Social Norms Shift Behavioral and Neural Responses to Foods

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Abstract

■ Obesity contributes to 2.8 million deaths annually, making interventions to promote healthy eating critical. Although preliminary research suggests that social norms influence eating behavior, the underlying psychological and neural mechanisms of such conformity remain unexplored. We used fMRI to investigate whether group norms shift individuals' preferences for foods at both behavioral and neural levels. Hungry participants rated how much they wanted to eat a series of healthy and unhealthy foods and, after each trial, saw ratings that ostensibly represented their peers' preferences. This feedback was manipulated such that peers appeared to prefer each food more than, less than, or as much as participants themselves. After a delay, participants rerated each food. Participants' second ratings shifted to resemble group norms. Initial consensus, as compared to disagreement, with peers produced activity in the nucleus accumbens, a region associated with reward prediction errors. Furthermore, the strength of this activity predicted the extent to which participants' ratings conformed to peer ratings, suggesting that the value associated with consensus drives social influence. Ventromedial prefrontal cortex (vMPFC), a region associated with value computation, initially responded more strongly to unhealthy, as compared to healthy, foods. However, this effect was "overwritten" by group norms. After individuals learned their peers' preferences, vMPFC responses tracked the popularity, but not the healthfulness, of foods. Furthermore, changes in vMPFC activity tracked social influence over behavioral ratings. These data provide evidence that group norms can shift food preferences, supporting the use of norms-based interventions to promote healthy eating. ■

INTRODUCTION

More than one third of American adults are considered obese (Ogden, Carroll, Kit, & Flegal, 2013). Research implicates obesity in a number of serious health problems (World Health Organization, 2009; Flegal, Graubard, Williamson, & Gail, 2007; Perry et al., 1995; Rimm et al., 1995), and an estimate of the national annual economic impact of obesity exceeds $98 billion (Tsai, Williamson, & Glick, 2011). Although multiple factors cause obesity, excess caloric intake is a prime contributor (Caballero, 2007).

Intriguingly, recent studies suggest that social norms influence dietary choices and even body mass index (BMI; Robinson, Thomas, Aveyard, & Higgs, 2014; Christakis & Fowler, 2007). Such findings make social norms a promising target for interventions to promote healthy eating and prevent obesity. However, the psychological and neural mechanisms that explain how social norms shape eating behaviors remain unclear. Although descriptive norms influence what and how much people eat (e.g., Robinson, Fleming, & Higgs, 2013; Lally, Bartle, & Wardle, 2011; Croker, Whitaker, Cooke, & Wardle, 2010), the use of self-report and observational designs in prior work leaves open at least two possible explanations for these effects. First, participants might publicly comply with situational expectations by temporarily changing their behaviors to match those around them while privately maintaining their original preferences (Dijksterhuis, 2001). Conversely, participants might *internalize* social norms, updating their subjective preferences, as well as their behaviors, to match their group.

Here, we drew upon emerging neuroscientific models of social influence to adjudicate between these possibilities. Recent fMRI investigations suggest that social influence for nonfood stimuli, such as faces and consumer goods, shares characteristics with reinforcement learning (Mason, Dyer, & Norton, 2009; Day, Roitman, Wightman, & Carelli, 2007; Schultz, 2006; Kelley, 2004). In particular, the nucleus accumbens (NAcc), a region responsive to reward prediction errors, responds when individuals learn they share opinions with others (consensus). This activity further predicts later conformity to group norms (Falk, Way, & Jasinska, 2012; Klucharev, Hytönen, Rijpkema, Smidts, & Fernández, 2009), suggesting that people experience consensus with groups as valuable and conform to maximize this rewarding experience. Furthermore, research has shown that regions associated with subjective valuation, including those within the ventromedial prefrontal cortex (vMPFC; Grabenhorst & Rolls, 2011), respond more to stimuli that individuals' peers rate positively, as compared to negatively. This suggests that social norms influence not only behavioral ratings for stimuli but also how people

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internally evaluate these stimuli (Zaki, Schirmer, & Mitchell, 2011). However, it remains unclear whether norms can likewise shift preferences for even primary rewards, such as foods.

Here, we used fMRI to test whether social norms (i) shift individuals' reported preferences for foods and (ii) shift internal responses to foods by modulating neural responses to these foods at a later time. We hypothesized that (i) participants would shift their ratings of foods to match those of their peers, (ii) participants' NAcc responses to group consensus would predict their tendency to conform, and (iii) participants would evince greater vMPFC activity while rerating popular versus unpopular foods. Testing these hypotheses clarifies the neural mechanisms underlying norm-based effects on dietary preferences and extends prior work on conformity by examining whether norms shift preferences for even primary rewards.

METHODS

Participants

Twenty-five Stanford University undergraduates participated for payment or course credit. We excluded data from three participants because of excessive head motion (>2.8 mm in any direction) and a fourth participant who failed to respond on >20% of trials. Analyses include data from the remaining 21 participants (18 women, mean age = 20.10 years). All participants were right-handed, healthy native English speakers with normal or corrected-to-normal vision who did not have a history of a neurological disorder and were not taking any medications that would interfere with fMRI data collection. Participants refrained from eating for 4 hr before the experiment to ensure that they were hungry (cf. Hare, Malmaud, & Rangel, 2011; see also van der Laan, de Ridder, Viergever, & Smeets, 2011; Siep et al., 2009; LaBar et al., 2001). The Stanford Institutional Review Board approved all methods for this study.

Stimuli

A total of 150 color images of foods on black backgrounds were compiled from sets provided by Blechert, Meule, Busch, and Ohla (2014), Hare, Camerer, and Rangel (2009), and Plassmann, O'Doherty, and Rangel (2007). Foods were sorted into two groups according to healthfulness. Unhealthy foods were highly processed (e.g., chips and candy), fatty (M = 16.84 g/100 g), and calorically dense (M = 398.04 kcal/100 g), whereas healthy foods were less processed (e.g., fruits and vegetables), less fatty (M = 2.34 g/100 g) and less calorically dense (M = 118.84 kcal/100 g). The nutritional qualities of foods in these groups differed significantly (all ps < .001).

Procedure

Participants completed a paradigm adapted from previous research on social influence (Zaki et al., 2011; Klucharev et al., 2009). Participants were told they were part of a large-scale study on the food preferences of the Stanford undergraduate community and that hundreds of other Stanford undergraduates had already provided their

