific activation peaks were found in 43 subjects (90%) on the left and 32 subjects (67%) on the right. Thus, there seem to be both food and face-selective peaks or nodes in fusiform, but food nodes on the right are not identifiable in all subjects.

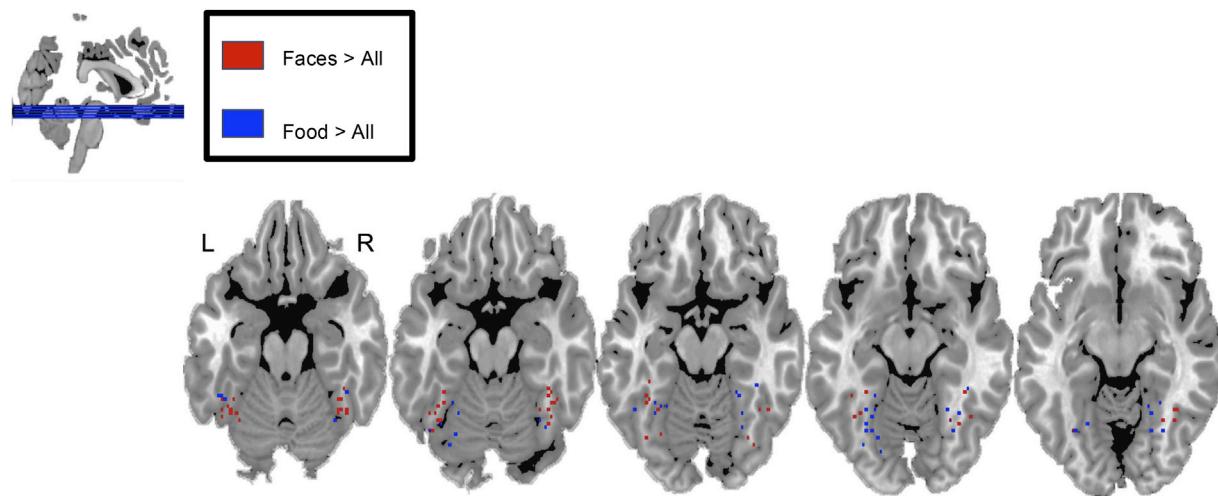
This result is consistent with the face literature, as right fusiform activation tends to be more robust and consistently found in subjects (Gauthier et al., 1999; Haxby et al., 1999; Ishai et al., 2005; Rhodes et al., 2004), although see (Elbich and Scherf, 2017) for individual differences that are linked to a left lateralized response. We next examined whether there were significant differences in the spatial location of these nodes by looking for significant differences in the x-, y-, and z-plane of the coordinates. Peak spatial location between face and food activation was found to be significant across the x-plane in the right hemisphere (Right:  $t(47) = -5.44, p < 0.001$ ; Left:  $t(47) = -0.22, p = 0.413, n. s.$ ), y-plane in the left hemisphere (Right:  $t(47) = -0.28, p = 0.391, n. s.$ ; Left:  $t(47) = -1.80, p = 0.039$ ), and z-plane in both right and left hemispheres (Right:  $t(47) = -2.87, p = 0.003$ ; Left:  $t(47) = -4.24, p < 0.001$ ). Thus, face peaks on the right tended to be more lateral and inferior relative to food peaks, whereas face peaks on the left tended to be anterior and inferior to food peaks; see Fig. 2. Individual coordinates for each subject can be found within Supplementary Tables 1 and 2.

In order to explore whether food-selective activation is truly distinct or overlapping with the classically defined, FFA, we recruited an additional subject to complete a longer version of the task-based experiment at two separate time points. This analysis was completed on one subject given the commonly used procedure to use a localizer task to identify subject-specific FFA based on face-selectivity. In this subject, we were able to localize a food-selective and face-selective patch within the fusiform gyrus at both time points. In fact, localization of food activation in the fusiform was found to be nearly identical on the subjects' brain maps (See Fig. 3) and coordinates for face- and food-selective peaks differed by only one voxel. Although face- and food-selective peaks could be identified bilaterally at both time points, the patch of cortex responding to food was most easily identified on the left, specifically within the lateral occipital sulcus for this subject. Results indicate that a localizer procedure could reliably estimate the region that is functionally activated within the fusiform cortex to food.

The two previous analyses indicate that face- and food-selective nodes are somewhat dissociable, while the ROI analysis indicates a degree of overlap in left fusiform activation. We next assess overlapping activation to faces and food at the individual level by identifying voxels that are significant ( $p < 0.05$ ) for BOTH the contrast of Faces > Places AND Clocks and Food > Places & Clocks. We visualized this information in group-level probability maps that depict the number of subjects that activate a given voxel (Fig. 4A). This is a whole brain analysis (i.e. unmasked), but the image is presented at a threshold that reflects regions that greater than 50% of the sample activated to both Faces and Food relative to other objects. This analysis suggests that there is overlap in



**Fig. 1.** Region of Interest Analysis of FFA response to all conditions. Bar graphs for fusiform ROIs indicate group average estimates (t-statistic values) of activation to faces, food, places, or clocks. Error bars indicate standard error. ROIs are displayed on axial slices of brain, including left fusiform face area (aqua) and right fusiform face area (red). Borders of bar graphs correspond to color of ROI used in axial brain image. Significance is depicted as follows: (\*\* =  $p < 0.005$ ; \*\*\* =  $p < 0.001$ ).



