# Nonpreferred Stimuli Modify the Representation of Faces in the Fusiform Face Area

**Vadim Axelrod and Galit Yovel**


## Abstract

■ The ventral visual cortex has a modular organization in which discrete and well-defined regions show a much stronger response to certain object categories (e.g., faces, bodies) than to other categories. The majority of previous studies have examined the response of these category-selective regions to isolated images of preferred or nonpreferred categories. Thus, little is known about the way these category-selective regions represent more complex visual stimuli, which include both preferred and nonpreferred stimuli. Here we examined whether glasses (nonpreferred) modify the representation of simultaneously presented faces (preferred) in the fusiform face area. We used an event-related fMR-adaptation paradigm in which faces were presented with glasses either on or above the face while subjects performed a face or a glasses discrimination task. Our findings show that the sensitivity of the fusiform face area to glasses was maximal when glasses were presented on the face than above the face during a face discrimination task rather than during a glasses discrimination task. These findings suggest that nonpreferred stimuli may significantly modify the representation of preferred stimuli, even when they are task irrelevant. Future studies will determine whether this interaction is specific to faces or may be found for other object categories in category-selective areas. ■




## INTRODUCTION

Modular organization of the ventral visual cortex is a robust and reliable finding reported in numerous fMRI studies (for a review, see Op de Beeck, Haushofer, & Kanwisher, 2008). A category-selective activation has been found for a number of categories including faces, scenes, words, and bodies. The majority of studies that examined the representation of objects in these category-selective regions have presented isolated images of preferred or nonpreferred object categories. A few studies that did present pairs of stimuli have either presented them side by side (Reddy & Kanwisher, 2007) or as overlapping transparent stimuli (Yi, Kelley, Marois, & Chun, 2006). Thus, stimuli in these studies were unrelated, and it is therefore still unknown how category-selective brain areas represent a complex stimulus, which is composed of both preferred and nonpreferred categories. In the current study, we examined the representation of one image, which includes both preferred and nonpreferred categories in a category-selective area. Specifically, we examined the representation of faces (preferred) with glasses (nonpreferred) in a face-selective area (Figure 1).

Many fMRI studies have shown that the fusiform face area (FFA) represents the identity of faces (e.g., Avidan & Behrmann, 2009; Ewbank & Andrews, 2008; Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Grill-Spector, Knouf, & Kanwisher, 2004). The most prevalent paradigm that has been used to assess the nature of the representation of faces is the fMR adaptation (e.g., Avidan & Behrmann, 2009; Davies-Thompson, Gouws, & Andrews, 2009; Ewbank & Andrews, 2008; Gilaie-Dotan & Malach, 2007; Yovel & Kanwisher, 2005). In this paradigm, the BOLD signal to different faces is compared with the response for same faces. Because repeated presentation of the same stimulus results in a lower BOLD signal, a higher response to different than same faces is taken as evidence that a brain region discriminates between the different stimuli (Grill-Spector & Malach, 2001; but see, Sawamura, Orban, & Vogels, 2006). Using fMR adaptation, studies have shown that the FFA is sensitive to the identity of familiar faces (Avidan & Behrmann, 2009; Rotshtein et al., 2005) and nonfamiliar faces (Gilaie-Dotan & Malach, 2007; Yovel & Kanwisher, 2005) and to upright but not inverted faces (Mazard, Schiltz, & Rossion, 2006; Yovel & Kanwisher, 2005) and generates a holistic representation of the internal facial features (Schiltz & Rossion, 2006).

The goal of the current study was to assess whether nonface stimuli may influence the representation of face identity in a face-selective region. Effects of facial and nonfacial external features (i.e., hair, glasses) on the perceived identity of the internal facial features have been demonstrated in two face illusions, the Clinton–Gore (Sinha & Poggio, 1996) or the Bush–Cheney illusions (Sinha & Poggio, 2002), in which combination of the external features of Gore/Cheney and the internal facial features of Clinton/Bush, respectively, modified the identity of the internal features, which were mistakenly perceived to be consistent with the external features. These findings

Tel Aviv University, Israel

 