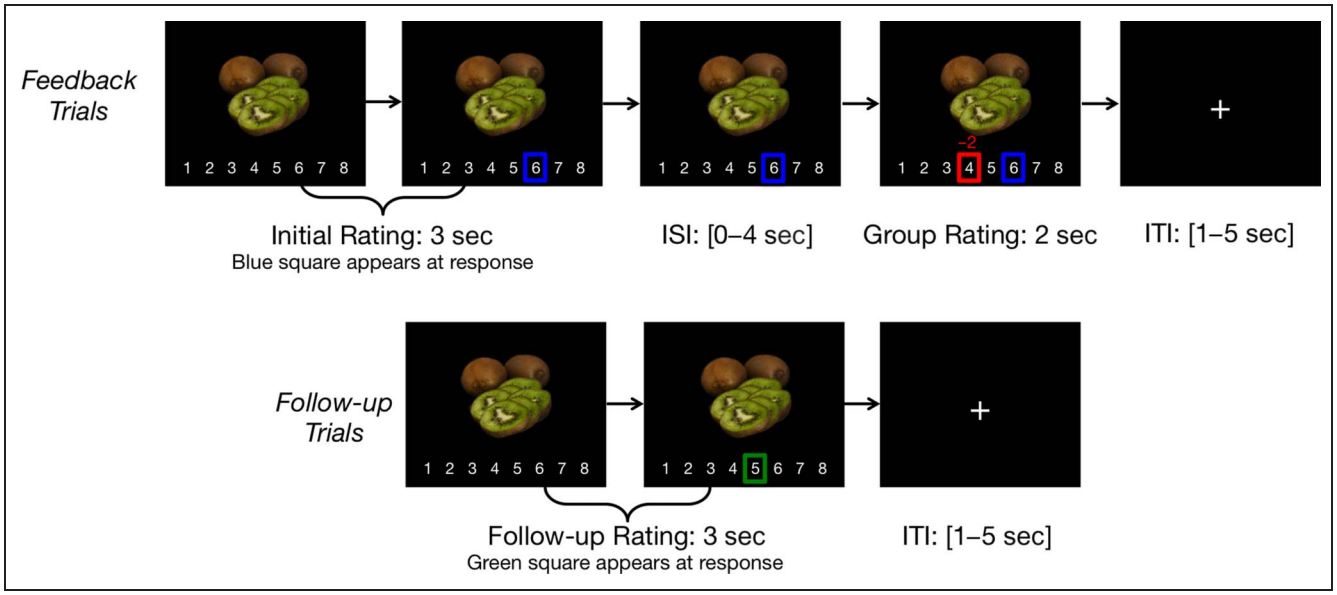

Figure 1. Task schematic. In feedback trials, participants saw images of foods for 3 sec and rated how much they would like to eat each food (initial ratings). A blue box appeared around their selection until the end of the 3-sec response period and remained for an additional jittered 0-sec to 4-sec ISI. Ostensible group ratings were displayed for 2 sec (sorting trials into peers lower, peers higher, or peers agree group norms conditions) before a 1-sec to 5-sec jittered intertrial interval (ITI). In follow-up trials, participants again saw and rated each food (follow-up ratings). A green square appeared around their choice until the 1-sec to 5-sec jittered ITI.

preferences for foods. To familiarize participants with the task, they completed a series of six training trials before entering the fMRI scanner.

While in the scanner, participants first completed 150 feedback trials (see Figure 1 for schematic). In these trials, participants viewed each food for 3 sec and provided initial ratings of how much they would like to eat that food on a scale from 1 (*dislike*) to 8 (*like*). A blue box appeared around their selection. Participants were told, truthfully, that we would randomly select and enact one trial at the end of the experiment. If the participant's rating for that randomly chosen food was 4 or lower, they would not receive the food, but if their rating was 5 or higher, they would receive the food. This technique encourages participants to honestly state their preferences by rendering their choices incentive compatible (cf. Hare et al., 2009).

After making each rating, participants were presented for 2 sec with what they believed was the average rating made by the last 200 Stanford undergraduate participants. This rating appeared as a red box around a number on the scale. If the participant's rating was identical to the group's rating, the word "Agree" appeared above the box. Otherwise, an integer appeared (e.g., "−2") to indicate the difference between the group's rating and their own. In actual fact, we manipulated group ratings to produce three norm conditions. On approximately one third of trials, foods were rated 1, 2, or 3 scale points lower by the group than the participant (peers lower). On approximately one third of trials, group ratings were the same as those provided by the participant (peers agree). On approximately one third of trials, group ratings were 1, 2, or 3 points above the participant's rating (peers higher).

Approximately 5 min after feedback trials, participants completed 150 follow-up trials (also evenly split into two blocks), which involved rerating each food on the same scale they used in feedback trials. A green box appeared around participants' follow-up ratings. Unlike the first block of feedback trials, no group ratings were provided during follow-up trials.

Behavioral Data Acquisition and Analysis

We presented stimuli and collected participants' ratings using Matlab's PsychToolbox extension (www.mathworks.com; Kleiner, Brainard, & Pelli, 2007). We used a paired-samples t test at the participant level to assess whether participants' initial ratings for unhealthy and healthy foods differed during feedback trials. To test whether group norms in feedback trials affected participants' subsequent ratings in follow-up trials—and especially to test if individuals conformed to group opinions during these trials—we conducted a mixed effects analysis of participants' follow-up ratings on the trial level using the lme4 and lmerTest packages in R (www.r-project.org; Bates, Maechler, Bolker, & Walker, 2014; Kuznetsova, Brockhoff, & Christensen, 2014; R Core Team, 2014). We removed trials on which participants failed to provide initial or follow-up ratings (total of 66 trials, mean of 3.14 per participant) to ensure that all trials had all relevant data for the mixed effects model. With follow-up rating as the response variable, we entered group norm condition (i.e., peers lower, peers agree, and peers higher) as a fixed effect and participant as a random effect. We also entered participants' initial ratings for each trial as a fixed effect covariate to ensure that our dependent measure of interest—participants' conformity to group norms—was not influenced by differences in participants' initial preferences for foods in each condition. This approach is also used to control for the potential influence of regression to the mean on analyses of follow-up ratings (cf. Izuma & Adolphs, 2013). More specifically, the principle of regression to the mean suggests that foods that received very high or very low initial ratings should receive follow-up ratings that are closer to participants' average ratings. By including initial ratings as covariates in analyses of follow-up ratings, we statistically minimize this influence: The effect of group norms must explain variance in follow-up ratings beyond differences in initial ratings. We then constructed a second mixed effects model to examine whether the effect of group ratings on participants' follow-up ratings differed based on the healthfulness of foods. This model was equivalent to the previous one, but it also included terms for healthfulness and the Condition × Healthfulness interaction as fixed effects.

We also analyzed behavioral ratings on the participant level. We assessed if group norms influenced whether participants were likely to increase, decrease, or not change their rating from initial to follow-up rating. As in the mixed effects model, we removed trials that were missing either of these ratings. We then computed participants' shift rates by calculating the percentage of trials within each condition for which they decreased, increased, or did not change their rating. If social norms influenced the value participants assigned to foods in follow-up ratings, we expected them to be most likely to decrease their ratings in the peers lower condition, increase their ratings in the peers higher condition, and not change their rating in the peers agree condition.

To quantify individual differences in participants' tendency to conform to group ratings, we computed behavioral conformity scores for each participant. Drawing upon methods used by Klucharev et al. (2009), we calculated the Pearson's r correlation coefficient between (a) the difference between the group's ratings and the participant's initial ratings and (b) the difference between the participant's follow-up ratings and their initial ratings. These correlation coefficients were computed across all trials within each participant. We then transformed raw scores to z scores using Fisher's (1921) r to z transformation to ensure that coefficients were normally distributed for subsequent analyses. High behavioral conformity scores indicate that a particular participant showed a strong tendency to shift their follow-up ratings toward group ratings on a trial-by-trial level.

fMRI Data Acquisition, Processing, and Analysis

Participants were scanned at Stanford's Center for Cognitive and Neurobiological Imaging using a 3-T GE Discovery fMRI. Images were gradient-echo, echoplanar T2-weighted (EPI) scans. Volumes were acquired continuously every 2 sec and comprised 46 axial slices of 2.9-mm thickness. Participants completed two runs of feedback trials and two runs of follow-up trials. A T1-weighted structural image was captured between the feedback and follow-up runs.

We discarded the first six volumes of each run (12 sec of fixation) and completed standard preprocessing using SPM8 (Wellcome Department of Cognitive Neurology, London, UK), including correction for slice time and head motion. Functional volumes were realigned to the anatomical image, spatially normalized to the standard MNI-152 template by segmenting the anatomical image and smoothed using a Gaussian kernel with an FWHM of 6 mm.

We analyzed neuroimaging data in Neuroelf (www.neuroelf.net) using general linear models (GLMs) where events were modeled as epochs convolved with canonical hemodynamic response functions. We used Neuroelf's per-subject GLM function to concatenate runs within each subject before modeling subjects as random effects. All GLMs included motion parameters as regressors of no interest to statistically remove motion-related variance and a high-pass filter of 128 sec to remove low-frequency noise. We also modeled noncritical parts of each trial and trials in which participants did not respond within the 3-sec response window as regressors of no interest to ensure that only the intertrial interval was treated as baseline for each GLM. All statistical maps were restricted to a gray matter mask provided by Neuroelf. We calculated a significance threshold through a whole-brain Monte Carlo simulation implemented via Neuroelf's Alphasim function. This simulation indicated that clusters comprising at least 25 contiguous voxels at a voxel-wise statistical threshold of $p < .005$ corresponded to a corrected false discovery rate of <5%.

Neural Responses to Healthfulness during Initial Image Viewing

Our first analysis explored neural responses to foods before participants observed group preferences. We constructed a GLM that modeled the 3-sec window during feedback trials in which participants initially viewed and rated foods, splitting trials into two conditions according to healthfulness. We then identified clusters that responded to the healthfulness of foods using an unhealthy > healthy contrast.