**Fig. 2.** Peak coordinates of face and food patches for all subjects. Axial slices of the brain with individual peak voxel activation to Faces > All Other Objects (red) or Food > All Other Objects (blue). Coordinates depicted in this image can be found in [Supplementary Tables 1 and 2](#).

face and food activation within the fusiform and that this is spatially consistent at the group level. Probability maps for the contrasts of Faces > All Other Objects and Food > All Other Objects (Fig. 4B&C) depict similar information for face- and food-selective voxels. These maps show consistent face-selective clusters in bilateral fusiform, bilateral amygdala, and orbitofrontal cortex while food-selective clusters are in early visual cortex and left lateralized occipital temporal cortex. Taken together, many subjects activate bilateral fusiform for both faces and food relative to places and clocks. However, there appears to be more spatial overlap in face-selective voxels than food-selective voxels within the fusiform.

In addition to the union maps, we next discuss the more traditional, whole-brain analysis of the group. Statistical maps presented in Fig. 5 are corrected for multiple comparisons using TFCE permutation tests in randomize (see Methods) and presented at a  $p < 0.05$  threshold. Please see Tables 2–4 for regional definitions of peak voxels that correspond to contrasts depicted in Fig. 5. We first present the three contrasts that are most conceptually similar to the union maps. In Fig. 5, Part A, regions that are significantly activated by the contrast of Faces & Food > Places & Clocks show significant activation in bilateral fusiform, bilateral amygdala, medial and bilateral orbitofrontal cortex, insula, precuneus, putamen, and nucleus accumbens, indicating that both faces and food activate regions traditionally associated with face processing, as well as regions implicated in processing reward. Next, we assessed regions that were selective for Faces or Food with the contrasts of Faces > Food, Places, & Clocks (Fig. 5B) and Food > Faces, Places, & Clocks (Fig. 5C). Face-selective clusters included regions typically associated with face processing, including right lateralized fusiform, bilateral amygdala, bilateral temporal pole, inferior frontal gyrus, and medial/lateral orbitofrontal cortex. The contrast of Food > Faces, Places, & Clocks (Fig. 5C) shows a large cluster that encompasses early visual cortex, left lateralized occipital and left lateralized fusiform cortex, as well as left lateral orbitofrontal cortex. These contrasts include faces or food contrasted with every other object type (including food or faces, respectively). Thus, we also depict the regions that are significantly activated for Faces relative to the ‘control’ categories of Places & Clocks (Fig. 5D) and Food relative to Places & Clocks (Fig. 5E), as well as a Figure depicting these two contrasts overlaid on the same brain with overlapping voxels highlighted in pink. Overlapping voxels include primarily the left fusiform, as well as left amygdala (Fig. 5F). Finally, we include direct contrasts of Faces and Food in [Supplementary Fig. 4](#). Direct contrasts of Faces to Food show significant activation in right lateralized fusiform, bilateral amygdala, orbitofrontal cortex, temporal pole, and angular gyrus. The direct contrast of Food relative to Faces shows significant activation in a large swathe of

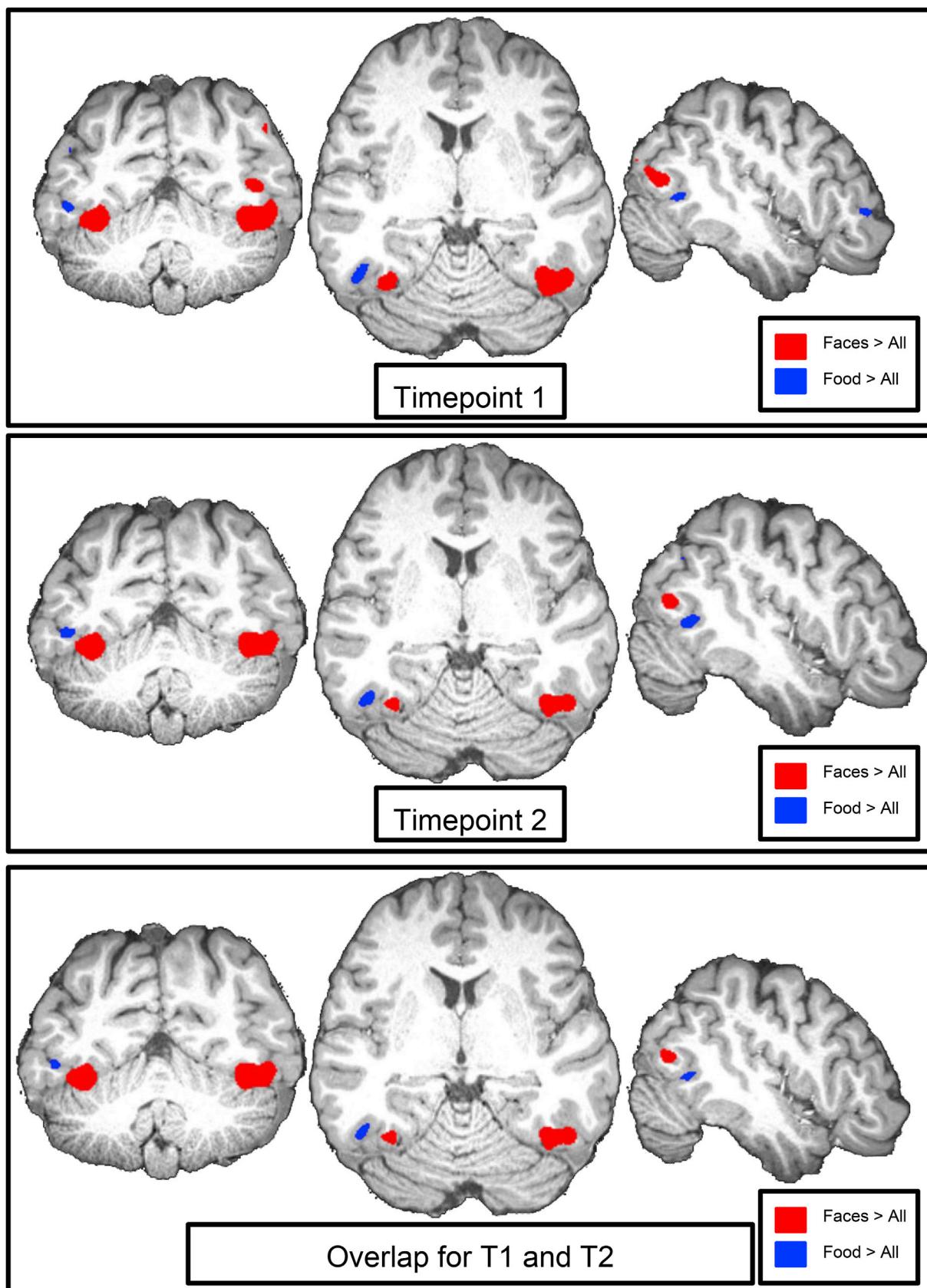
early visual cortex that extends into parahippocampal and left inferior temporal gyrus (See [Supplementary Fig. 4](#) and [Supplementary Table 3](#)).

