Neural Evidence for Reduced Apprehensiveness of Familiarized Stimuli in a Mere Exposure Paradigm

2 authors, including:

Yi Zhang
Bridgewater College
8 PUBLICATIONS **67** CITATIONS

Neural Evidence for Reduced Apprehensiveness of Familiarized Stimuli in a Mere Exposure Paradigm

Leslie A. Zebrowitz and **Yi Zhang**
Brandeis University

Abstract

Mere familiarization with a stimulus increases liking for it or similar stimuli ('mere exposure' effects) as well as perceptual fluency, indexed by the speed and accuracy of categorizing it or similar stimuli ('priming' effects). Candidate mechanisms proposed to explain mere exposure effects include both increased positive affect associated with greater perceptual fluency, and also reduced negative affect associated with diminished apprehensiveness of novel stimuli. Although these two mechanisms are not mutually exclusive, it is difficult for behavioral measures to disentangle them, since increased liking or other indices of greater positive affect toward exposed stimuli could result from increases in positive feelings or decreases in negative feelings or both. The present study sought to clarify this issue by building on research showing a dissociation at the neural level in which the lateral orbital frontal cortex (LOFC) is activated more by negatively valenced than by neutral or positively valenced stimuli, with the reverse effect for medial orbital frontal cortex (MOFC). Supporting the reduced apprehensiveness hypothesis, we found lower LOFC activation to familiarized faces and objects (repetition suppression). We did not find evidence to support the positive affect hypothesis in increased activation to familiarized stimuli in MOFC or in other parts of the reward circuit that respond more to positively valenced stimuli (repetiton enhancement), although enhancement effects were shown in some regions.

Mere familiarization with a stimulus has remarkable effects. A large literature shows 'mere exposure' effects, in which familiarization with faces or objects increases liking for them even without explicit recall that they have been previously seen (specific exposure effect, *SEE*; Bornstein, 1989; Zajonc, 1968; 2001). Other research has extensively documented 'behavioral priming' effects, in which familiarization with a stimulus increases the speed and accuracy of naming or categorizing it under impoverished viewing conditions even without explicit recall that it had been previously seen, as in subliminal presentation or amnesia (Lander, Bruce, Smith, & Hancock, 2009; Martin & Greer, 2011; Tulving & Schacter, 1990). Both of these behavioral effects generalize to stimuli that are similar to the familiarized ones (generalized exposure effect, *GEE*/conceptual priming; Gordon & Holyoak, 1983; Koutstaal et al., 2001; Monahan, Murphy, & Zajonc, 2000; Rhodes, Halberstadt, & Brajkovich, 2001; Winkielman, Halberstadt, Fazendeiro, & Catty, 2006; Zebrowitz, White, & Wieneke, 2008). The fact that the effects of stimulus familiarization go beyond responses to the specific stimuli that people have experienced increases the psychological and social ramifications of this phenomenon. For example, mere exposure effects may contribute to greater liking for strangers from an ingroup than an outgroup (Smith, Dijksterhuis, & Chaiken, 2008; Zebrowitz, Bronstad, & Lee, 2007; Zebrowitz, White, & Wieneke, 2008). The goal of the present study was to increase understanding of

Corresponding author: Leslie A Zebrowitz, Brandeis University, Department of Psychology MS 062, Waltham, MA 02454, zebrowitz@brandeis.edu, Phone: 781-736-3263, FAX: 781-736-3291.
Requests for reprints should be sent to Professor Leslie A. Zebrowitz, Department of Psychology, MS 062, Brandeis University, Waltham, MA 02454: zebrowitz@brandeis.edu.

SEE and GEE by investigating neural responses associated with mere exposure to other-race faces as well as novel objects.

The mechanisms underlying the well-established behavioral effects of stimulus familiarization are still not completely understood (Moreland & Topolinski, 2010). Candidates to explain increased liking of exposed stimuli include increases in positive affect associated with increased processing fluency (Reber, Winkielman, & Schwarz, 1998; Topolinski & Strack, 2009) and decreases in negative affect associated with apprehensiveness of novel stimuli (Zajonc, 2001). Although these two mechanisms are not mutually exclusive, it is difficult for liking measures to disentangle them, since increased liking could result from increases in positive feelings or decreases in negative feelings or both. One approach to disentangling the two possible mechanisms has used electromyography (EMG) to assess incipient facial expressions to stimuli, since facial EMG can detect mild affective reactions to subtle stimuli that do not elicit fully developed emotional expressions (Cacioppo, Bush, & Tassinary, 1992; Dimberg, Thunberg, & Elmehed, 2000). Research has shown that both stimulus familiarity and processing fluency increase incipient smiles, as reflected by increased EMG activity over the cheek region, with no effects on incipient frowns, as reflected by increased EMG activity over the brow region (deVries, Holland, Chenier, Starr, & Winkielman, 2010; Harmon-Jones & Allen, 2001; Winkielman,& Cacioppo, 2001; Winkielman, Halberstadt, Fazendeiro, & Catty, 2006). Although these results have been taken to support the positivity of familiarity as opposed to the negativity of novelty, it is possible that a reduction in apprehensiveness would increase incipient smiles. The present study sought to shed additional light on the negativity of novelty and the positivity of familiarity by building on research that has examined neural effects of familiarization.

Previous research on neural effects of familiarization has focused primarily on clarifying the mechanism for priming effects. This work reveals decreased activation to repeated visual stimuli (repetition suppression) in several brain regions with reliable fMRI effects in occipito-temporal cortex, including the fusiform gyrus (e.g., Elliott & Dolan, 1998; Koutstaal et al., 2001; Gobbini & Haxby, 2006). Consistent with a perceptual fluency interpretation of these effects, occipital cortex shows weaker activation to stimuli that are easier to categorize than those made difficult by the addition of noise (Banko, Kortvelyes, Kovacs, & Vidnyanszky, 2011). Many other regions also have reliably shown repetition suppression effects (e.g., Gobbini & Haxby, 2006; Koutstaal et al., 2001), and some research has found that it is repetition suppression in inferior prefrontal and middle frontal regions that predicts behavioral priming effects, such as categorization speed. (Bunzeck et al., 2006; Schacter, Wig, & Stevens, 2007). That effect is consistent with perceptual fluency, inasmuch as it suggests a decrease in controlled processing and greater automatic processing of the familiarized stimuli. Neural attenuation effects have also been shown to generalize to similar stimuli, akin to the behavioral GEE. In particular, activation was lower in temporal, parietal, and posterior cingulate cortex not only for previously seen objects than for novel ones, but also for objects similar to those previously seen (Koutstaal et al., 2001), with comparable effects for previously seen and similar scenes (Blondin & Lepage, 2005).