Neural Responses to Group Feedback

We next analyzed the 2-sec window during which participants learned how their ratings compared to their peers' ratings. We identified regions that were preferentially engaged by consensus, compared to disagreement (i.e., more active when peers learned that their ratings agreed, as compared to disagreed, with the group's ratings). Consensus was modeled by contrasting peers agree > peers higher + peers lower conditions. We also identified regions that preferentially responded to the experience of group disagreement using a disagree > consensus contrast (i.e., peers higher + peers lower > peers agree).

Our neural model of social influence posits that people experience consensus with others as rewarding. Hence, people conform to group norms to maximize this experience of reward. As such, we hypothesized that participants who experience consensus as more rewarding will show a greater tendency to conform to group ratings. To test this hypothesis directly, we correlated participants' neural responses to consensus with their tendency to conform behaviorally. In particular, the aforementioned consensus > disagreement contrast revealed that a cluster within the NAcc responded to consensus, as compared to disagreement, at the group level (see Results). As such, we tested whether the strength of this NAcc response to consensus correlated with behavioral conformity at a participant-by-participant level. To do so, we extracted parameter estimates representing each participant's NAcc response to consensus and correlated these estimates with participants' behavioral conformity scores (see above for details on calculating behavioral conformity scores).

Neural Responses to Foods during Follow-up Trials

To test whether peer preferences shifted neural as well as behavioral responses to foods, we conducted a whole-brain analysis of the 3-sec period in which participants rerated foods in follow-up trials. We examined activity while participants rerated foods initially paired with peers higher, as compared to peers lower, group feedback, to isolate brain regions whose activity tracked peer preferences (i.e., using a peers higher > peers lower contrast). Note that this analysis was run during follow-up trials, in which group feedback was not displayed. As such, results from this analysis reveal the residual effects of peer preferences on individuals' brain activity after a delay.

We complemented this whole-brain approach with an ROI analysis that tested whether peer preferences modulated activity in prefrontal areas more generally responsive to reward. We used the neuroimaging meta-analysis website of NeuroSynth (www.neurosynth.org) to identify brain regions that are significantly associated with the term "reward." The resulting meta-analysis of 329 studies produced a statistical map that included 49 significant activations throughout the brain. We focused our analyses on the vMPFC by constructing 6-mm spheres around the two most ventral maxima that were located within the medial frontal gyrus and were within 10 mm of the midline

(10 > x coordinate > −10). We then extracted beta estimates of neural activity in these independently defined ROIs while participants rerated foods in follow-up trials, and we compared ROI activity in response to foods previously paired with peers higher, as compared to peers lower, feedback using paired-samples t tests.

To assess whether peer ratings and healthfulness interact to predict neural activity, we constructed a second GLM in which we split follow-up trials into six [3 (Group norm: peers lower vs. peers agree vs. peers higher) × (2 Healthfulness unhealthy vs. healthy)] conditions. We extracted resulting beta estimates of neural activity from the vMPFC clusters identified through (a) the first peers higher > peers lower whole-brain contrast and (b) the two clusters identified by the NeuroSynth ROI approach described above. We then analyzed estimates of vMPFC activity during food rerating periods in these three clusters using a 2 (Group norm: peers higher vs. peers lower) × 2 (Healthfulness: unhealthy vs. healthy) repeated-measures ANOVA. As in our behavioral analyses, we statistically controlled for participants' own initial ratings by adding them as a trial-by-trial parametric regressor of no interest in both GLMs.

The above GLMs assessed general effects of group norm conditions on subsequent brain activity while participants rerated foods. However, they do not isolate changes in brain activity that specifically accompany shifts in participants' behavioral responses. For instance, the above analyses do not identify brain activity that reflects an individual's increased rating of a food that she believes is popular among her peers. To isolate such activity, we created a third GLM that models neural activity during follow-up trials as a function of both (i) group norms condition during feedback trials (i.e., peers lower, peers agree or peers higher) and (ii) whether or not participants conformed behaviorally to that norm during follow-up trials. Hence, we split peers lower trials into peers lower + rating decreased and peers lower + rating not decreased conditions, we split peers agree trials into peers agree + rating not changed and peers agree + rating changed trials, and peers higher trials were split into peers higher + rating increased and peers higher + rating not increased trials.

We used this GLM to test two questions. First, we tested whether changes in vMPFC activity during follow-up trials were related to changes in participants' behavioral ratings. We found that vMPFC responses to foods in the peers higher condition were increased compared to foods in the other two conditions (see Results). Consequently, we focused our analyses on the peers higher condition to test whether this effect related to changes in participants' reported preferences for each food. If vMPFC activity indeed tracks participants' preferences—and if group norms shift both vMPFC activity and preferences simultaneously—we would expect increased vMPFC activity specifically on trials when participants were rerating foods that they believed their peers liked and that they reported liking more after learning about their peers' preference. Operationally, this means that we would expect vMPFC to be higher for peers higher + rating increased trials than for peers higher + rating not increased trials. To test this hypothesis, we performed a peers higher + rating increased > peers higher + rating not increased contrast on this GLM.

Second, we used this GLM to test whether vMPFC activity during follow-up trials truly tracks participants' subjective value of foods or whether it tracks the experience of consensus with peers. This experiment allowed us to empirically test whether vMPFC activity reflected participants' updated valuation of each food or the experience of merely providing ratings that were aligned with those of their peers Separating these two potential explanations sheds light on the psychological mechanisms that produce our results. If vMPFC activity tracks the value of foods—not the experience of consensus—we would expect vMPFC activity to be higher for peers higher + rating increased trials (i.e., trials on which participants increased their valuation of the food and provided ratings that aligned with their peers) than for peers agree + rating not changed trials (i.e., trials on which participants did not update their valuation of the food but still provided ratings that aligned with the group norm). To test this hypothesis, we conducted a peers higher + rating increased > peers agree + rating not changed contrast.

RESULTS

Behavioral Results

Participants' initial ratings did not differ between healthy and unhealthy foods [$t(20) = -0.59, p = .56$]. However, as hypothesized, participants' follow-up ratings shifted in the direction of peer ratings. A trial-level mixed effects model of participants' follow-up ratings yielded a significant effect of Group norm ($p < .001$; Figure 2A, Table 1). Participants' follow-up ratings were lowest for foods in the peers lower condition ($M = 4.28$), higher for foods in the peers agree condition ($M = 4.42$), and highest for foods in the peers higher condition ($M = 4.46$). When healthfulness was added as a factor to the mixed model, the effect of Group norm remained ($p < .001$, Table 1), but no effect of healthfulness or Healthfulness × Norm interaction emerged (ps > .12, Figure 2B). Hence, peer preferences shifted participants' reported preferences for unhealthy foods just as strongly as for healthy foods.

As expected, the participant level analysis of shift direction showed that participants were most likely to decrease their ratings for foods in the peers lower condition, not change their ratings in the peers agree condition, and increase their ratings for foods in the peers higher condition (Table 2).