*Question 3: Do individual differences influence activation to face and food stimuli?*

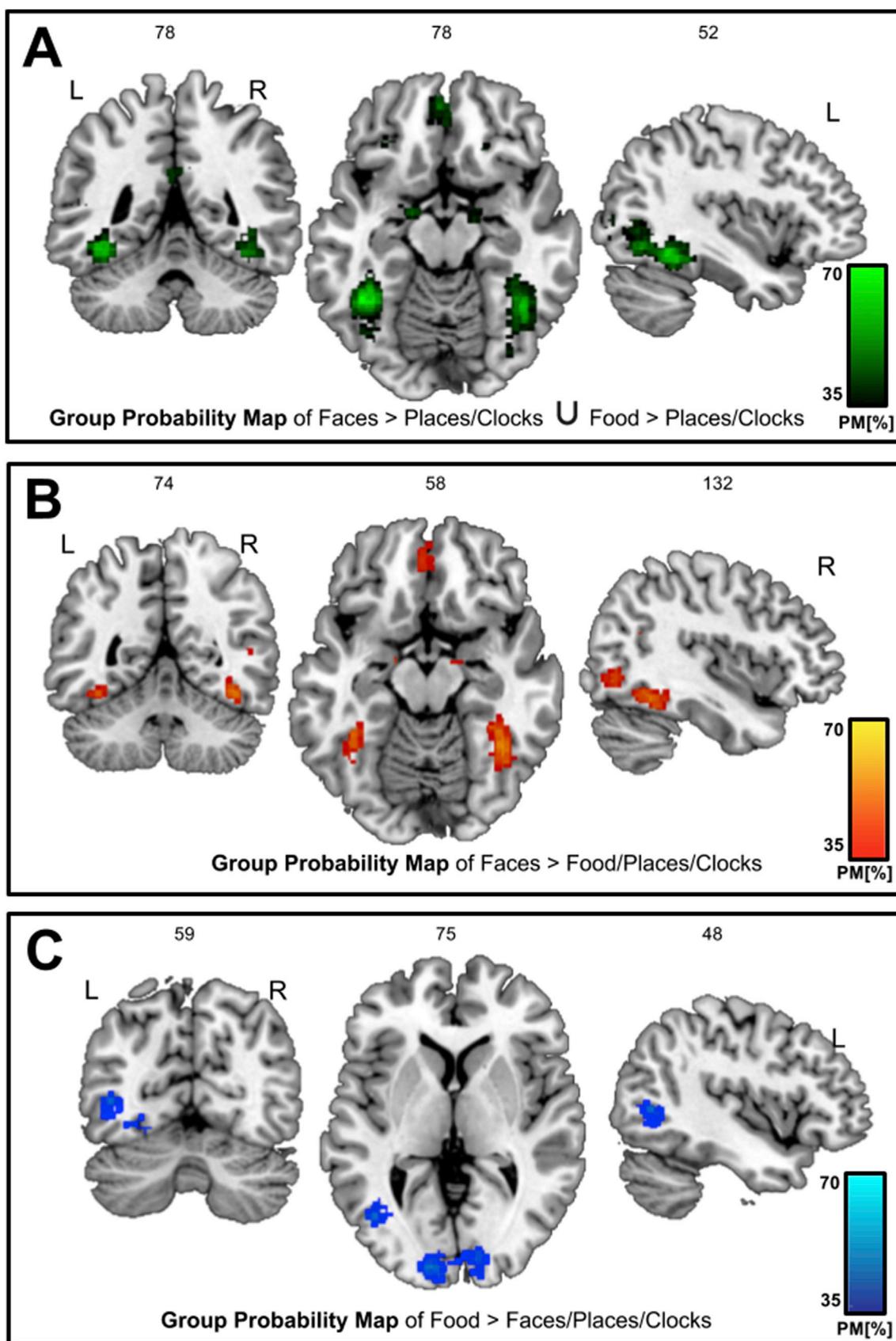
Because there does seem to be some degree of overlap in the gross location of face- and food-peaks and previous work has related activation to food images in the fusiform to healthy weight status, we next asked whether individual differences in BMI are reflected in activation in the fusiform. To assess this, we extracted t-values from each individual within the region of the left fusiform that responds to faces and food more than other objects. This region was extracted using a mask derived from the group-level union map, which reflects voxels that are activated for both faces and food relative to control objects. We find that as BMI increases, relative activation to Faces > Food decreases ( $r = -0.294$ ;  $p = 0.024$ ). That is, while most individuals activate the FFA more strongly to faces relative to food, this activation is reduced as BMI increases. This relationship was consistent when using corrected BMI (BMIC;  $r = -0.309$ ;  $p = 0.017$ ).