In addition to evidence for attenuated neural responses to familiarized stimuli, research has also reported *increased* activation to repeated stimuli (repetition enhancement) in temporal, parietal, and inferior frontal cortex as well as anterior cingulate, caudate, and precuneus (Blondin & Lepage, 2005; Henson et al., 2002; James & Gauthier (2006); Koustaal et al. 2001). Although some contextual and stimulus moderators of suppression vs. enhancement effects have been identified, with enhancement shown for stimuli that are low in visual quality, high in perceptual similarity, or non-nameable (James & Gauthier, 2006; Turk-Browne, Yi, Leber, & Chun, 2007), these cannot account for the fact that both effects are

sometimes shown concurrently in different brain regions, and this phenomenon remains an active research question.

Whereas increased automatic processing associated with perceptual fluency could explain behavioral priming effects, it is unclear why it would, in and of itself, explain greater liking in mere exposure effects. A more compelling explanation for the positive affective responses elicited by familiarized stimuli in mere exposure paradigms would involve changes in activation in the 'reward circuit' whose function is to guide goal-related behavioral responses, such as approach and avoidance (Delgado, 2007). The present study focused on the orbito-frontal cortex, which responds differentially to positively and negatively valenced stimuli. Specifically, the lateral orbito-frontal cortex (LOFC) responds more to negatively valenced than neutral or positively valenced stimuli (Cloutier, Heatherton, Whalen, & Kelley, 2008; Liang, Zebrowitz, & Zhang, 2010; Kensinger & Schacter, 2005; O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001), and the medial (MOFC) responds more to positively valenced than neutral or negatively valenced stimuli (Cloutier, et al., 2008; Ishai, 2007; Kampe, Frith, Dolan, & Frith, 2001; Kawabata & Zeki, 2004; Liang et al., 2010; O'Doherty et al., 2003; Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007).

Two possible effects of stimulus familiarization in OFC can be predicted from existing theory. The hypothesis that increased liking for exposed stimuli results from a reduction in negative affect elicited by apprehensiveness of novel stimuli (Zajonc, 2001) suggests that stimulus familiarization should be associated with repetition suppression in LOFC, which responds most to negatively valenced stimuli. The hypothesis that increased liking results either from the misattribution of positive affect associated with perceptual fluency to positive features of the stimulus (e.g., Bornstein & D'Agostino, 1994) or from a direct effect of perceptual fluency on positive affect (e.g., Reber, Winkielman, & Schwarz, 1998; Winkielman & Cacioppo, 2001) suggests that stimulus familiarization should be associated with repetition enhancement in MOFC, which responds most to positively valenced stimuli.[1] Such neural-enhancing effects of stimulus familiarization are plausible given that that stimulus repetition not only can suppress neural activation, but also enhance it, as discussed above. To our knowledge, only one study has reported an effect of stimulus familiarization in OFC. Specifically, repetition of neutral face pairs yielded greater suppression in LOFC than did repetition of fear face pairs, and the magnitude of this effect was positively correlated with the difference in reaction time priming for neutral vs. fear faces (Bentley, Vuilleumier, Thiel, Driver, & Dolan, 2003).

The present research extends the Bentley et al. (2003) finding in four ways. First, whereas Bentley et al. (2003) assessed priming effects, we examined effects of familiarization within a mere exposure paradigm that has reliably influenced liking judgments (Bornstein & D'Agostino, 1992; Zebrowitz, et al., 2008). Second, we examined neural activation in OFC not only to previously seen faces (SEE), but also to novel faces from a previously exposed category (GEE). Third, we extended research on neural mechanisms for SEE and GEE to other race faces. Specifically, we exposed White perceivers to either Black or Korean faces, and then compared neural activation to these faces with activation to novel faces from the exposed racial category (SEE); we also compared activation to novel faces from the exposed category with activation to novel faces from the other racial category (GEE). Finally, we investigated whether any effects of familiarization on changes in OFC activation were

---

[1]While our predictions of LOFC suppression or MOFC enhancement are based on the substantial evidence that the LOFC responds more strongly to negatively valenced than neutral or positively valenced stimuli, while MOFC responds more strongly to positively valenced than other stimuli, it should be noted there are also nonlinear effects, with both regions responding more strongly to stimuli of either valence than to neutral stimuli (Elliott, Newman, Longe, & Deakin, 2003; Krendl et al., 2007; Liang, Zebrowitz, & Zhang, 2009; Winston et al., 2007).

parallel for faces and objects by examining SEE and GEE effects for Chinese characters and polygons.

Method

Participants

A total of 32 Caucasian participants (16 men) were recruited from the greater Boston area and randomly assigned to one of two exposure conditions: Black faces and Chinese characters (BC) or Korean faces and polygons (KP). All were right-handed, between the ages of 18 and 35 (Mean = 23.6), and had normal or corrected to normal eye sight. Participants were compensated with a check for $50 upon finishing the study.

Stimuli

Exposure stimuli for the BC exposure group included 10 Black male faces with neutral expressions and 10 Chinese characters. *Exposure stimuli* for the KP exposure group included 10 Korean male faces with neutral expressions, five 8-sided and five 12-sided polygons. *Generalization stimuli* included an additional 10 novel Black faces, 10 novel Chinese characters, 10 novel Korean faces, and 10 novel 8- and 12- sided polygons. The number of generalization stimuli from each category was equal to that used in previous behavioral studies (Zebrowitz et al., 2008).

Faces were drawn from previous behavioral studies (Zebrowitz, Bronstad and Lee, 2007; Zebrowitz et al., 2008), and matched in attractiveness based on ratings collected in those studies. The Black exposure faces were matched with Korean exposure faces, and the Black generalization faces with the Korean generalization faces. Each face was rotated so that the eyes were on a horizontal axis, and cropped so that the middle of the eyes was at the same position for each image. The polygon stimuli were sampled from a previous mere exposure study (Vanderplas & Garvin, 1959), while the Chinese characters were picked by a native Chinese experimenter to match the polygons on visual complexity.

The mean luminance and contrast of all stimuli were standardized by Matlab 5.2. A scrambled version of each of the exposure stimuli was created by a Matlab algorithm as its own mask during the exposure session.

Experimental Paradigm

Participants were told the study was about visual perception of faces and objects. A research staff member first described the scanning procedures and asked participants to remove all metal objects. After participants signed the consent form, they were given earplugs (29dB rating) and asked to lie down on a foam-padded table in the scanning machine. Those who needed vision correction were fitted with scanner-compatible lenses. A head coil was mounted around their head. They were also given a squeeze ball to communicate with the investigator. Participants were instructed not to move their head during the experiment. They were given the following instructions:

> "Before the scanning begins, we will show you a series of pictures of faces and objects very quickly. There will always be a cross in the center of the screen. Please look at each picture when it appears and look at the cross when there is no picture. This part of the experiment will take about 3 minutes. After this part, we will begin scanning. We will show you more pictures of faces and objects, and your task will be to press one of the buttons to rate how much you like each of them: not much (press button #1); a little (press button #2); quite a bit (press button #3). You will have up to 4 seconds to respond."