Neural Responses during Initial Food Viewing

Interestingly, although participants reported equal initial preferences for unhealthy and healthy foods, the contrast

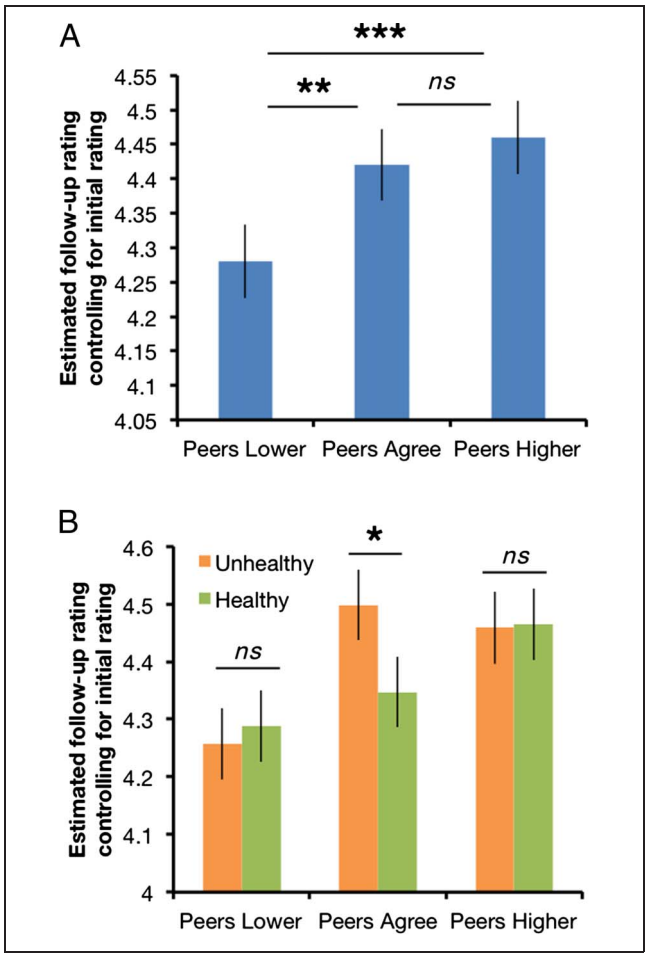

Figure 2. Behavioral results showing that participants' follow-up ratings are modulated by previous exposure to group norms. (A) Participants' follow-up ratings shifted to resemble peer ratings: Foods in the peers lower condition were rated lower than those in the peers agree condition, and foods in the peers higher condition received the highest ratings. (B) Peer ratings have equivalent influence participants' follow-up ratings for both unhealthy and healthy foods. Error bars represent *SEM*. Estimated marginal means and *SEM*s were estimated from mixed model analyses, and both models statistically controlled for participants' initial ratings (***, $p < .001$; **, $p < .01$; *, $p < .05$; *ns*, $p > .05$).

Table 2. Mean Proportion of Trials in Each Condition for Which Participants Decreased, Did Not Change, or Increased Their Ratings from Initial to Follow-up Ratings

Condition	*Rating Decreased*	*Rating Unchanged*	*Rating Increased*
Peers lower	37.19%	50.39%	12.42%
Peers agree	26.28%	61.23%	12.49%
Peers higher	28.32%	50.41%	21.27%

of unhealthy > healthy while participants initially viewed foods revealed a significant cluster of activity in the vMPFC (see Figure 3 and Table 3 for all regions). Hence, participants evinced increased vMPFC activity while initially viewing unhealthy foods, as compared to healthy foods.

Neural Responses to Group Feedback

The consensus > disagreement contrast of neural activity while participants observed group ratings revealed a large cluster of increased activity in the NAcc (Figure 4A, B; Table 4). Furthermore, consensus-related NAcc activity correlated with behavioral conformity scores across individuals [$r(19) = .52$, $p = .02$; Figure 4C]. That is, the strength of individuals' NAcc responses to consensus predicted their tendency to conform to peer ratings. The disagreement > consensus contrast produced significant clusters in the right superior frontal gyrus, bilateral superior parietal lobule, and right precuneus (Figure 5; Table 4).

Neural Responses to Foods during Follow-up Trials

A whole-brain analysis revealed a cluster in the vMPFC that responded more while participants rerated foods that the group previously rated positively than while

Table 1. Results of Trial-level Mixed Effect Models Showing the Effects of Condition and Healthfulness on Participants' Follow-up Ratings, Controlling for Their Initial Ratings

Predictor	*F*	*df*	*p*
Model Not Including Healthfulness			
Group norm condition	8.30	(2, 3062.57)	<.001*
Initial rating	11,049.36	(1, 2941.87)	<.001*
Model Including Healthfulness			
Group norm condition	8.23	(2, 3059.57)	<.001*
Healthfulness	1.42	(1, 3057.01)	.23
Condition × Healthfulness interaction	2.14	(2, 3057.46)	.12
Initial rating	11,080.78	(1, 2938.07)	< .001*

Degrees of freedom estimated using Satterthwaite approximation.

* $p < .001$.

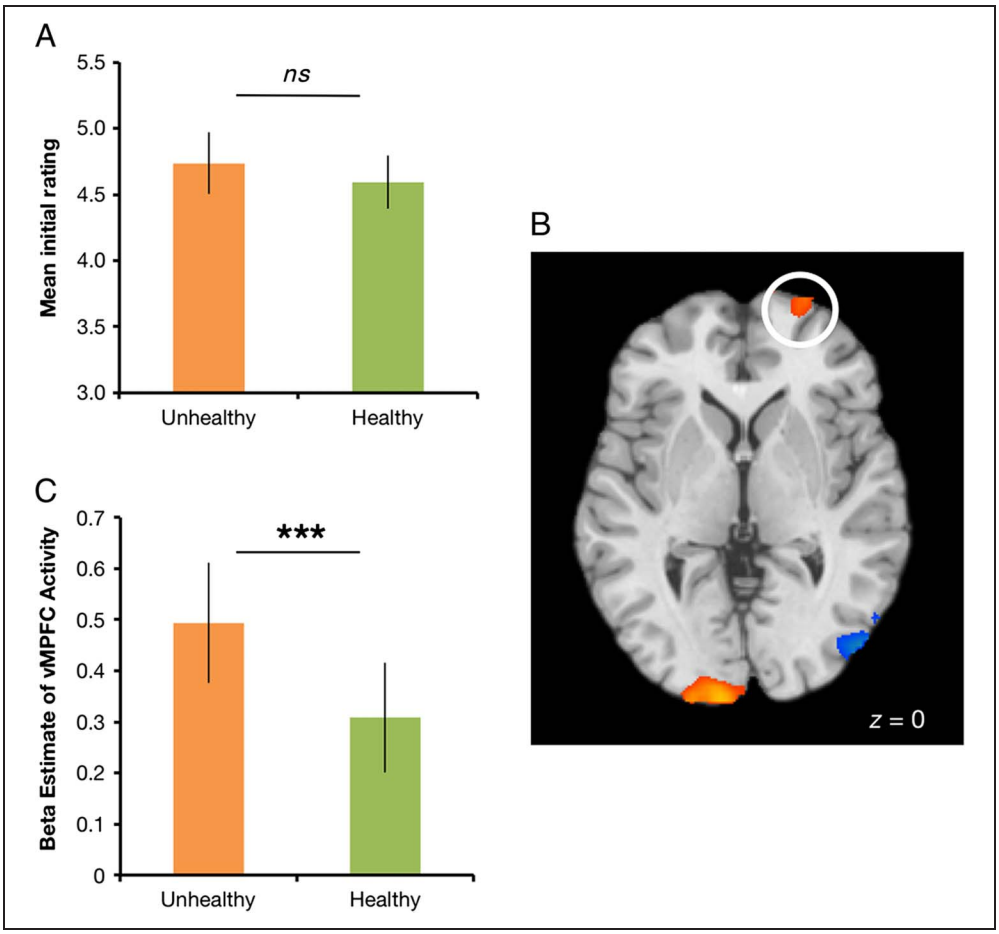

Figure 3. Comparisons of behavioral and neural responses to healthy and unhealthy foods during feedback trials. (A) Mean initial behavioral ratings for unhealthy and healthy ratings, showing no significant difference (*ns*, $p > .05$). (B) Regions preferentially active when participants view unhealthy foods, compared to healthy foods, with a significant cluster of the vMPFC highlighted (peak voxel MNI coordinates: 27, 69, 0). (C) Beta estimates of activity in the vMPFC cluster while participants view unhealthy and healthy foods (***, $p = .001$). Error bars represent *SEM*.

they viewed foods that were rated less positively (peers higher > peers lower; Figure 6A; Table 5). Note that this analysis pertains to follow-up trials, during which individuals did not observe group ratings, and it also controls for individuals' initial ratings. As such, activity revealed by this contrast likely represents neural responses because of prior group feedback, rather than currently displayed social information or the characteristics of foods in each condition. Conversely, a whole-brain peers lower > peers higher contrast revealed no significant clusters.