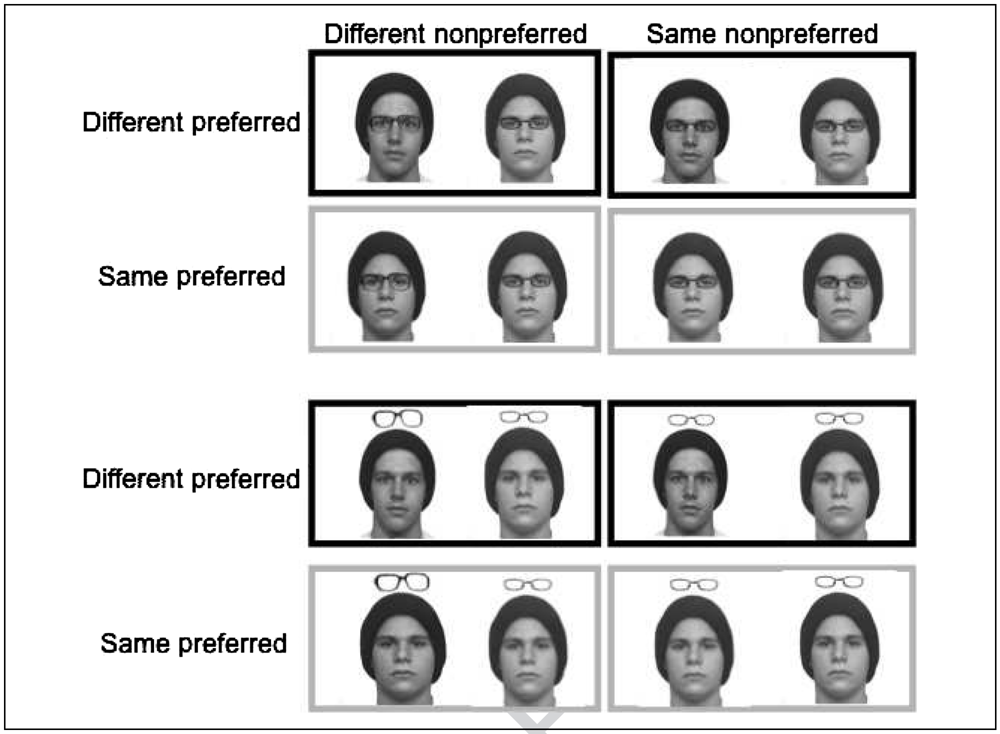


**Figure 1.** Stimuli used in the fMR-adaptation task: The fMR-adaptation task included sequential presentation of different or same faces with different or same glasses presented on the face or above the face. Subjects performed a face discrimination task.

suggest that internal and external facial stimuli may generate a holistic representation in which the internal features may be modified by changes in facial (e.g., hair) external features or nonfacial (e.g., glasses) external features. To assess the effect of nonface stimuli on the representation of face stimuli in the face-selective cortex, we manipulated independently the identity of face and nonface stimuli (glasses; Figure 1). If the FFA is sensitive to the identity of glasses, we will find release from adaptation to same faces that differ in glasses identity (Figure 2A). If the FFA is not sensitive to glasses, it will show the same magnitude of adaptation to faces, regardless of the identity of the glasses (Figure 2B). If the FFA is sensitive to the identity of glasses, that may be due to two factors: sensitivity to the shape of the glasses per se and/or to the influence of the external features on the representation of the identity of the face. By manipulating the glasses relative location (Figure 1) during a face discrimination task, we were able to study whether the FFA is sensitive to the nonface stimuli per se or to their effect on the representation of the internal facial features. To assure that the location effects that we may find are not due to effects of attention/retinotopy, in a second experiment we examined the effect of location during a glasses discrimination task.



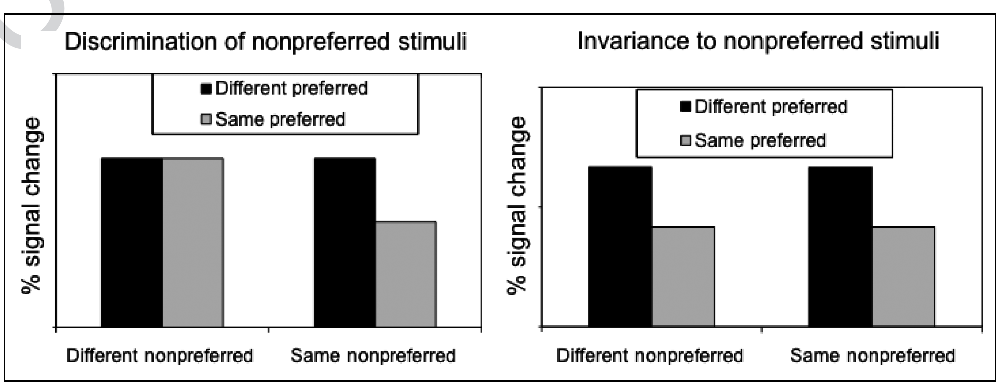


**Figure 2.** Predicted response of the FFA to nonpreferred stimuli (glasses). (A) If the FFA is sensitive to glasses identity, it will show release from adaptation to faces that differ in glasses, resulting in a higher response to same faces with different glasses than same faces with same glasses (gray bars). (B) If the FFA is invariant to the identity of glasses, it will show a higher response to different than same faces (fMR-adaptation effect for face identity) regardless of the identity of the glasses and the response to same faces that differ in glasses will be similar to the response of same faces with same glasses (gray bars).