*Question 4: What is the connectivity profile of these face- and food-peaks at rest?*

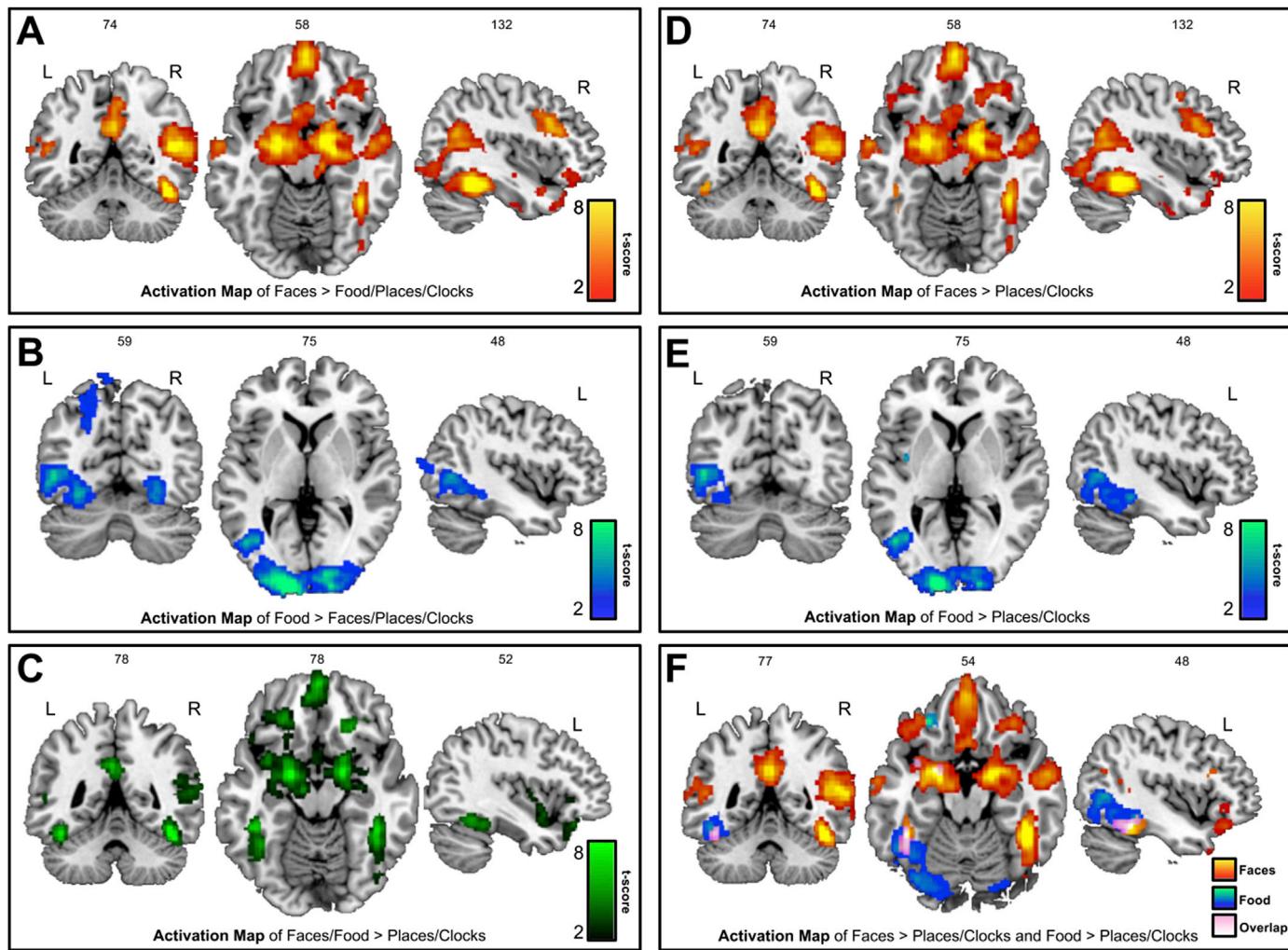
In order to assess connectivity between the fusiform and other regions of the brain in the absence of a task, we then completed an exploratory connectivity analysis to identify differences in connectivity profiles between face- and food-peaks and the rest of the brain during a resting state paradigm. Individually-defined face- and food-selective peaks within the fusiform were used to create 9 mm ROIs spheres for each subject. Intrinsic connectivity between these peaks and six other ROIs were then examined. ROIs included regions involved in face and reward processing, and included: amygdala (AMY), orbitofrontal cortex (OFC), nucleus accumbens (NACC), insula (INS), anterior temporal pole (ATL), occipital face area (OFA), and the superior temporal sulcus (STS). After correction for multiple comparisons using a Bonferroni corrected p-value of 0.002, significant connectivity was found between the INS, ATL, OFA, and STS for both face- and food-peaks. Bilateral NACC and AMY were not significant within either network, while OFC was only significant for the face-peaks. (Face Fusiform peak: Right NACC:  $t(14) = -0.153$ ,  $p = 0.440$ , n. s.; Left NACC:  $t(24) = -0.973$ ,  $p = 0.17$ , n. s.; Right AMY:  $t(14) = -3.04$ ,  $p = 0.004$ , n. s.; Left AMY:  $t(24) = -1.99$ ,  $p = 0.031$ , n. s.; Right OFC:  $t(14) = -4.40$ ,  $p < 0.001$ ; Left OFC:  $t(24) = -5.36$ ,  $p < 0.001$ ). Bilateral food fusiform peaks showed a similar pattern (Food Fusiform