Table 3. Brain Areas that Respond Preferentially to Unhealthy, as Compared to Healthy, Foods during Feedback Trials (Unhealthy > Healthy Contrast)

Region	*Volume (vox)*	*MNI Coordinates*			*t*
		x	*y*	*z*	
vMPFC	30	27	69	0	4.16
Middle occipital gyrus	122	51	−78	−3	−5.44
Lingual gyrus/inferior occipital gyrus	358	−15	−105	−15	6.70

t values are maxima for each cluster, as computed by Neuroelf.

Corroborating this whole-brain analysis, two independently defined vMPFC areas associated with "reward" (identified through NeuroSynth) responded more strongly to foods previously associated with positive group ratings (the peers higher condition) than those previously associated with negative group ratings (the peers lower condition). This effect was significant in one independently defined cluster (MNI coordinates = 4, 52, −12; $t(20) = 2.49$, $p = .02$; Figure 6B), and there was a similar (though nonsignificant) trend in the same direction for the second cluster (MNI coordinates = −6, 56, −10; $t(20) = 1.68$, $p = .11$). Thus, a meta-analytic approach supports the hypothesis that participants evinced greater vMPFC activity when rerating popular foods, as compared to unpopular foods.

We also tested whether the effect of group feedback on activity in the vMPFC depended on the healthfulness of foods. Repeated-measures ANOVAs on the cluster identified through the whole-brain peers higher > peers lower contrast revealed a significant effect of Group norm [$F(1, 20) = 13.63, p = .001$] but no effect of Healthfulness [$F(1, 20) = 1.25, p = .28$] or Norm × Healthfulness interaction [$F(1, 20) = 0.98, p = .33$]. ANOVAs on activity in the two NeuroSynth ROI clusters also produced no significant effects of Healthfulness or Norm × Healthfulness interactions (*p*s > .35; Table 6). Hence, peer preferences

appeared to have equivalent effects on brain activity in response to both healthy and unhealthy foods.

We next tested whether the effects of group norms on behavioral ratings and vMPFC activity were related to each other using a GLM that split trials depending on whether participants behaviorally conformed versus did not conform (see Methods). The peers higher + rating increased > peers higher + rating not increased contrast revealed a cluster in the vMPFC. Although this cluster failed to pass cluster level correction, it was within proximity of the cluster revealed by the whole-brain peers higher > peers lower contrast (see Figure 7A; Table 7). For completeness, we performed a peers lower + rating not decreased > peers lower + rating decreased contrast and found no significant clusters in the vMPFC.

We then used this GLM to test whether vMPFC activity during follow-up trials represented changes in valuation, rather than experiences of consensus with one's group after updating one's ratings. The peers higher + rating increased > peers agree + rating not changed contrast revealed a robust cluster in the vMPFC that passed cluster level correction (Figure 7B; Table 7). Given that these contrasts rely on a small subset of trials in each condition, they are likely underpowered and should be interpreted cautiously. Nonetheless, they provide interesting exploratory evidence for brain–behavior relationships. Specifically, these results suggest that vMPFC activity tracks participants' updated value of foods following exposure to group norms. We also conducted a peers agree + rating not changed > peers lower + rating decreased contrast and found no significant differences in activity in the vMPFC.

DISCUSSION

These data demonstrate that social norms can shift individual preferences for even a primary reward—food—and elucidate the neural mechanisms driving such conformity. Participants evinced increased NAcc activity when they experienced consensus with a group than when they disagreed with the group, and the strength of this response predicted their tendency to shift their

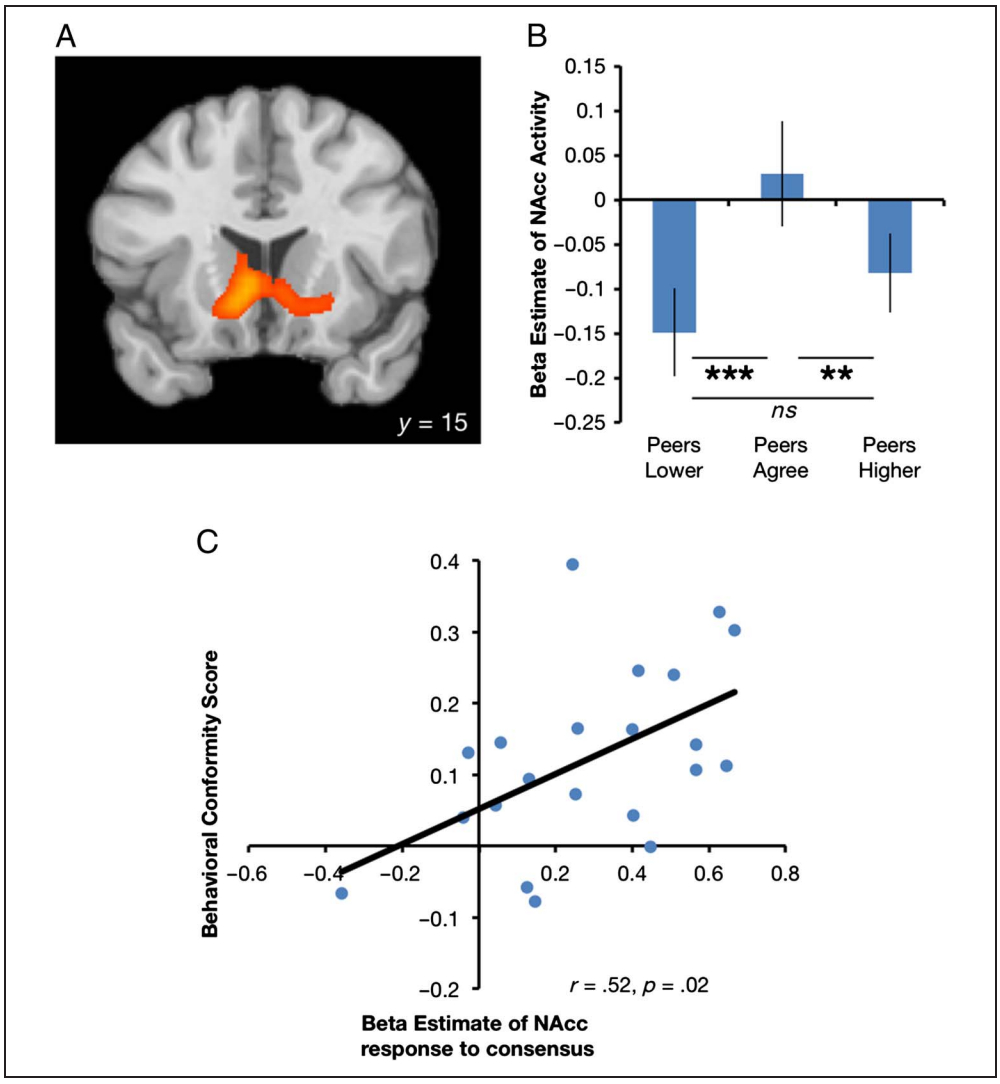

Figure 4. Neural response to group consensus, compared to disagreement, during feedback trials and its relationship with behavioral conformity. (A) Results of the consensus > disagreement contrast. The NAcc region is more active when participants experience consensus than disagreement with group norms (peak voxel MNI coordinates: −6, 15, −3; *ns*, $p > .05$). (B) Beta estimates of activity in the NAcc cluster while participants view feedback in each condition; error bars represent *SEM*. ***, $p < .001$; **, $p < .01$; (C) Participant level correlation between NAcc activity from the consensus > disagreement contrast and their behavioral conformity (see Methods for details on calculating behavioral conformity scores).

Table 4. Brain Areas that Respond Preferentially to Consensus or Disagreement while Viewing Group Ratings in Feedback Trials

		MNI Coordinates			
Regions	*Volume (vox)*	*x*	*y*	*z*	*t*
Consensus > Disagreement					
NAcc	253	−6	15	−3	5.59
Insula	30	36	6	9	4.41
Postcentral gyrus	45	54	−12	54	4.66
Postcentral gyrus	56	−48	−12	60	5.10
Superior temporal gyrus	29	51	−15	−9	3.74
Inferior parietal lobule	101	−66	−33	33	5.03
Middle temporal gyrus	85	−60	−36	0	4.30
Superior temporal gyrus	268	72	−39	18	6.71
Superior temporal gyrus	25	72	−39	3	4.05
Disagreement > Consensus					
Superior frontal gyrus	64	27	6	54	4.02
Precuneus/superior parietal lobule	674	27	−54	39	6.98
Superior parietal lobule	120	−27	−54	42	4.66
Cerebellum	25	−36	−63	−42	3.98

t values are maxima for each cluster, as computed by Neuroelf.