During the exposure manipulation, the exposure stimuli (10 Black faces and 10 Chinese characters or 10 Korean faces and 10 polygons) were each presented for 100 ms followed immediately by a scrambled image mask for another 100 ms and then an inter-stimulus interval of 800 ms. This exposure manipulation was repeated 10 times, with a different random order of stimuli for each presentation. The number repetitions was identical to the procedure employed by Zebrowitz et al. (2008) who found significant effects on liking. Lasting for approximately 3 minutes, the exposure manipulation was performed while participants were in the scanner but before scanning began.

Immediately following the exposure manipulation, MRI scanning was conducted while the 40 generalization stimuli were presented randomly mixed with the 20 exposure stimuli that the participant had just seen. The order of the stimuli was pseudo-randomly counterbalanced by Optseq2 (Dale, 1999) with an additional 60 seconds of randomly jittered intervals, including 10 periods of 2 seconds, 4 periods of 4 seconds, and 4 periods of 6 seconds. Additionally, there was equal likelihood of images of each stimulus type appearing before and after images of other stimulus types, counterbalanced across exposure condition. Participants were notified via intercom that they would now be shown stimuli to be rated, and they pressed the squeeze ball to indicate their permission to start the scanning session. Each image was shown for 2 seconds followed by a 4 second inter-stimulus interval, during which time, participants used one of the three keys to rate the likeability of the image.

Data Acquisition

MRI scanning was conducted at the MGH/MIT/HST/Martinos Center. Stimuli were presented by E-Prime version 1.1 running on a Dell Latitude D800 laptop, together with a video projector in the MRI scanning room. The images were back-projected onto the mirror mounted on the head coil. Two hundred and thirteen volumes were acquired on a Siemens 3T Allegra head-only MR Scanner with high-speed imaging gradients, with the first 3 volumes dropped for saturation artifacts. Structural imaging that provides detailed anatomic information included high resolution whole brain RF-Spoiled GRASS images (SPGR; 128 slice sagittal 1 mm $\times$ 1 mm in plane resolution with 1.25 mm thickness). Functional imaging involved an automated shim procedure to improve B0 magnetic field homogeneity and T2*-weighted echo-planar pulse sequences sensitive to BOLD contrast (Kwong et al., 1992). Functional imaging runs consisted of whole-brain acquisitions (TR = 2s, TE = 30 ms, 32 interleaved slices, $3.125 \times 3.125 \times 4$ mm voxels with 4 mm slices). All images were performed using a birdcage transmit/receive head coil.

Imaging Data Analysis

Preprocessing—Using FEAT Version 5.4 (FSL 3.1, 2004) we applied the following pre-statistics processing: motion correction; non-brain removal; spatial smoothing using a Gaussian kernel of FWHM 5 mm; high pass signal cutoff at 50 seconds; and registration to the standard Montreal Neurological Institute (MNI) average template. For motion correction, we used MCFLIRT, a linear registration process that overcomes subtle movements of the brain (http://www.fmrib.ox.ac.uk/fsl/mcflirt/index.html). No participants showed movement above 1 mm in any single dimension throughout the run

GLM modeling—We then performed whole brain individual level analyses on each subject to generate a single statistical map corresponding to 6 regressors representing the response to each stimulus category relative to baseline using GLM within FEAT: exposure face, exposure object, generalization Black, generalization Korean, generalization Chinese character, generalization polygon. Regressors were modeled by convolving a delta function at each event onset with a canonical hemodynamic response function and its temporal derivative.

Exposure contrasts—Two contrasts were computed for each participant to test SEE: previously seen faces vs. novel faces from the same category; previously seen objects vs. novel objects from the same category. Two additional contrasts were computed for each participant to test GEE: novel faces from the exposed category vs. novel faces from the unexposed category; novel objects from the exposed category vs. novel objects from the unexposed category. Main effects of SEE/GEE were determined by mixed-effects analyses performed on the exposure contrasts at the group level using FSL's FLAME. Z (Gaussianised T/F) statistical maps were thresholded using an uncorrected voxel threshold of *P*<.001 (with the exception of a more sensitive threshold of *P*<.01 in the case of GEE for faces in order to detect OFC). Interaction effects of SEE/GEE with exposure condition were tested by mixed-effects analysis using the same threshold as the corresponding main effect. All thresholded statistical maps were submitted to a small-volume correction criterion that used a Monte Carlo simulation (AlphaSim by AFNI) (Ward, 2000) with 5000 iterations. The minimum cluster size needed for an overall alpha of P < .05 was 7 voxels for contrasts with an uncorrected voxel threshold of P < .001 and 16 voxels for those thresholded at P < .01.

Results

Neural Response to Familiarized Faces

Specific Exposure Effect—Previously seen faces showed repetition suppression in left LOFC (Table 1, Figure 1). There was also repression suppression in caudate. There were no repetition enhancement effects for previously seen faces in MOFC. Repetition suppression also was found for other race faces in several clusters in occipito-temporal cortex and in the left inferior frontal gyrus, consistent with previous research. Finally, although not specifically predicted, additional repetition suppression effects were shown in anterior cingulate, paracingulate, dorsal medial prefrontal cortex (dmPFC), ventral medial prefrontal cortex (vmPFC), and left temporal pole (Table 1). The contrast examining whether repetition suppression effects were moderated by exposure group revealed no interaction effects in the regions showing the foregoing main effects, indicating comparable effects of exposure to Black faces and Korean faces on the neural response to the exposed faces vs. novel ones from the same category.

Generalized Exposure Effect

The GEE contrast revealed lower activation to novel other race faces from a previously exposed racial category than a non-exposed category in both left and right LOFC (Table 1, Figure 1). Faces from a previously exposed category did not show enhanced activation in MOFC. Lower activation to faces from a previously exposed racial category also was found in several clusters in occipito-temporal cortex. Finally, the GEE contrast revealed lower activation to novel faces from a previously exposed racial category in vmPFC, as found in the SEE, and in insula (Table 1). The contrast examining whether exposure group moderated the foregoing GEEs revealed interactions with exposure group in right LOFC, where lower activation to novel faces from the exposed than the unexposed category was greater in the Korean than the Black face exposure condition (Table 1).