**Fig. 3.** Test-Retest Reliability of Face and Food Patches within the Fusiform for a single subject. A single subject completed a longer version of the face/food localizer task at two separate timepoints, separated by one week. Whole brain t-statistic maps for this subject are depicted on the subject's anatomical image with face-selective activation (Faces > All Other Objects) in red and food-selective activation (Food > All Other Objects) in blue. Top panel: Timepoint 1; Middle Panel: Timepoint 2; Bottom panel: Voxels that were activated at both timepoints. T-statistic maps are presented with a high threshold ( $t = 6.0$ ) in order to emphasize the consistent activation within the fusiform.



**Fig. 4.** Probability maps of the percentage of subjects with significant activation in a given voxel for contrasts of interest. (A) Probability map depicting the union of voxels that are activated by both Faces > Places and Food > Places and Clocks. (B) Probability map depicting the voxels that are activated by Faces > All Other Objects. (C) Probability map depicting the voxels that are activated by Food > All Other Objects. Scale indicates percentage of subjects that activate a given voxel (35–70%).



**Fig. 5.** Whole-brain statistical maps from group-level analysis. Data are corrected for multiple comparisons at  $p < 0.05$  using TFCE and permutation testing and all scales depict t-statistic values from 2 to 8. Statistical maps are overlaid on the ch2bet image using mrintron. Coordinates that correspond to the location of the crosshair for that slice are above each section. (A) Faces > Food, Places, & Clocks in red-yellow scale (B) Food > Faces, Places, and Clocks in blue-green scale (C) Faces & Food > Places & Clocks in black-green scale (D) Faces > Places & Clocks in red-yellow scale (E) Food > Places & Clocks in blue-green scale (F) Overlap of Faces > Places & Clocks (red-yellow scale) and Food > Places & Clocks (blue-green scale); Overlapping activation is depicted in pink to white scale.

Peak: Right NACC:  $t(14) = -1.104$ ,  $p = 0.144$ , n. s.; Left NACC:  $t(24) = -2.17$ ,  $p = 0.02$ , n. s.; Right AMY:  $t(14) = -1.412$ ,  $p = 0.090$ , n. s.; Left AMY:  $t(24) = -0.299$ ,  $p = 0.383$ , n. s.; Right OFC:  $t(14) = -3.13$ ,  $p = 0.004$ , n. s.; Left OFC:  $t(24) = -3.18$ ,  $p = 0.002$ , n. s.). All other ROIs (OFA, STS, ATL, INS) showed significant connectivity with both face- and food-peaks (All  $t's > 4.3$ , all  $p's < 0.002$ ); see Fig. 6.

Interestingly, when we compared whether there are significant differences in connectivity between nodes of the face and food networks, the two nodes that are significant are the anterior temporal and orbitofrontal nodes (ATL;  $t(24) = 2.28$ ; OFC;  $t(24) = 1.8$ ; all other  $t$ 's greater than 1.29 and  $p$ 's greater than 0.10). In the ATL and OFC, connectivity values were both greater for Face peak connectivity relative to Food peak connectivity, a point we take up further in the discussion.

## Discussion

In the current study, we investigated neural response in fusiform cortex within two categorical domains: faces and food. To our knowledge, this is the first paper to directly compare response within parts of visual cortex to faces and food, although there is a great deal of work on response of the visual cortex to these categories in separate fields of cognitive and clinical neuroscience. The activation of the fusiform to food

images cannot be explained by either the expertise hypothesis or the face-selectivity hypothesis and our data challenge these two theories. Food images are not face-like and therefore, this response is not compatible with the face-selectivity hypothesis. The wide variety of food images used in the current design were not difficult to discriminate from one another and therefore, these results also challenge the expertise hypothesis, which suggests the fusiform is recruited for the fine-grained discrimination of similar exemplars. Rather, these results are more compatible with the distributed model proposed by Haxby (Haxby et al., 2000, 2001), which suggests that the ventral temporal cortex is topographically organized to identify attributes of form rather than specific objects. Based on Haxby's distributed model, each object form has a distinct pattern of activation that is distributed throughout ventral temporal cortex rather than localized to a specific cortical region. Evidence for this theory comes from multi-voxel pattern analyses that demonstrate information regarding all types of objects are represented throughout ventral visual cortex, even within regions that show greatest response to one particular category of objects (Haxby et al., 2001).

However, even the distributed model of object perception does not address why specific nodes in the fusiform may be activated in response to visual images of food or faces more than other object categories. We suggest that an attribute that we refer to as motivational relevance (but

**Table 2**

MNI coordinates and brain regions of group-level whole brain analyses.