## EXPERIMENT 1

### Methods

#### *Subjects*

Ten healthy volunteers (age = 19–36 years, 7 women) participated in Experiment 1. One subject was discarded from the data analysis because of excessive movement during scanning. All subjects gave informed consent to participate in the study, which was approved by the ethics committee of the Tel Aviv Sourasky Medical Center.

#### *Apparatus*

MRI data were collected in a 3-T GE MRI scanner. EPI sequence was used to collect fMRI data with the following parameters: repetition time = 1.5 sec, echo time = 35 msec, flip angle = 90°, 22 slices per repetition time, slice thickness = 4 mm no gap, matrix = 64 × 64, and field of view = 256 mm.

While lying in the scanner, subjects received a response box, which they used according to experiment instructions. Stimuli were presented with Matlab (Psychtoolbox; Brainard, 1997). The stimuli were projected to a screen located at the back of the scanner through a projector. The subjects viewed the stimuli through a mirror that was placed on the upper part of the head coil in front of their eyes.

#### *Stimuli*

All visual stimuli were grayscale. Functional localizer images were miscellaneous photographs of 80 different faces and 80 different types of objects (e.g., ball, apple, barrel); scrambled objects were a random mixture of pixels of each of the object images. Stimuli of the fMR-adaptation experiment were photographs of 12 different male faces drawn from the Harvard Face Database. The faces subtended 4.5° of visual angle in width and 6.8° of visual angle in height. The height of stimuli in which glasses were located above the faces was 9.1°. Images of glasses were copied and pasted to the face image using the Adobe Photoshop CS2 software. The size of the face stimuli was 3 × 4 cm.

#### *Procedure*

*Functional localizer scan.* The localizer included three object categories: faces, objects, and scrambled objects, presented in a block design. The order of the categories was counterbalanced within and across scans. Localizer scan duration was 4:27 minutes. Each localizer scan consisted of four blocks for each category and five blocks of a baseline fixation point. To ensure general vigilance, we instructed the subjects to press a response box button whenever two identical images appeared consecutively (one-back task).

*fMR-adaptation scans.* fMR adaptation to faces and glasses was measured using a rapid event-related design that included eight conditions in a 2 × 2 × 2 factorial design: face identity (different, same), glasses identity (different, same), and glasses location (on face/above face). Each trial consisted of four images. For same trials, all four images were identical. Different trials included two pairs of different stimuli (A–B–A–B, where A and B were two different images). Stimulus duration was 0.3 sec and interstimulus interval was 0.2 sec. The intertrial interval was 1 sec. In total, the length of each trial was 3 sec: (0.3 sec + 0.2 sec) × 4 + 1 sec. Each scan included 12 repetitions for each condition (72 repetitions per condition for whole experiment) and 24 null trials. The stimuli were projected at the center of the screen with random location jittering of 30 pixels to prevent discrimination on the basis of apparent motion of face features that are presented with a short interstimulus interval duration. The experiment consisted of six scans, and each scan lasted 6:12 minutes.

Subjects were instructed to press one key if the faces were identical and another key if they were different, regardless of the glasses identity. To eliminate possible errors in judging same faces that differed in glasses as different faces, subjects were familiarized with the faces at the beginning of the experiment (during the anatomical scan). For each of the 12 identities, pairs of same faces with different glasses were presented side by side for 5 sec, and subjects inspected them. This familiarization session lasted 5 minutes, during which subjects were instructed to carefully observe the images without performing any task (passive viewing).