Neural Response to Familiarized Objects

Specific Exposure Effect—Previously seen objects elicited less activation than novel ones from the same category in right LOFC (Table 2, Figure 2). Repetition suppression to previously seen objects was also found in occipito-temporal cortex. Finally, there was lower activation to previously seen than novel objects in dmPFC, paralleling the effect for faces (Table 2). The contrast examining whether exposure group moderated the SEE revealed no interaction effects in the regions showing the foregoing main effects, indicating comparable

effects of repeated exposure to Chinese characters and polygons on the neural response to the exposed objects vs. novel ones from the same category.

Previously seen objects also elicited greater neural activation than novel ones in several regions, a repetition enhancement effect (Table 2). However, repetition enhancement was not shown in either MOFC or in other regions in the reward circuit that respond more to positively valenced stimuli than to neutral or negative ones. The repetition enhancement effects were not moderated by exposure group.

Generalized Exposure Effect—The GEE contrast for objects revealed lower activation to novel objects from a previously exposed category than a non-exposed category in left LOFC (Figure 2). The GEE contrast also revealed lower activation to novel objects from a previously exposed category than a non-exposed category in several clusters within occipito-temporal cortex. Many additional regions showed lower activation to novel stimuli from the familiarized than the unfamiliarized category, including dmPFC, which had shown lower activation in the SEE for objects, and caudate, which had shown lower activation in the SEE for faces (Table 3, Figure 2). Whereas decreased neural activation to familiarized objects were shown in both GEE and SEE, the repetition enhancement effects shown in SEE did not generalize, and there also was no repetition enhancement in MOFC.

Liking ratings

Analyses of variance were performed on liking ratings for faces and for objects with three levels of stimulus familiarity (exposed, novel from exposed category, novel from new category) as a within subjects variable. Contrary to prediction, the results revealed no significant effects of stimulus familiarity on liking for faces ($M_{exposed}$ = 1.80, SD = .44; $M_{novel, exposed category}$ = 1.75, SD = .39; $M_{novel, new category}$ = 1.81, SD = .44, $F(2, 60)$ = .41, p = .66) or on liking for objects ($M_{exposed}$ = 1.85, SD = .54; $M_{novel, exposed category}$ = 1.84, SD = .52; $M_{novel, new category}$ = 1.95, SD = .58, $F(2,30)$ = .81 p = .45.

Discussion

As predicted, we found lower activation in LOFC to previously exposed faces and objects than to novel ones (SEE) as well as to novel faces and objects from a previously exposed category than from a non-exposed category (GEE). These results demonstrate a consistent participation of the reward circuit in repetition suppression effects that generalizes across different types of stimuli (faces and objects) and different types of familiarity (specific and general), substantially extending the Bentley et al. (2003) finding that priming yielded greater LOFC attenuation to fear than neutral faces.

The fact that familiarization attenuated neural activation in LOFC, a part of the reward circuit that responds more to negatively than neutral or positively valenced stimuli (Cloutier et al., 2008; Liang et al., 2010; Kensinger & Schacter, 2005; O'Doherty et al., 2001), supports Zajonc's (2001) argument that mere exposure effects on liking derive from a reduction in apprehensiveness elicited by novel stimuli. Caudate attenuation in the Face SEE and Object GEE also supports this argument, since research has reported stronger caudate activation to negatively valenced stimuli (Cloutier, Heatherton, Whalen, & Kelley, 2008; Delgado, Locke, Stenger, & Fiez, 2003; Kensinger & Schacter, 2005; Liang, Zebrowitz, & Zhang, 2010; O'Doherty et al., 2001). On the other hand, there was no increased activation in MOFC or in other regions in the reward circuit that respond more to positively valenced stimuli, such as nucleus accumbens (Aharon, Etcoff, Ariely, Chabris, O'Connor et al., 2001; Cloutier, et al., 2008; Ishai, 2007; Kampe et al., 2001; Kawabata & Zeki, 2004; Liang et al., 2010; O'Doherty et al., 2003; Winston et al., 2007). These results suggest that the effects of stimulus famliarization on liking and other indices of positive affect (deVries et al., 2010;

Harmon-Jones & Allen, 2001; Reber et al., 1998; Winkielman & Cacioppo, 2001; Winkielman et al., 2006) reflect a reduction in negative valence rather than a direct increase in positive valence. It is important to note that the failure to find increased activation in MOFC cannot be attributed to attenuation in neural activation across the entire brain inasmuch as several regions showed a repetition enhancement effect in the object SEE. That result is consistent with previous evidence, particularly in posterior cingulate, one region where we also found the effect (Gobbini & Haxby, 2006; Henson, Shallice, & Dolan, 2000; Kosaka et al., 2003; Koutstaal, 2001; Soldan, Zarahn, Hilton, & Stern, 2008).

In addition to multiple demonstrations of an association between stimulus familiarization and an attenuated neural response in LOFC, the present study also found repetition suppression in several other regions. The attenuation we found in occipital-temporal cortex has been well-documented in previous research (e.g., Elliott & Dolan, 1998; Koutstaal et al., 2001; Gobbini & Haxby, 2006), but ours is the first to show the effect for other race faces.[2] We also replicated previous evidence for repetition suppression in inferior frontal cortex, consistent with greater automaticity in processing familiarized stimuli (Bunzeck et al., 2006; Schacter et al., 2007). Finally, we found attenuation in mPFC to familiarized faces and objects. The precise functions of various regions in mPFC remain a topic of active discussion, but some research indicates that it plays a role in encoding the emotional and motivational value of stimuli (O'Reilly, 2010). This suggests that there was less processing of the value of stimuli when making liking judgments if they had been previously exposed.

The finding that familiarization with novel stimuli is associated with a reduction in their negative valence, as indexed by LOFC attenuation, is consistent with socially significant negative reactions to unfamiliar stimuli outside the laboratory. For example, the GEE effect for faces is consistent with research demonstrating that inter-group contact can reduce prejudice even when the ideal conditions for increasing positive responses to outgroup members are not met (Allport, 1954; Pettigrew & Tropp, 2006). It is noteworthy that the GEE effect in LOFC was weaker in the case of Black than Korean face exposure. This is consistent with the tendency for White perceivers to show stronger levels of activation to Black faces in brain regions that respond to threat or negative stimulus valence (Eberhardt, 2005; Ito & Bartholow, 2009). It is also consistent with the Bentley et al. (2003) finding that LOFC attenuation to repeated face pairs was weaker for fear faces than neutral ones. Effects of stimulus familiarization on LOFC attenuation are also consistent with recent evidence that residential mobility enhances both a preference for more familiar 'big box' stores and also the strength of the mere exposure effect, with the latter result mediated by mobility-evoked anxiety (Oishi, Miao, Koo, Kisling, & Ratliff, 2011). The fact that people responded more positively to familiarized stimuli when they were experiencing anxiety due to an unfamiliar environment suggests that stimulus repetition serves to reduce apprehensiveness.