Contrast	Cluster size	Peak Voxel Coordinates (MNI)					
		Region	t-score	X	Y	Z	
Faces > Food, Places, and Clocks	9578	R Amygdala	11.5	18	-4	-16	
		L Amygdala	10.4	-18	-4	-14	
		R Anterior Temporal Gyrus	7.11	58	-2	-16	
		L Putamen	7.06	20	6	-12	
		R Superior Temporal Gyrus	6.64	52	-8	-12	
		Medial OFC	6.2	4	40	-20	
		3955	R Angular Gyrus	9.37	60	-46	10
		1062	Precuneus	7.86	2	-50	30
		943	R Fusiform	12.3	44	-50	-20
		855	R Inferior Frontal Gyrus	7.33	46	16	26
		843	L Superior Temporal Sulcus	7.16	-54	-42	2
		213	L Middle Temporal Gyrs	5.88	-60	-6	-12
		25	L Fusiform	7.6	-42	-44	-22
		18	Frontal Pole	5.33	6	62	30
Food > Faces, Places, and Clocks	12697	10	L Middle Temporal Gyrus	4.39	-68	-30	-4
		10	L Lateral Orbitofrontal Cortex	4.57	-38	30	-20
		8	Early Visual Cortex	13.6	-16	-102	10
		8	Lateral Occipital Cortex	8.37	-16	-102	10
		8	Fusiform Cortex	5.61	-48	-48	-12
		8	L Lateral Orbitofrontal Cortex	7.2	-24	34	-16

can also be described as salience and/or value) may play an important role in driving activation in the fusiform. This is supported by work showing increased fusiform activation for high energy versus low energy foods (Holsen et al., 2005; Killgore et al., 2003; Rothemund et al., 2007; Uher et al., 2006), as well as by work showing increased fusiform activation for high value faces.

The importance of object value in driving fusiform activation is also supported by work examining the fusiform hypoactivation to faces seen in patients with autism spectrum disorder (ASD) (Chevallier et al., 2012; Scherf et al., 2010; Schultz, 2005; Whyte et al., 2016). For example, one case study on a child with ASD documented fusiform activation in response to his favorite cartoon character, but not to non-preferred cartoon characters or human faces (Grelotti et al., 2005). This work suggests that the underlying neural architecture of the fusiform may be operational in ASD, but may be inappropriately ‘tuned’ due to atypical or diminished social motivational drives (Chevallier et al., 2012; Schultz,

2005; Troiani et al., 2014; Troiani and Schultz, 2013).

Face-selective responses in the fusiform are thought to be immature early in life and change throughout the course of development (Scherf et al., 2007; Golarai et al., 2007; Deen et al., 2017). However, because studies of children's neural responses in these regions have focused on comparing faces with scenes, we still know little about how the motivational value of objects drives the development of object representations in the brain. To this point, a recent study by Foss-Feig et al. (2016) found that images of children's individualized hobbies corresponded to increases in fusiform activation. Thus, it may be that a combination of motivation and a prolonged visual history are necessary for activation and coding within the fusiform. It will be important for future neuro-imaging work in both children and adults to consider the relative value of stimulus categories.

It may be the case that even the face-selective portion of the fusiform is not responsive to faces, per se, but rather to a combination of stimulus

**Table 3**

MNI coordinates and brain regions of group-level whole brain analyses (continued).

Contrast	Cluster size	Peak Voxel Coordinates (MNI)					
		Region	t-score	X	Y	Z	
Faces and Food > Places and Clocks	3467	L Amygdala	9.21	-20	-4	-14	
		R Amygdala	9	-22	0	-20	
		R Temporal Pole	7.54	-28	6	-24	
		R Putamen	6.74	20	8	-14	
		L Lateral Orbitofrontal Cortex	6.59	-26	36	16	
		L Midbrain	5.87	-8	-14	-14	
		L Insula	5.79	-36	6	12	
		L Hippocampus	5.4	-30	-20	-10	
		L Putamen	5.38	-20	10	-8	
		L Nucleus Accumbens	5.18	-10	12	-6	
		R Fusiform	9.86	42	-44	-18	
		R Angular Gyrus	9.04	60	-44	10	
		R Lateral Occipital Cortex	8.39	50	-70	8	
		1933	Medial Orbitofrontal Cortex	8.19	0	60	-10
		739	Precuneus	7.34	-4	-52	26
512	2909	L Fusiform	8.24	-42	-44	-18	
		L Superior Temporal Gyrus	5.95	-48	-40	10	
		111	Thalamus	5.75	2	-8	10
		95	R Orbitofrontal Cortex	6.74	24	30	-14
		27	L Anterior Temporal Cortex	4.81	-30	-6	-40
		17	Superior Frontal Gyrus	5.55	0	20	62
		7	L Lateral Occipital Cortex	6.11	-44	-80	-6
3	3	Subcallosal Orbitofrontal Cortex	5.21	0	18	-20	

**Table 4**

MNI coordinates and brain regions of group-level whole brain analyses (continued).

Contrast	Cluster size	Peak Voxel Coordinates (MNI)				
		Region	t-score	X	Y	Z
Faces > Places and Clocks	10983	L Amygdala	10.8	-18	-4	-14
		R Amygdala	10.6	18	-4	-16
		Med Orbitofrontal Cortex	8.02	0	60	-10
		R Anterior Middle Temporal	6.88	58	-2	-16
		L Putamen	6.47	-22	8	-8
		R Temporal Pole	6.01	32	6	-22
		R Fusiform	11.9	44	-50	-20
		R Angular Gyrus	9.04	60	-44	10
		R Lateral Occipital Cortex	8.39	50	-70	8
		Precuneus	7.93	2	-50	30
		Frontal Pole	5.57	-2	44	62
		R Inferior Frontal Gyrus	6.85	44	14	26
		L Posterior Middle Temporal Gyrus	7.74	-64	-38	8
		L Anterior Middle Temporal Gyrus	6.42	-60	-6	-14
		L Fusiform	8.09	-40	-44	-18
Food > Places and Clocks	7213	R Precentral Gyrus	4.74	42	2	52
		L Middle Frontal Gyrus	5.36	-46	22	24
		R Inferior Frontal Gyrus	4.72	56	36	8
		Early Visual Cortex	12.2	-12	-102	10
		L Lateral Occipital Cortex	7.59	-46	-68	2
		L Fusiform	6.59	-44	-40	-14
		L Insula	7.79	-36	6	-12
		L Lateral Orbitofrontal Cortex	8.04	-24	34	-16
		L Amygdala	6.58	-20	2	0