#### *Data Analysis*

fMRI data analysis was conducted using statistical parametric mapping (SPM2; Wellcome Department of Imaging Neuroscience, London, UK). In both functional localizer and fMR-adaptation experiments, the first eight volumes were acquired during the presentation of a blank screen and were discarded from the analysis. The data were preprocessed using slice timing correction, realignment, normalization to a standard template (Montreal Neurological Institute, voxel size = 3 × 3 × 3), and spatial smoothing with an 8 × 8 × 8-mm FWHM Gaussian kernel. A general linear model was estimated for each subject (HRF boxcar function for the localizer model and FIR function for the fMR-adaptation experiments). The localizer scans were used to define the face-selective region and the lateral occipital cortex (LOC) the object region. The face-selective FFA region was defined as voxels in the fusiform gyrus that showed a significantly higher response to faces than objects ($p < .00001$, uncorrected), the face-selective occipital face area (OFA) region was defined as voxels in the lateral inferior occipital cortex that showed a significantly higher response to faces than objects ($p < .00001$, uncorrected), and the object-selective region (LOC) was defined

**Table 1.** Experiment 1: Behavioral Performance (% Correct and RT in Parentheses) on the Face Discrimination Task Measured in the Scanner

| | *Glasses on Face* | | *Glasses above Face* | |
|---|---|---|---|---|
| | *Different Glasses* | *Same Glasses* | *Different Glasses* | *Same Glasses* |
| Different face | 98% (1.91 sec) | 97% (1.85 sec) | 98% (1.86 sec) | 99% (1.87 sec) |
| Same face | 99% (1.86 sec) | 98% (1.88 sec) | 98% (1.86 sec) | 98% (1.91 sec) |

as voxels in lateral occipital complex, which show a significantly higher response to objects than scrambled objects ($p < .00001$, uncorrected). In the fMR-adaptation experiments, time courses were extracted for each regressor using the MarsBaR ROI toolbox for SPM. Peak values of time courses (6 sec from trial onset) were extracted and analyzed using SPSS (Version 14; SPSS Inc., Chicago, IL).

## Results and Discussion

### *Behavioral Findings*

Performance levels on the face discrimination task were at ceiling level, and there were no significant differences between the conditions in both accuracy and RT (Table 1).

### *fMRI Findings*

Figure 3 shows the averaged percent signal change in the FFA across nine subjects. Because there was no significant interaction between hemispheres and the experimental factors, the data were collapsed across hemispheres using a weighted average on the basis of the relative volumes of the right and left FFA regions. To find out whether the representation of faces in the FFA is invariant to the identity of glasses, we first examined the response to glasses stimuli presented on the face (Figure 3A).

Replicating previous findings, we found a higher response to different than same identity faces, $t(8) = 5.802$, $p < .001$, when glasses were identical. However, when glasses were different, we found a release from fMR adaptation to same faces, which generated a response that did not differ from the response to different faces, $t(8) = 0.725$, $p = .489$. A two-way ANOVA with face identity (different, same) and glasses identity (different, same) as repeated measures confirmed a significant interaction between the identity of preferred and that of nonpreferred stimuli, $F(1, 8) = 10.866$, $p = .011$ (Figure 3A).

These findings suggest that the representation of faces in the FFA is not invariant to the identity of the nonpreferred stimuli. Two alternative explanations may account for this effect: The most straightforward explanation is that the FFA is sensitive to the identity of glasses. Another possibility is that the shape of glasses modifies the representation of the face such that same faces that differ in glasses are represented in the FFA as two different identities. This idea is consistent with the mentioned above famous face illusion, the Clinton–Gore (Sinha & Poggio, 1996) or the Bush–Cheney illusion (Sinha & Poggio, 2002), which showed that external features such as hair and glasses may modify the representation of face identity. If the FFA is sensitive to the identity of glasses per se rather than to their effect on the identity of the face, it will also show release from adaptation to glasses when they are presented above the face.