Although our results suggest that LOFC attenuation is implicated in the well-documented greater liking for exposed stimuli (Bornstein, 1989) and for novel stimuli from an exposed category (Monahan et al., 2000; Zebrowitz et al., 2008), our conclusions must be tempered by the fact that we did not find significant effects of our exposure manipulation on liking. This can be attributed to insufficient sensitivity of the 3-point liking scale to pick up subtle differences in evaluative responses associated with familiarization. Indeed, the experimental protocol in the present study was very similar to two experiments conducted by Zebrowitz et

---

[2]The finding that attenuation in inferior lateral occipital/fusiform gyrus was shown on the right side for the SEE effect and on the left side for the GEE effect in the case of both faces and objects is consistent with previous evidence that the right fusiform response is highly specific to a particular exemplar, with more generalization to similar stimuli in left fusiform (Blondin & Le Page, 2005; Eger, Schweinberger, Dolan, & Henson, 2005); Koustaal et al., 2001; Simons et al., 2003). The finding that fusiform gyrus showed effects for objects as well as faces is consistent with previous evidence demonstrating fMRI adaptation to inanimate objects in fusiform face area (Ewbank, Schluppeck, & Andrews, 2005).

al. (2008) that did find significant GEE effects when 7-point scales were used to rate liking. The current study used the same Korean faces, the same number of repetitions in the exposure manipulation, the same number of generalization stimuli within each category, approximately the same ISI (800 ms vs. 1000 ms), and the same 2s duration for the liking ratings. Although the exposure duration for each stimulus differed (100 ms in the current study vs. 50 ms in Zebrowitz et al., 2008, Experiment 1), both durations fall within the range of 5 ms to 500 ms that showed maximum likeability effects in previous research by Bornstein and D'Agostino (1992). Moreover, the 100 ms mask presented after each stimulus in the present study rendered the visibility of the stimuli closer to the shorter duration previously employed. A second experiment in Zebrowitz et al. (2008) found the same liking effects using Black faces and subliminal exposures, demonstrating the robustness of the effects. Although showing parallel effects of stimulus familiarization on LOFC attenuation and liking within the same study would reinforce our conclusions, the fact that a mere exposure effect on liking has been reported hundreds of times, including a behavioral study that closely matches the current paradigm, strongly implicates a role for LOFC attenuation in the effect. More specifically, LOFC attenuation to familiarized stimuli supports the hypothesis that the mere exposure effect reflects reduced apprehensiveness about novel stimuli.

Conclusions

The present study demonstrated that familiarization with other race faces or uncommon objects yields reduced neural activation in LOFC not only to the specific familiarized faces or objects but also to novel faces or objects from the familiarized category. Whereas previous research suggests that decreased activation in occipital cortex or in inferior frontal regions associated with controlled processing may explain behavioral priming effects (Banko et al., 2011; Bunzeck et al., 2006; Schacter et al., 2007), it is unclear how greater perceptual fluency or automaticity can in and of itself explain increased liking for familiarized stimuli or novel stimuli from a familiarized category, the 'mere exposure' effect (Bornstein, 1989; Monahan, Murphy, & Zajonc, 2000; Zebrowitz, White, & Wieneke, 2008; Zajonc, 1968). The evidence we have provided for lower activation to familiarized stimuli in LOFC, a region that responds more to negative than neutral or positive stimuli (Cloutier, Heatherton, Whalen, & Kelley, 2008; Liang, Zebrowitz, & Zhang, 2010; Kensinger & Schacter, 2005; O'Doherty et al., 2001), is consistent with Zajonc's (2001) argument that mere exposure effects derive from a reduction in negative affect associated with apprehensiveness about novel stimuli. In contrast, our failure to find any evidence that exposure increases activation in reward regions that respond more to positively valenced stimuli suggests that greater liking for familiarized stimuli may not derive from a tendency for increased perceptual fluency to directly increase positive affect.

Acknowledgments

References

Aharon I, Etcoff N, Ariely D, Chabris CF, O'Connor E, Breiter HC. Beautiful faces have variable reward value: fMRI and behavioral evidence. Neuron. 2001; 32(3):537–551. [PubMed: 11709163]

Allport, GW. The nature of prejudice. Vol. 1954. Oxford, England: Addison-Wesley; 1954.

Banko EM, Gal V, Kortvelyes J, Kovacs G, Vidnyanszky Z. Dissociating the Effect of Noise on Sensory Processing and Overall Decision Difficulty. Journal of Neuroscience. 2011; 31:2663–2674. [PubMed: 21325535]

Bentley P, Vuilleumier P, Thiel CM, Driver J, Dolan RJ. Effects of attention and emotion on repetition priming and their modulation by cholinergic enhancement. Journal of Neurophysiology. 2003; 90(2):1171–1181. [PubMed: 12649315]

Blondin F, Lepage M. Decrease and increase in brain activity during visual perceptual priming: An fMRI study on similar but perceptually different complex visual scenes. Neuropsychologia. 2005; 43(13):1887–1900. [PubMed: 16168731]

Bornstein RF. Exposure and affect: Overview and meta-analysis of research, 1968–1987. Psychological Bulletin. 1989; 106:265–289.

Bornstein RF, D'Agostino PR. Stimulus recognition and the mere exposure effect. Journal of Personality and Social Psychology. 1992; 64:545–552. [PubMed: 1447685]

Bornstein RF, D'Agostino PR. The attribution and discounting of perceptual fluency: Preliminary tests of a perceptual fluency/attributional model of the mere exposure effect. Social Cognition. 1994; 12(2):103–128.

Bunzeck N, Schutze H, Duzel E. Category-specific organization of prefrontal response-facilitation during priming. Neuropsychologia. 2006; 44(10):1765–1776. [PubMed: 16701731]

Cacioppo JT, Bush LK, Tassinary LG. Microexpressive facial actions as a function of affective stimuli - replication and extension. Personality and Social Psychology Bulletin. 1992; 18:515–526.10.1177/0146167292185001

Cloutier J, Heatherton TF, Whalen PJ, Kelley WM. Are attractive people rewarding? Sex differences in the neural substrates of facial attractiveness. Journal of Cognitive Neuroscience. 2008; 20(6):941–951. [PubMed: 18211242]

Dale AM. Optimal stimulus sequences for event-related fMRI. Human Brain Mapping. 1999; 8:109–114. [PubMed: 10524601]

Delgado MR. Reward-related responses in the human striatum. Annals of the New York Academy of Science. 2007; 1104:70–88.