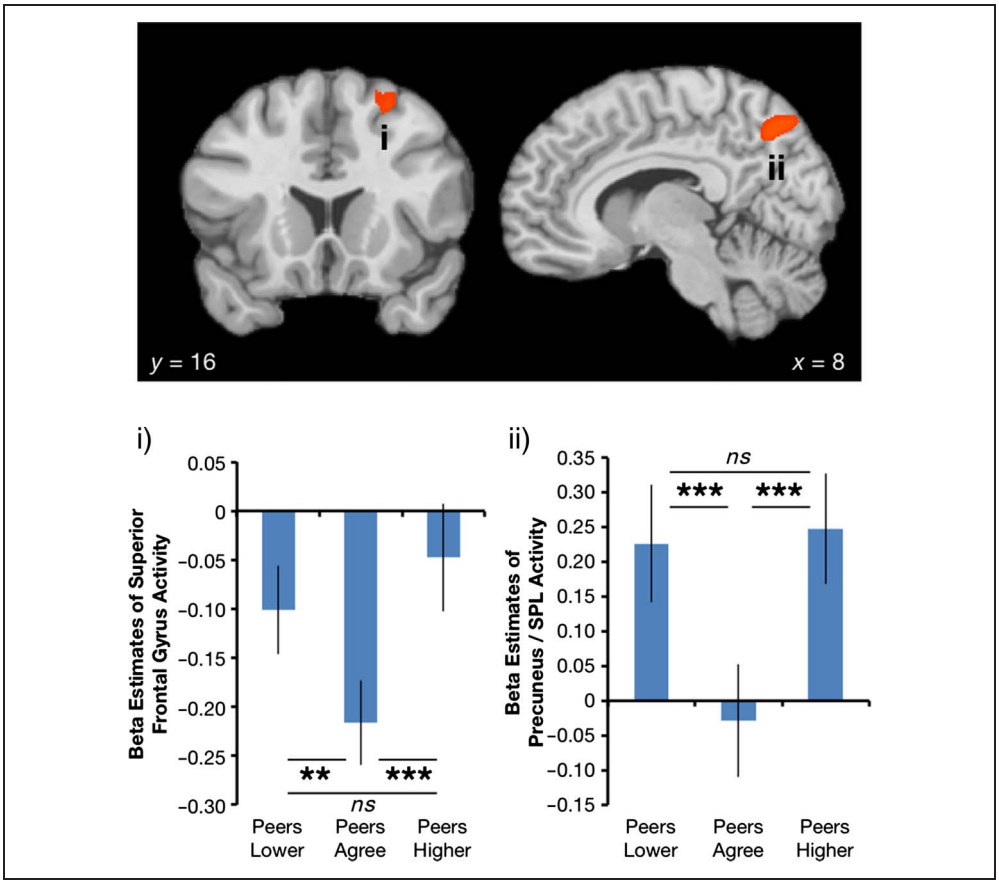

Figure 5. Neural responses to group disagreement, compared to consensus, during feedback trials. Results of the disagreement > consensus contrast. Clusters are located in right superior frontal gyrus (i; peak voxel MNI coordinates: 27, 6, 54) and right precuneus (extending into superior parietal lobule (SPL; peak voxel MNI coordinates: 27, −54, 39). (i) Beta estimates of activity in the right superior frontal gyrus cluster while participants view feedback in each condition; error bars represent *SEM*. (ii) Beta estimates of activity in the right precuneus/superior parietal lobule while participants view feedback in each condition; error bars represent *SEM* (***, $p < .001$; **, $p < .01$; *ns*, $p > .05$).

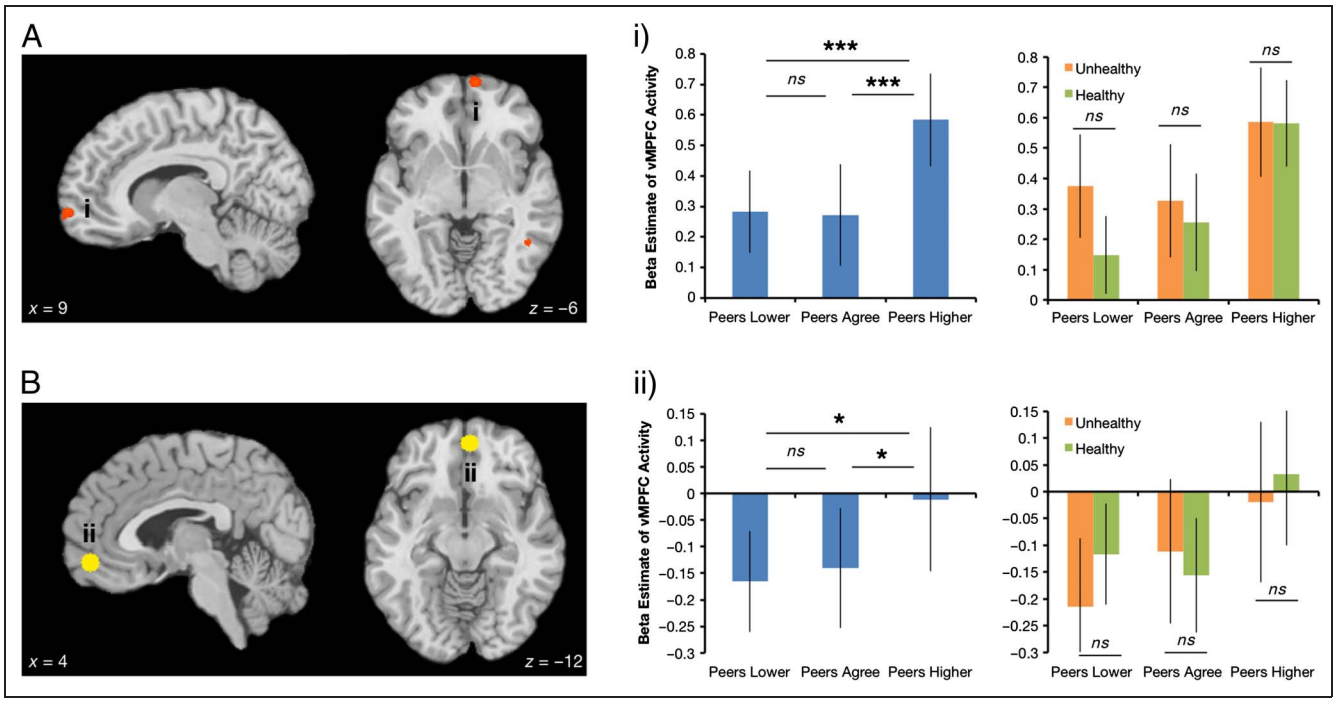

Figure 6. Whole-brain and ROI analyses showing that previous exposure to group norms modulates vMPFC activity during follow-up trials. (A) Results of the whole-brain contrast showing regions more responsive to foods during follow-up trials that were previously rated higher by peers than those rated lower by peers. (i) Beta estimates of vMPFC cluster activity attained from the whole-brain analysis (peak voxel MNI coordinates: 9, 66, −6) displayed by group norm condition and split by the healthfulness of foods. (B) vMPFC ROI attained from a "reward" NeuroSynth meta-analysis. (ii) Beta estimates of activity in the vMPFC ROI (center voxel MNI coordinates: 4, 52, −12) again displayed by group norm condition and split by healthfulness. Error bars represent *SEM* (***, $p < .001$; *, $p < .05$; *ns*, $p > .05$).

preferences to match group norms. However, participants not only shifted their reported ratings to fit those of their peers, but whole-brain and ROI analyses reveal that they engaged vMPFC more strongly while viewing popular, as compared to unpopular, foods.