qualities that primarily make up faces, but are also shared by some other kinds of objects. That is, neuronal tuning in ventral visual cortex could be organized along a number of stimulus quality continuums, with modular categorical responses reflecting consistent activation along a number of these dimensions. Speaking to this point, we have previously found that another region involved in ‘category-specific’ processing, the parahippocampal place area, is driven by a number of stimulus features, including several low-level visual properties and high-level semantic properties (Troiani et al., 2012). Other studies have illustrated stimulus continuums that drive activation in an organized way across ventral visual cortex, including low-level image statistics (Rice et al., 2014), 3D shape continuums (Tootell et al., 2008), animacy (Sha et al., 2015), real world object-size (Konkle and Oliva, 2012), combinations of these features (Konkle and Caramazza, 2013; Long et al., 2017), semantic similarity (Huth et al., 2012), and affective value (Lebrecht et al., 2012). Future work should explore whether a stimulus set varying on a number of these stimulus dimensions drive fusiform activation.

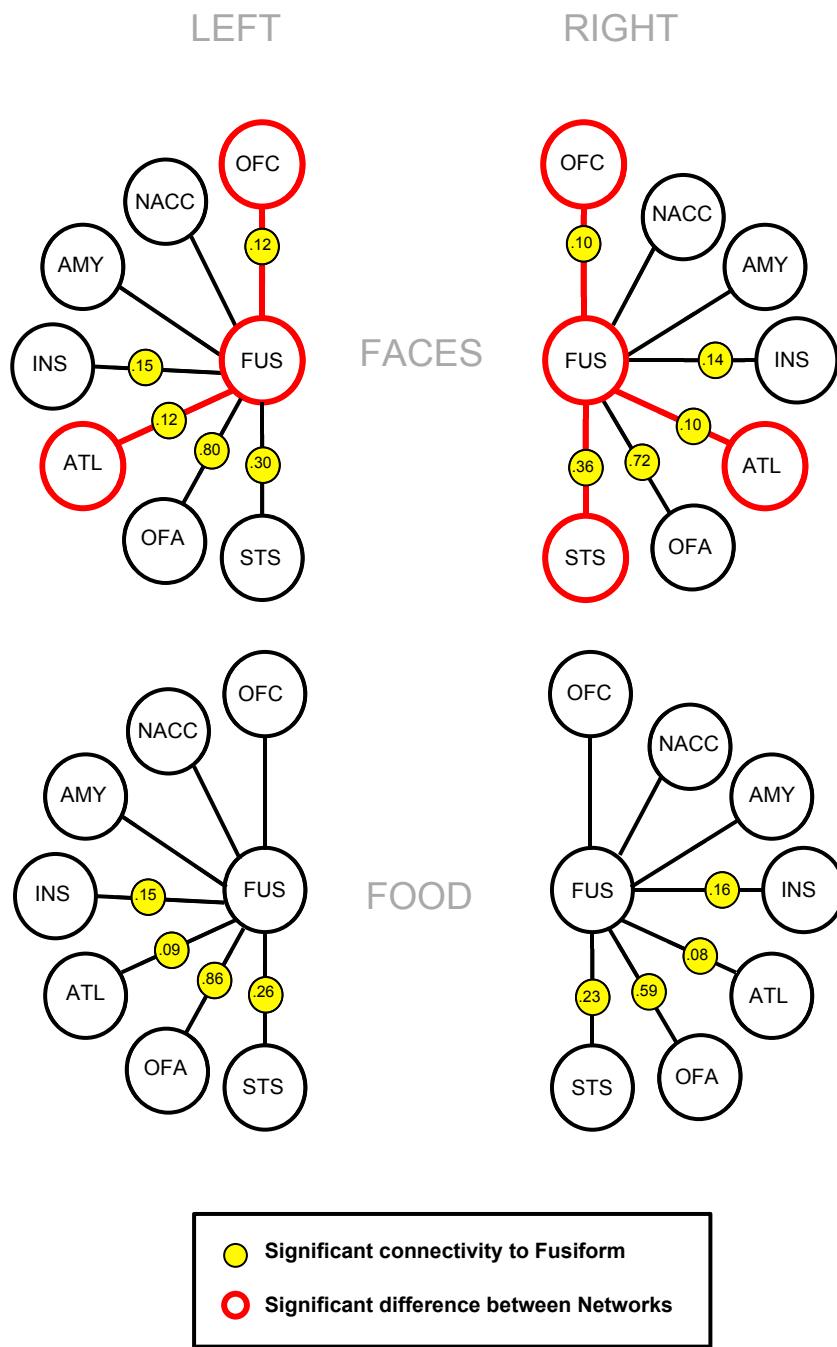
The exploratory connectivity analysis revealed greater activation to Faces rather than Food in the ATL and OFC. The ATL and OFC are connected by the white matter tract known as the uncinate fasciculus, which is thought to play a key role in social cognition. Thus, increased connectivity between the face-selective fusiform and the ATL and OFC is consistent with other connectivity work and underscores the importance of these regions in face- or social-specific processing (Alm et al., 2015; Olson et al., 2015; Unger et al., 2016; Von Der Heide et al., 2013). There is increasing realization that while individualized brain regions may code for specific types of information, multiple regions form networks that work in tandem to achieve complex cognitive tasks (Sporns, 2013). For example, recent research suggests that one node of the face processing network, the ATL, functions as a “neural switchboard”. That is, connectivity between other nodes of the face network, including the FFA, and the ATL vary based on the information required for a specific task or context (Wang et al., 2017). Rather than being a repository of person information, the ATL operates under the hub-and-spoke model such that if a face were presented one could expect increased connectivity between the ATL and FFA, and if a name were presented one could expect increased connectivity between the ATL and the VWFA. From this perspective, activation and connectivity in the fusiform region (and networks of brain regions connected to the fusiform) may also be