Delgado MR, Locke HM, Stenger VA, Fiez JA. Dorsal striatum responses to reward and punishment: Effects of valence and magnitude manipulations. Cognitive, Affective, & Behavioral Neuroscience. 2003; 3:27–38.

de Vries M, Holland RW, Chenier T, Star MJ, Winkielman P. Happiness cools the warm glow of familiarity: Psychophysiological evidence that mood modulates the familiarity-affect link. Psychological Science. 2010; 21:321–328.10.1177/0956797609359878 [PubMed: 20424063]

Dimberg U, Thunberg M, Elmehed K. Unconscious facial reactions to emotional facial expressions. Psychological Science. 2000; 11:86–89.10.1111/1467-9280.00221 [PubMed: 11228851]

Eberhardt JL. Imaging Race. American Psychologist. 2005; 60(2):181–190. [PubMed: 15740450]

Eger E, Schweinberger SR, Dolan RJ, Henson RN. Familiarity enhances invariance of face representations in human ventral visual cortex: fMRI evidence. NeuroImage. 2005; 26(4):1128–1139. [PubMed: 15961049]

Elliott R, Dolan RJ. Neural response during preference and memory judgments for subliminally presented stimuli: A functional neuroimaging study. Journal of Neuroscience. 1998; 18(12):4697–4704. [PubMed: 9614244]

Elliott R, Newman JL, Longe OA, Deakin JFW. Differential Response Patterns in the Striatum and Orbitofrontal Cortex to Financial Reward in Humans: A Parametric Functional Magnetic Resonance Imaging Study. Journal of Neuroscience. 2003; 23(1):303–307. [PubMed: 12514228]

Ewbank MP, Schluppeck D, Andrews TJ. fMR-adaptation reveals a distributed representation of inanimate objects and places in human visual cortex. [Article]. NeuroImage. 2005; 28(1):268–279. [PubMed: 16054842]

Gobbini MI, Haxby JV. Neural response to the visual familiarity of faces. Brain Research Bulletin. 2006; 71(1–3):76–82. [PubMed: 17113931]

Gordon PC, Holyoak KJ. Implicit learning and generalization of the "mere exposure" effect. Journal of Personality and Social Psychology. 1983; 45:492–500.

Harmon-Jones E, Allen JB. The role of affect in the mere exposure effect: Evidence from psychophysiological and individual differences approaches. Personality and Social Psychology Bulletin. 2001; 27:889–898.

Henson R, Shallice T, Dolan R. Neuroimaging evidence for dissociable forms of repetition priming. Science. 2000; 287(5456):1269–1272. [PubMed: 10678834]

Henson R, Shallice T, Gorno-Tempini ML, Dolan RJ. Face repetition effects in implicit and explicit memory tests as measured by fMRI. Cerebral Cortex. 2002; 12(2):178–186. [PubMed: 11739265]

Ishai A. Sex, beauty and the orbitofrontal cortex. International Journal of Psychophysiology. 2007; 63(2):181–185. [PubMed: 16759727]

Ito TA, Bartholow BD. The neural correlates of race. [Review]. Trends in Cognitive Sciences. 2009; 13(12):524–531. [PubMed: 19896410]

James TW, Gauthier I. Repetition-induced changes in BOLD response reflect accumulation of neural activity. Human Brain Mapping. 2006; 27:37–46.10.1002/hbm.20165 [PubMed: 15954142]

Kampe KKW, Frith CD, Dolan RJ, Frith U. Reward value of attractiveness and gaze. Nature. 2001; 413(6856):589–590. [PubMed: 11595937]

Kawabata H, Zeki S. Neural Correlates of Beauty. Journal of Neurophysiology. 2004; 91(4):1699–1705. [PubMed: 15010496]

Kensinger EA, Schacter DL. Retrieving accurate and distorted memories: Neuroimaging evidence for effects of emotion. NeuroImage. 2005; 27:167–177. [PubMed: 15919215]

Kosaka H, Omori M, Iidaka T, Murata T, Shimoyama T, Okada T, et al. Neural substrates participating in acquisition of facial familiarity: an fMRI study. NeuroImage. 2003; 20(3):1734–1742. [PubMed: 14642483]

Koutstaal W, Wagner AD, Rotte M, Maril A, Buckner RL, Schacter DL. Perceptual specificity in visual object priming: functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex. Neuropsychologia. 2001; 39(2):184–199. [PubMed: 11163375]

Krendl AC, Macrae CN, Kelley WM, Fugelsang JA, Heatherton TF. The good, the bad, and the ugly: An fMRI investigation of the functional anatomic correlates of stigma. Social Neuroscience. 2006; 1(1):5–15. [PubMed: 18633772]

Kwong KK, Belliveau JW, Chesler DA, Goldberg IE, Weisskoff RM, Poncelet BP, et al. Dynamic magnetic-resonance-imaging of human brain activity during primary sensory stimulation. Proceedings of the National Academy of Sciences of the United States of America. 1992; 89(12):5675–5679. [PubMed: 1608978]

Lander K, Bruce V, Smith E, Hancock PJB. Multiple repetition priming of faces: Massed and spaced presentations. Visual Cognition. 2009; 17(4):598–616.

Liang XY, Zebrowitz LA, Zhang Y. Neural activation in the "reward circuit" shows a nonlinear response to facial attractiveness. Social Neuroscience. 2010; 5(3):320–334. [PubMed: 20221946]

Martin D, Greer J. Getting to know you: From view-dependent to view-invariant repetition priming for unfamiliar faces. Quarterly Journal of Experimental Psychology. 64(2):217–223.

Monahan JL, Murphy ST, Zajonc RB. Subliminal mere exposure: Specific, general, and diffuse effects. Psychological Science. 2000; 11:462–466. [PubMed: 11202490]

Moreland RL, Topolinski S. The mere exposure phenomenon: A lingering melody by Robert Zajonc. Emotion Review. 2010; 2(4):329–339.

O'Doherty J, Kringelbach ML, Rolls ET, Hornak J, Andrews C. Reward and punishment representations in the human orbitofrontal cortex. Nature Neuroscience. 2001; 4:95–102.

O'Doherty J, Winston J, Critchley H, Perrett D, Burt DM, Dolan RJ. Beauty in a smile: The role of medial orbitofrontal cortex in facial attractiveness. Neuropsychologia. 2003; 41(2):147–155. [PubMed: 12459213]

Oishi S, Miao FF, Koo M, Kisling J, Ratliff KA. Residential mobility breeds familiarity-seeking. Journal of Personality and Social Psychology.