Our findings that (a) group consensus is associated with relatively more NAcc activity than disagreement and (b) that the strength of this signal predicts behavioral conformity are congruent with reward learning models of social influence (e.g., Klucharev et al., 2009). As such, these data may suggest that individuals conform because agreement with others is experienced as valuable (cf. Baumeister & Leary, 1995), and conformity maximizes

Table 5. Brain Areas that Are More Active while Participants Re-rated Foods Previously Rated Higher by Peers than Those Later Lower by Peers during Follow-up Trials (Peers Higher > Peers Lower Contrast)

		MNI Coordinates			
Region	*Volume (vox)*	*x*	*y*	*z*	*t*
vMPFC	43	9	66	−6	3.84
Cerebellum	27	−36	−42	−27	3.60
Inferior temporal gyrus/fusiform	45	45	−51	−9	4.15

t values are maxima for each cluster, as computed by Neuroelf.

Table 6. Results of Repeated-measures ANOVAs on Neural Activity in vMPFC Clusters while Participants Re-rated Foods during Follow-up Trials

	MNI Coordinates				
Region	*x*	*y*	*z*	*F*	*p*
Main Effect of Group Norm					
$vMPFC_{higher > lower\ contrast}$	9	66	−6	13.63	.001*
vMPFC ROI	4	52	−12	6.69	.02*
vMPFC ROI	−6	56	−10	3.20	.09#
Main Effect of Healthfulness					
$vMPFC_{higher > lower\ contrast}$	9	66	−6	1.25	.28
vMPFC ROI	4	52	−12	0.90	.35
vMPFC ROI	−6	56	−10	0.29	.60
Norm × Healthfulness Interaction					
$vMPFC_{higher > lower\ contrast}$	9	66	−6	0.98	.33
vMPFC ROI	4	52	−12	0.09	.76
vMPFC ROI	−6	56	−10	0.75	.40

* $p < .05$.

# $p < .10$.

opportunities for such reward. Furthermore, the correlation between NAcc activity and behavioral conformity supports the ideas that individuals differ in the extent to which they value consensus and that this variance tracks individual levels of conformity. A reward model has been used to explain how social influence shapes aesthetic preferences for artistic designs, music, and the attractiveness of others (e.g., Izuma & Adolphs, 2013; Zaki et al., 2011; Campbell-Meiklejohn, Bach, Roepstorff, Dolan, & Frith, 2010; Klucharev et al., 2009). Here we extend this growing literature by demonstrating that peer attitudes are powerful enough to shift evaluations of and neural responses to even primary rewards such as foods.

It is worth noting that this pattern of results could either reflect increased NAcc responsivity to agreement or decreased responsivity to disagreement. Although our design does not include the control conditions necessary to adjudicate between these interpretations, both are of interest conceptually. Positive prediction error would imply that agreement with group norms is experienced as rewarding and people conform to maximize this reward. Negative prediction errors suggest that individuals experience unanticipated disutility in response to group disagreement and thus conform to correct their behavior so it agrees with peer opinions. This second interpretation also carries the intriguing implication that individuals generally expect others to agree with them—consistent with classic social psychological work on the false consensus effect (Ross, Greene, & House, 1977)—and are unpleasantly surprised by disagreement. Adjudicating between these possible explanations should be a target of future research.

Group norms also modulated both self-reported and neural responses to foods in follow-up trials. Critically, our data suggest that the behavioral and neural effects of group norms are not only parallel but actually related to each other: vMPFC activity was highest for trials on which participants increased their behavioral ratings to conform to the peers higher group norm. These results suggest that group norms are capable of shaping participants' *internal evaluation* of stimuli, supporting findings from previous research on facial attractiveness and music (Zaki et al., 2011; Campbell-Meiklejohn et al., 2010). Our discovery that this pattern also occurs in foods implies that prior studies showing that social norms shift eating behaviors likely reflect changes in individuals' subjective preferences for foods, not simply their transient public compliance with social norms (Robinson et al., 2014; Robinson, Blissett, & Higgs, 2013; Robinson & Higgs, 2012).

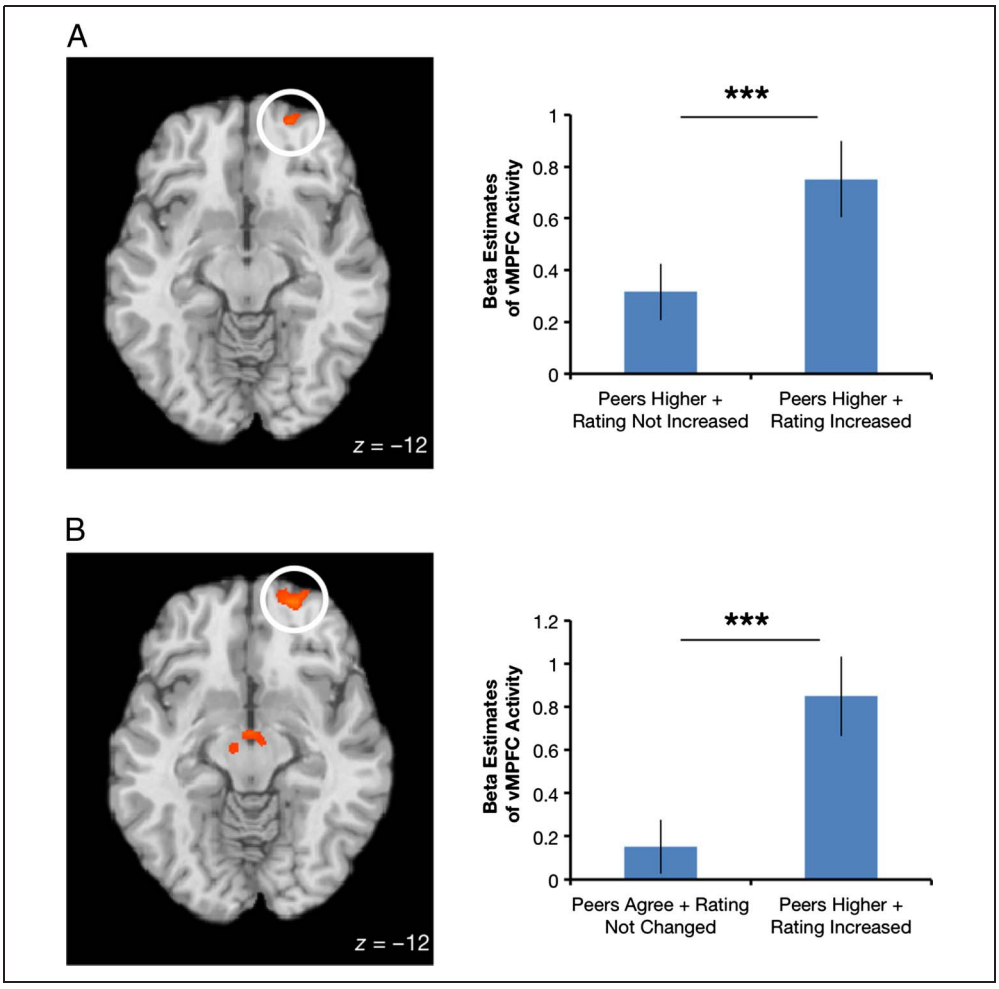

Figure 7. Neural responses while rerating foods during follow-up trials, where trials are split both by peer norms and participants' behavioral responses (the peers higher + rating increased > peers higher + rating not increased and the peers higher + rating increased + peers agree + rating not changed contrasts). (A) Results of the peers higher + rating increased > peers higher + rating not increased contrast. The vMPFC cluster was more active when participants increased their rating for foods they believed their peers like than when they did not increase their rating for those foods (peak MNI coordinates: 21, 57, −12). (B) Results of the peers higher + rating increased > peers agree + rating not changed contrast. The vMPFC cluster was more active when participants increased their rating to match the peers higher norm than when they did not change their rating to match the peers agree norm (peak MNI coordinates: 21, 57, −12; ***, $p < .001$).