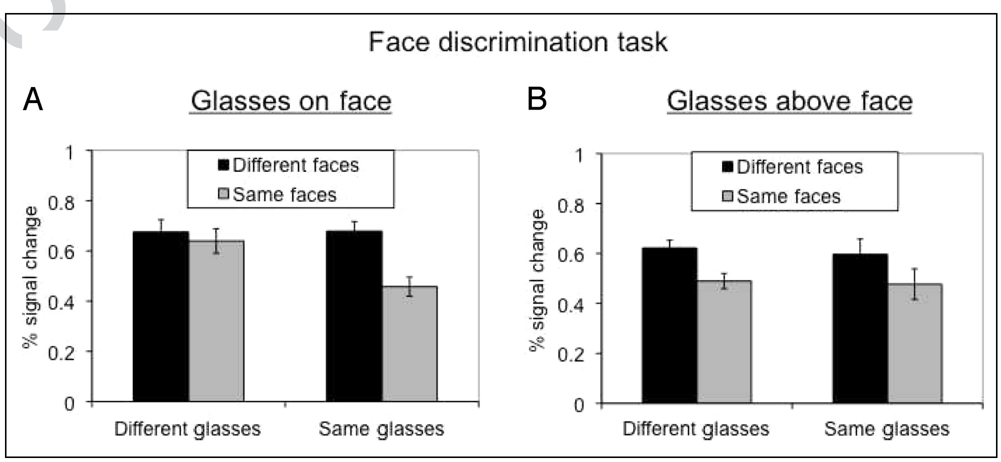


**Figure 3.** fMR adaptation in the FFA during a face discrimination task (Experiment 1) to faces and glasses as a function of glasses location relative to the face: (A) When glasses were on the face, the response was higher to different than same glasses when faces were identical (gray bars), and there was no difference between different and same faces that differed in glasses. (B) When glasses were above the face, results revealed fMR adaptation to faces regardless of the identity of glasses. Furthermore, there was no difference between the responses to different than same glasses when faces were identical (gray bars), which indicates that the FFA is not sensitive to glasses identity when they are presented above the face during a face discrimination task (error bars represent the standard error of the difference between the responses to different and same faces).

Figure 3B shows the response of the FFA when glasses are presented above the face. Contrary to the results we obtained when glasses were presented on the face, we found a higher response to different than same faces regardless of the identity of the glasses. The results of a two-way ANOVA with face identity (different, same) and glasses identity (different, same) as repeated measures revealed a significant main effect for Face Identity, $F(1, 8) = 17.363$, $p = .004$, with no effect for glasses identity or an interaction between them. Thus, the FFA was insensitive to the identity of the glasses when they were presented above the face.

To assess fMR adaptation to glasses identity as a function of their location, we compared the responses for different and identical glasses for same face identity only (comparison of gray bars in Figure 3). When glasses were on the face, the response to different glasses was higher than the response to same glasses (i.e., fMR adaptation for nonpreferred stimuli), $t(8) = 3.920$, $p = .004$). When the glasses were above the face, the difference between different and same glasses was nonsignificant, $t(8) = 0.332$, $p = .750$. A two-way ANOVA with glasses identity (different, same) and location (on face, above face) showed a significant main effect for the Glasses Identity, $F(1, 8) = 19.337$, $p = .002$, and a significant Glasses Identity × Glasses location interaction, $F(1, 8) = 6.537$, $p = .033$. These findings suggest that during a face discrimination task, the FFA discriminated between glasses when they were presented on the face (Figure 3A) but not when they were above the face (Figure 3B).

Analysis of the OFA revealed a similar pattern to the one we found in the FFA. When glasses were on the face, we found a Glasses Identity × Face Identity interaction, $F(1, 7) = 5.7$ $p < .05$, indicating a larger adaptation for faces when glasses are same when they are different. Interestingly, the OFA showed a significant adaptation to face identity also when glasses were different, $t(7) = 2.6$, $p < .05$, which suggests some invariance to glasses identity. When glasses were above the face, we found a main effect of Face Identity, $F(1, 7) = 21.4$ $p < .005$, but no interaction with glasses identity reflecting adaptation to faces regardless of glasses identity.

Unlike the face-selective areas, the LOC showed no interaction of glasses identity and face identity ($p = .3$) when glasses are on the face. There was a trend for adaptation to faces when glasses were on the face, $F(1, 6) = 3.87$, $p = .05$, but not when they were above the face ($p = .14$). Thus, unlike the face-selective areas, the LOC did not show reliable adaptation to faces. The LOC also did not show adaptation to glasses, both when presented on the face ($p = .12$) or above the face ($p = .44$).

The results we obtained support the hypothesis that face-selective cortical areas do not discriminate between glasses per se (when presented above the face) but are sensitive to their effect on the representation of face identity (when presented on the face). Notably, however, because subjects performed a face discrimination task, glasses presented above the face were located in the periphery of the visual field. It is possible that under such viewing conditions, differences in the shape of glasses were not detected. Indeed, previous studies have suggested that the FFA is biased to foveal stimuli (Hasson, Levy, Behrmann, Hendler, & Malach, 2002; Malach, Levy, & Hasson, 2002; Levy, Hasson, Avidan, Hendler, & Malach, 2001). Although this question has never been tested directly, it is possible that the FFA may not show adaptation to stimuli presented in the periphery but only to fovealy presented stimuli. Thus, the results we obtained may merely reflect a foveal bias rather than the effect of the glasses presented on the face on the representation of face identity. To decide between these two alternatives, we conducted a second experiment.