O'Reilly RC. The What and How of prefrontal cortical organization. Trends in Neurosciences. 2010; 33:355–361. [PubMed: 20573407]

Pettigrew TF, Tropp LR. A meta-analytic test of intergroup contact theory. Journal of Personality and Social Psychology. 2006; 90:751–783. [PubMed: 16737372]

Reber R, Winkielman P, Schwarz N. Effects of perceptual fluency on affective judgments. Psychological Science. 1998; 29:45–48.

Rhodes G, Halberstadt J, Brajkovich G. Generalization of mere exposure effects to averaged composite faces. Social Cognition. 2001; 19:57–70.

Schacter DL, Wig GS, Stevens WD. Reductions in cortical activity during priming. Current Opinion in Neurobiology. 2007; 17:171–176. [PubMed: 17303410]

Simons JS, Koutstaal W, Prince S, Wagner AD, Schacter DL. Neural mechanisms of visual object priming: evidence for perceptual and semantic distinctions in fusiform cortex. NeuroImage. 2003; 19(3):613–626. [PubMed: 12880792]

Smith PK, Dijksterhuis A, Chaiken S. Subliminal exposure to faces and racial attitudes: Exposure to Whites makes Whites like Blacks less. Journal of Experimental Social Psychology. 2008; 44(1): 50–64.

Soldan A, Zarahn E, Hilton HJ, Stern Y. Global familiarity of visual stimuli affects repetition-related neural plasticity but not repetition priming. NeuroImage. 2008; 39(1):515–526. [PubMed: 17913513]

Topolinski S, Strack F. Motormouth: Mere exposure depends on stimulu-specific motor simulations. Journal of Experimental Psychology: Learning, Memory, and Cognition. 2009; 35:423–433.

Tulving E, Schacter DL. Priming and human memory systems. Science. 1990; 247(4940):301–306. [PubMed: 2296719]

Turk-Browne NB, Yi D-J, Leber AB, Chun MM. Visual quality determines the direction of neural repetition effects. Cerebral Cortex. 2007; 17:425–433.10.1093/cercor/ [PubMed: 16565294]

Vanderplas JM, Garvin EA. The Association Value of Random Shapes. Journal of Experimental Psychology. 1959; 57(3):147–154. [PubMed: 13641586]

Ward, BD. Simultaneous inference for fMRI data. 2000. [On-line] http://afni.nimh.nih.gov/pub/dist/doc/manual

Winkielman P, Cacioppo JT. Mind at ease puts a smile on the face: Psychophysiological evidence that processing facilitation leads to positive affect. Journal of Personality and Social Psychology. 2001; 81:989–1000. [PubMed: 11761320]

Winkielman P, Halberstadt J, Fazendeiro T, Catty S. Prototypes are attractive because they are easy on the mind. Psychological Science. 2006; 17:799–806. [PubMed: 16984298]

Winston JS, O'Doherty J, Kilner JM, Perrett DI, Dolan RJ. Brain systems for assessing facial attractiveness. Neuropsychologia. 2007; 45(1):195–206. [PubMed: 16828125]

Zajonc RB. Attitudinal effects of mere exposure. Journal of Personality and Social Psychology. 1968; 9 Monograph Supplement, No. 2, part 2.

Zajonc RB. Mere exposure: A gateway to the subliminal. Current Directions in Psychological Science. 2001; 10:224–228.

Zebrowitz LA, Bronstad PM, Lee HK. The contribution of face familiarity to ingroup favoritism and stereotyping. Social Cognition. 2007; 25:306–338.

Zebrowitz LA, White B, Wieneke K. Mere exposure and racial prejudice: Exposure to other-race faces increases liking for strangers of that race. Social Cognition. 2008; 26:259–275. [PubMed: 19584948]
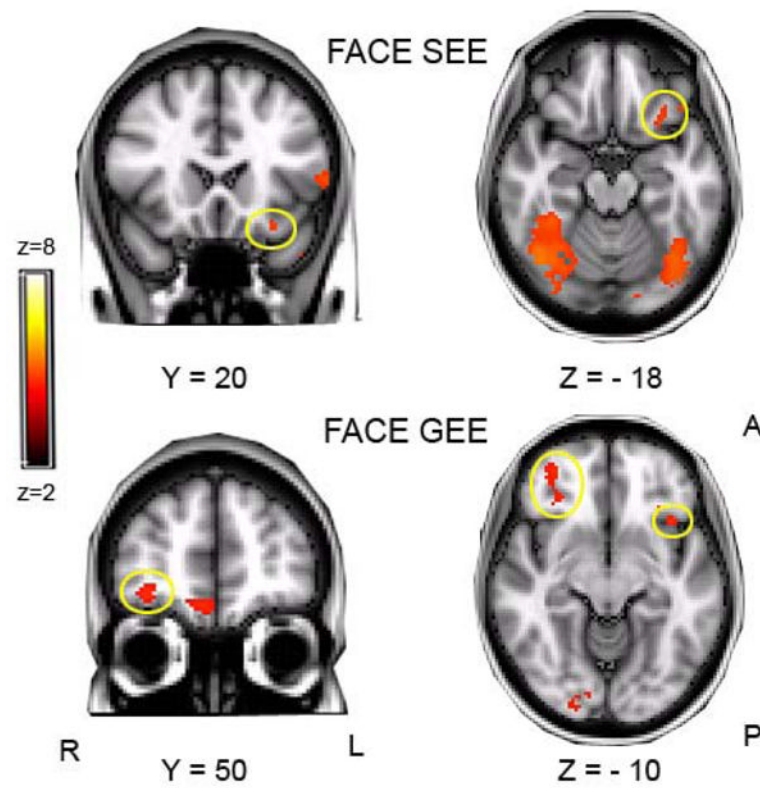
Figure 1.
Top panel Activation in SEE effect for faces (novel faces in the exposed category > previously seen faces) is shown in the left LOFC (circled), uncorrected p < .001 and extent threshold of 7 voxels.
Bottom panel: Activation in GEE effect for faces (novel faces from the unexposed category > novel faces from the exposed category) is shown in the bilateral LOFC (circled), uncorrected p < .01 and extent threshold of 16 voxels.
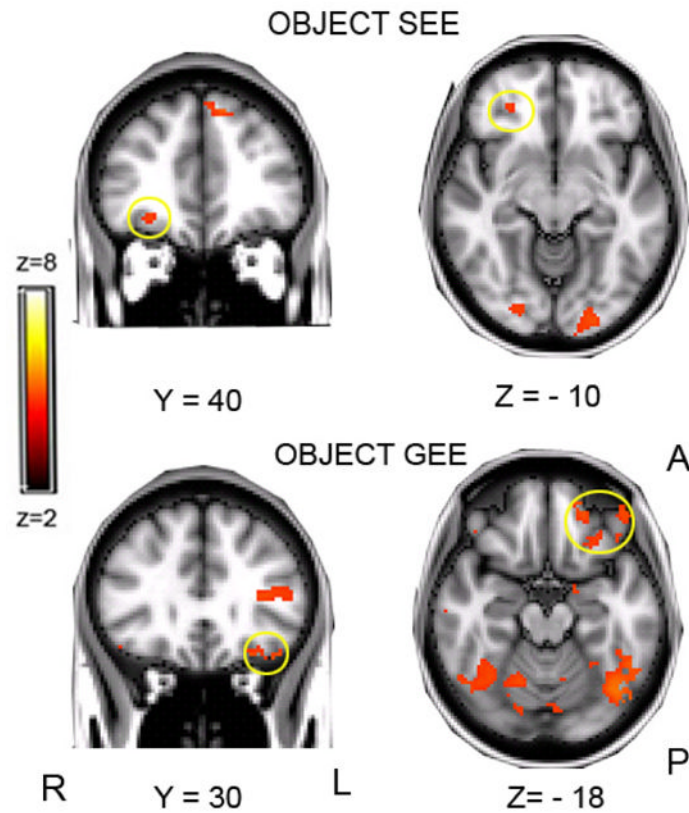
Figure 2.
Top panel Activation in SEE effect for objects (novel objects in the exposed category > previously seen objects) is shown in the left LOFC (circled), uncorrected p < .001 and extent threshold of 7 voxels.
Bottom panel: Activation in GEE effect for objects (novel objects from the unexposed category > novel objects from the exposed category) is shown in the left LOFC (circled), uncorrected p < .001 and extent threshold of 7 voxels.