Table 7. Brain Regions that Are More Active while Re-rating Foods in the Peers Higher Condition for which Participants Increased Their Ratings than When They (A) Did Not Increase Their Ratings for Foods in This Condition and (B) Maintained Their Rating for Foods in the Peers Agree Condition

Region	Volume (Vox)	MNI Coordinates			t
		x	y	z	
Peers Higher + Rating Increased > Peers Higher + Rating Not Increased					
vMPFC	10	21	57	−12	4.09
Thalamus	50	−18	−25	12	5.54
Inferior parietal lobule	65	−48	−33	57	4.51
Peers Higher + Rating Increased > Peers Agree + Rating Not Changed					
vMPFC	42	21	57	−12	4.64
Thalamus	39	6	−15	−9	4.09
Thalamus	53	−18	−21	12	4.42
Supramarginal gyrus/ inferior parietal lobule	47	−36	−39	36	4.85
Cerebellum	123	−36	−63	−36	5.16

t values are maxima for each cluster, as computed by Neuroelf.

These findings dovetail with prior demonstrations of functional dissociation between vMPFC and NAcc in responding to the reward value of stimuli (Hare, O'Doherty, Camerer, Schultz, & Rangel, 2008). Specifically, we found that the NAcc responded to group consensus but was not modulated by peer preferences, whereas the vMPFC was modulated by peer preferences but was not sensitive to consensus. Such a pattern supports the assertion that NAcc activity reflects prediction errors—in this case, to novel information about (dis)agreement with groups—whereas activity in medial vMPFC tracks goal values—in this case, the subjective value individuals assign to foods. Similarly, Falk et al. (Falk, Berkman, Whalen, & Lieberman, 2011; Falk, Berkman, Mann, Harrison, & Lieberman, 2010) show that individual differences in vMPFC activity (not NAcc activity) predict future compliance to persuasive messages. Although persuasive messaging and social influence are not identical psychological phenomena, Falk et al. (2011) suggest that vMPFC activity in their study indexes participants' implicit valuation of the persuasive messages in relation to one's personal goals. Our findings would support this claim, as we find that group norms shift vMPFC activity along with behavioral ratings of liking (i.e., participants' self-reported value).

Interestingly, during initial ratings, unhealthy foods produced more vMPFC activity than healthy foods, although individuals reported liking each type of food equally. Such findings replicate prior demonstrations that vMPFC responses track caloric density and fat content (van der Laan et al., 2011; Grabenhorst, Rolls, & Parris, 2010; O'Doherty, Buchanan, Seymour, & Dolan, 2006; de Araujo & Rolls, 2004; O'Doherty, Deichmann, Critchley, & Dolan, 2002). This finding also connects with prior demonstrations that neural and self-reported indices of preference can dissociate. In particular, Sharot, De Martino, and Dolan (2009) document a case in which striatal activity differentiated between stimuli that individuals claimed to like equally but later judged differentially. Although by no means conclusive, it is possible that our findings represent a similar state of affairs, in which vMPFC activity represents an internal preference for calorically dense foods that participants did not report.

However, after exposure to group norms, we found that this pattern was "overwritten": vMPFC responses at follow-up (after exposure to peer ratings) tracked the popularity and not the healthfulness of foods. This result strengthens the claim that social norms shape the internal valuation of stimuli by modulating activity in regions that process the reward value of stimuli. However, this finding also prompts further research into mechanisms underlying how shifting attention to different stimulus qualities (such as a food's healthfulness, pleasantness, or social desirability) modulates behavioral and neural responses to those stimuli. Researchers have shown that directing attention to the taste or healthfulness of foods can influence activity in vMPFC (Hare et al., 2011; Grabenhorst & Rolls, 2008). Here, we find that informing individuals of the social desirability of foods has similar effects on the vMPFC, suggesting that social desirability influences how people compute the value of primary rewards.

We also observed increased activity in right superior frontal gyrus and precuneus when participants experienced disagreement with group norms, as compared to consensus. Although we did not predict this pattern a priori, it suggests preliminary inferences concerning the role of these regions in responses to social disagreement. In particular, the right superior frontal gyrus is associated with cognitive control processes (Brown, Goltz, Vilis, Ford, & Everling, 2006; Wager & Smith, 2003; Braver & Cohen, 2001), including the control of emotion (Kanske, Heissler, Schönfelder, Bongers, & Wessa, 2011; Kober et al., 2010; Ochsner & Gross, 2005). Likewise, the precuneus is associated with updating social impressions across a number of contexts (Bhanji & Beer, 2013; Mende-Siedlecki, Baron, & Todorov, 2013; Mende-Siedlecki, Cai, & Todorov, 2012; Schiller, Freeman, Mitchell, Uleman, & Phelps, 2009). As such, activity in these regions during disagreement suggests that disagreement might prompt individuals to engage cognitive control and update their representations of peer preferences. However, this interpretation is speculative, and future work should more directly examine neural responses to social disagreement during social influence.

Prior research demonstrates that individual differences in BMI sometimes influence neural responses to foods

(e.g., Ng, Stice, Yokum, & Bohon, 2011; Stice, Spoor, Ng, & Zald, 2009). Given that this study was primarily focused on population level responses to social norms for food preferences, we did not collect detailed data on individual differences in BMI or general eating habits. However, future studies should explore how BMI and other individual differences affect neural and behavioral markers of social influence, as such data may provide interesting insight into why specific individuals may respond more or less strongly to social norms regarding food preferences.

Relatedly, previous research has found that individual differences in neural responses to foods (Demos et al., 2012) and food commercials (Gearhardt, Yokum, Stice, Harris, & Brownell, 2014; Yokum, Gearhardt, Harris, Brownell, & Stice, 2014) can predict future weight gain. Our findings suggest that social influence processes may have contributed to these researchers' results. For example, we found that greater caudate reactivity to consensus with one's peers predicts greater behavioral conformity at a later time, and Yokum et al. (2014) show that greater caudate reactivity to food commercials predicts future weight gain. Hence, participants who show heightened caudate reactivity to food commercials in this study may also be the individuals who consider it normative to consume that food. Demos, Heatherton, and Kelley (2012) find that the same relationship between caudate activity and weight change emerges when participants are looking at static images of foods. Although the absence of peer feedback in their paradigm makes a social influence interpretation indirect, there is an important intersection between this study and our study that should be explored further. Specifically, future research should test whether neural responses to food norms can predict actual eating behavior (and even weight gain) outside the scanner.

In addition to informing basic science models of social influence, these results hold potential translational value, particularly for developing interventions that prevent obesity by promoting healthy eating (Robinson et al., 2014; Cornier, Marshall, Hill, Maahs, & Eckel, 2011). Several studies have shown that social norms influence the quantity of food people consume (Robinson et al., 2014), but less is known about the effects of social influence on preferences for individual foods (Robinson & Higgs, 2012). Hence, our demonstration that social norms "steer" both behavioral and neural responses to foods supports the use of social norms as tools for promoting healthy eating.

Furthermore, our findings suggest methods for best designing these intervention strategies. For example, our data indicate that group norms can shift preferences for both healthy and unhealthy foods, suggesting that intervention strategies may be most effective if they highlight descriptive norms that simultaneously promote healthy foods and devalue unhealthy foods. We also found that participants who demonstrated stronger NAcc activity when experiencing consensus (and thus potentially assign greater value to consensus) were more likely to conform to group norms. Social norm interventions should target these individuals, and researchers should develop complementary methods for engaging individuals who are less driven by consensus.

Future research can expand on these results in at least three ways. First, our participant sample was predominately female, limiting our ability to claim that these results hold across genders. However, prior work has demonstrated similar neural correlates of influence in solely male (Zaki et al., 2011), solely female (Klucharev et al., 2009), and mixed gender samples (Campbell-Meiklejohn et al., 2010), suggesting that the current findings should indeed generalize across genders. Second, if these results are to inform interventions, it is important to establish how long the effects of norms on food preferences last. Huang, Kendrick, and Yu (2014) recently demonstrated that social influence affected ratings of facial attractiveness for up to 3 days. Researchers should conduct similar studies on the stability of social influence over food preferences to establish whether results differ for this stimuli type. Finally, future research should investigate whether modulating preferences for foods in laboratory paradigms like the one reported here can influence real-world eating behaviors.

In all, this study successfully utilized a social influence paradigm to provide a clearer understanding of the mechanisms through which social norms shape food preferences. These data both inform the neuroscientific study of conformity and, in the future, can support the development of efforts to curb diet-related health issues.

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