influenced by an individual’s context or current state.

The influence of state on fusiform activation has been investigated using food images. For example (LaBar et al., 2001), scanned participants while passively viewing images of food and tools in hunger and sated states. Neural activation within the anterior fusiform gyrus was reduced when comparing across the hungry and sated states, highlighting the influence of state-dependent activation on this region. In a separate study (Mohanty et al., 2008), found that activation in a network that included the amygdala and fusiform was more active during periods of hunger relative to periods of satiation. This activation during a hungry state was also associated with faster detection of food-relevant objects (donuts) relative to non-relevant objects (hex-nuts). Thus, within the food domain, there is evidence that fluctuations in state will influence activation in the fusiform. Although we did not measure hunger state of all the participants in this study,<sup>1</sup> other work has shown activation in the fusiform to food images following meal consumption (Simmons et al., 2013). Thus, in the unlikely case that the majority of our participants were hungry, there is previous evidence that this region still activates to food images even when sated. It would be very interesting in future work to consider the role of individual’s state in driving both fusiform response and changes in network connectivity.

Thus, although the fusiform is most commonly associated with face processing, our results suggest that this region also responds to food, another motivationally-relevant stimulus. Our multiple analyses suggest that food selectivity is going to be more left-lateralized. The ROI analysis using independently-defined masks show equivalent left fusiform activation to faces and food, but face-selectivity within the right fusiform ROI. Across all subjects, peaks were more readily identified for food-selectivity on the left relative to the right. In our single-subject analysis that examined test-retest reliability, the ‘patch’ activated by food was more readily localized in left ventral visual cortex. On the topic of left fusiform responsibility, it seems important to mention another category

<sup>1</sup> Hunger rating was acquired for the cohort of participants scanned at Temple University, previously described in Troiani et al. (2016). Participants rated their current hunger level on a scale from 1 to 10 (where 1 is not hungry and 10 is extremely hungry). Average hunger rating was 3.25, indicating that they were only slightly hungry.



that has been shown to activate the left fusiform: orthographic visual information. A portion of the left fusiform has been called the visual word form area (VWFA) (Fiez and Petersen, 1998) and responds preferentially to strings of letters and numbers. Although this may seem tangential to face- or food-related activation, the response to orthographic information bears importance to the general interpretation of the underlying properties that drive fusiform activation and network connectivity. Recently, it was shown that visual experience with a written language is necessary to activate this region (Saygin et al., 2016), indicating that a certain amount of familiarity may be necessary to drive this response. One explanation is that humans are experts at reading/recognizing visual word forms and thus, rely on the fusiform in a similar manner to faces (McCandliss et al., 2003). However, consideration of motivational value is important with regard to the VWFA, as humans also have inherent drives to communicate and process information (Kang et al., 2009). This

additional point highlights the necessity of considering motivational relevance within the broader perspective of domain specificity in the brain.

Although this study addressed fusiform response to food for the first time, there are several limitations. For individual difference metrics, we used self-reported height and weight to compute BMI, rather than directly measuring these variables. This is a significant limitation, as self-reported BMI is unreliable and underestimates true BMI (Merrill and Richardson, 2009). Although we have applied a correction procedure in an attempt to estimate true BMI, future studies should measure height and weight directly. Also, this sample does not include a large number of subjects who are very overweight or obese. Although results suggest that as weight increases, differentiation between face and food response becomes smaller, future studies should include more subjects who have greater BMIs. In addition, we did not collect the hunger level of all

participants or assess activation during different hunger states within the same individual. Future studies should measure this in order to assess the influence of state-based motivation. Face and food nodes are very close spatially, albeit with some variability across individuals (See Supplementary Fig. 2). Thus, in our resting state analysis, our sample size was only a subset of our larger sample ( $N = 25$  on the right and  $N = 15$  on the left) and the high degree of overlap between networks could be partially due to overlapping signals. Future work should include a larger sample and explore other connectivity approaches, such as diffusion weighted imaging, in order to develop a more complete understanding of the distinctions and overlap in these networks.

In sum, we find that the left fusiform cortex responds to both faces and food. We believe this response is based on the rewarding value of both of these stimuli, as this result is consistent with findings of food value-driven fusiform activation within the literature on the visual processing of food images. These results challenge existing theoretical explanations of the fusiform response to faces and support a distributed model of object processing. Further, these findings suggest intriguing new avenues for future research in these domains that may also have implications for clinical disorders that show atypical visual responses to faces and/or food.

## Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.neuroimage.2018.02.064>.

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