Table 1

Brain Regions showing Specific Exposure effects (SEE) and Generalized Exposure Effects (GEE) to Faces

Region	Side	Peak coordinates (mm)			Maximal significance (Z)	Cluster size (voxels)
		x	y	z		
SEE repetition suppression: novel faces in exposed category > previously seen faces, averaging across exposure group						
Anterior Cingulate/paracingulate	L	−12	32	22	3.71	26
Caudate	R	8	10	6	3.32	20
dmPFC/anterior paracingulate	M	0	60	16	5.10	2168
Fusiform gyrus	L	−36	−66	−18	4.19	762
Inferior lateral occipital/fusiform gyrus	R	42	−64	−16	4.88	1286
Inferior frontal gyrus	L	−56	22	6	3.76	74
LOFC	L	−34	40	−10	2.62	30
LOFC	L	−28	20	−18	3.42	27
Occipital pole	R	34	−90	8	3.44	17
Temporal pole	L	−42	14	−42	3.56	22
vmPFC	M	−2	58	−4	3.64	32
GEE repetition suppression: Novel faces in unexposed category > novel faces in exposed category, averaging across exposure group						
Inferior lateral occipital/fusiform gyrus	L	−46	−76	8	3.07	46
LOFC/insula	R	32	50	−8	2.98	151
LOFC	L	−38	20	−10	2.93	24
LOFC	L	−30	28	−8	2.81	17
Occipital pole	R	20	−92	−12	2.82	25
Occipital pole	R	40	60	−4	2.82	25
Superior lateral occipital	R	34	−70	48	3.5	85
vmPFC	M	8	42	−16	3.22	153
GEE repetition suppression moderated by exposure group						
Korean exposure > Black exposure						
Lateral OFC	R	34	26	−20	2.62	29

Note: Shown for each region are location of peak (MNI space), the maximum Z score, and number of voxels activated.

Table 2

Brain Regions showing Specific Exposure effects (SEE) to Objects

Region	Side	Peak coordinates (mm)			Maximal significance (Z)	Cluster size (voxels)
		x	y	Z		
SEE repetition suppression: Novel objects in exposed category > previously seen objects, averaging across exposure group						
dmPFC	L	−12	40	46	4.29	60
Fusiform gyrus	R	30	−84	−18	3.76	96
Occipital pole	R	18	−98	−4	4.22	328
Occipital pole	L	−24	−94	−8	3.87	160
Occipital pole	L	−14	−108	0	3.54	50
LOFC	R	28	40	−10	3.46	20
SEE repetition enhancement: Novel objects in exposed category < previously seen objects, averaging across exposure group						
Cuneal gyrus	R	8	−84	36	3.95	96
Heschl's gyrus	L	−52	−14	6	3.64	44
Middle frontal gyrus	R	64	−38	14	3.47	26
Occipital pole	L	−10	−88	32	3.34	17
Planum temporale	R	46	−36	18	3.34	17
Posterior cingulate	R	16	−44	0	3.44	66
Temporal pole	R	50	6	−8	3.59	21

Note: Shown for each region are location of peak (MNI space), the maximum Z score, and number of voxels activated.

Table 3

Brain Regions showing Generalized Exposure Effects (GEE) to Objects

Region	Side	Peak coordinates (mm)			Maximal significance (Z)	Cluster size (voxels)
		x	y	z		
GEE repetition suppression: Novel objects in unexposed category > novel objects in exposed category, averaging across exposure group						
Caudate	R	14	6	24	3.35	16
Cerebellum	R	28	−72	−40	3.74	176
Cerebellum	L	−6	−58	−26	3.77	112
Cerebellum	L	−10	−58	−14	3.54	44
Cerebellum	L	−26	−50	−50	3.57	28
Cuneal cortex	M	−4	−82	40	3.50	30
Cuneal cortex	M	0	−76	22	3.34	18
dmPFC	R	12	64	10	3.66	112
dlPFC	R	44	42	4	3.48	126
Frontal pole	L	−14	66	6	3.43	25
Fusiform gyrus/inferior temporal/inferior occipital	L	−40	−64	−22	5.10	2900
Hippocampus	L	−26	−22	−8	3.35	18
Inferior frontal	L	−42	36	14	4.15	310
Inferior lateral occipital	L	−50	−82	8	3.54	48
LOFC	L	−26	30	−20	3.79	62
LOFC	L	−48	46	−16	3.65	41
LOFC	L	−22	46	−18	3.78	35
Posterior middle temporal	L	−60	−42	−2	3.56	73
Precentral gyrus	L	−46	4	20	3.54	43
Superior frontal gyrus	L	−36	12	50	4.08	193
Superior lateral occipital	L	−20	−78	38	4.15	310
Superior lateral occipital	L	−22	−66	58	3.48	28
Superior lateral Occipital	R	38	−78	26	3.61	296
Superior lateral Occipital	R	48	−70	18	3.47	18
Supramarginal gyrus	L	−48	−42	50	3.92	223
Thalamus	L	−14	−8	16	3.45	24

Note: Shown for each region are location of peak (MNI space), the maximum Z score, and number of voxels activated.