## EXPERIMENT 2

The goal of Experiment 2 was to assess the extent to which the fMR adaptation we observed for glasses presented on the face but not above the face in Experiment 1 is merely due to the FFA's foveal bias or indeed reflects the effect of glasses shape on the identity of the face. In this experiment, glasses were presented at the center of the visual field, and subjects performed a glasses discrimination task. If the adaptation to glasses presented on the face during a glasses discrimination task is smaller than during a face discrimination task, we can conclude that the release from adaptation to glasses during a face discrimination task (Experiment 1) was due to their influence on the representation of the identity of the face.

To assess the sensitivity of the FFA to glasses identity, in Experiment 2 we compared the response of the FFA with different and same glasses that were presented on or above identical faces, using the same stimuli that we used in Experiment 1 (the same face identity conditions only, gray brackets in Figure 1). Given the strong sensitivity to glasses presented on the face that we found in Experiment 1, in this experiment we also assessed whether glasses presented alone have a special status in the FFA relative to other nonpreferred object category, which is not typically associated with faces (chairs). Thus, four conditions of different and same glasses or chairs were also included. Importantly, under all conditions, subjects fixated at the objects (glasses/chairs) to perform the discrimination task.

### Methods

#### *Subjects*

Nine healthy volunteers (age = 19–36 years, six women) participated in Experiment 2. One subject was discarded from the data analysis because of excessive movement during scanning. All subjects gave informed consent to participate in the study, which was approved by the ethics committee of the Tel Aviv Sourasky Medical Center.

**Table 2.** Experiment 2: Behavioral Performance (% Correct and RT in Parentheses) on the Glasses Discrimination Task Measured in the Scanner

| | *Glasses on Face* | | *Glasses above Face* | |
|---|---|---|---|---|
| | *Different Glasses* | *Same Glasses* | *Different Glasses* | *Same Glasses* |
| Different face | 100% (1.88 sec) | 99% (1.91 sec) | 100% (1.86 sec) | 100% (1.87 sec) |
| Same face | 99% (1.87 sec) | 100% (1.86 sec) | 98% (1.86 sec) | 100% (1.88 sec) |

*Stimuli*

Stimuli of the fMR-adaptation experiment the four conditions of same face trials that were used in Experiment 1: different or same glasses, which were presented either on or above the face (Figure 1, gray frames). Four additional conditions included different and same isolated glasses and different and same chairs. Glasses stimuli subtended 4.5° of visual angle in width and 2.2 in height. Chairs subtended 4.5° in width and 6.1° in height.

*Procedure*

The functional localizer was identical to the one we used in Experiment 1. The fMR-adaptation scans had the same parameters of stimulus duration, number of trials, and number of scans that we used in Experiment 1. Subjects were asked to press one key if the objects (glasses or chairs) were identical and another key if they were different, regardless of the face identity, which was identical within each trial. Importantly, nonpreferred stimuli (glasses or chairs) were located at the center of the screen in all conditions (for glasses above face, the glasses were at the center of the visual field and the faces in the lower visual field).

## Results and Discussion

*Behavioral Findings*

Performance levels on the glasses discrimination task were at ceiling level, and there were no significant differences between the conditions in both accuracy and RT (Table 2).

*fMRI Findings*

We first examined fMR adaptation to glasses presented simultaneously with faces as a function of their location relative to the face. Because there was no significant interaction between hemisphere and the experimental conditions, the data were collapsed across hemispheres using a weighted average on the basis of the relative size of the right and left FFA regions.

The FFA response to different glasses was higher than for same glasses both when glasses were presented on the face, $t(7) = 2.84$, $p = .025$, and above the face, $t(7) = 3.008$, $p = .02$ (Figure 4). A two-way ANOVA with location (on face, above face) and glasses identity (different, same) as repeated measures revealed a main effect of Glasses Identity, $F(1, 7) = 18.927$, $p = .03$. In contrast to results of Experiment 1, there was no Glasses Identity × Location interaction, $F(1, 7) = 0.756$, $p = .413$. These findings suggest that the FFA is sensitive to the identity of glasses when subjects fixate on glasses during a glasses discrimination task regardless of their location relative to the face.

The OFA response on the glasses task was overall similar to the FFA with a main effect for Glasses Identity, $F(1, 5) = 11.8$, $p < .03$, and no Glasses Identity × Location interaction, $F(1, 5) = 1.58$, $p = .32$. The LOC showed a marginally significant effect of Glasses Identity, $F(1, 7) = 4.15$, $p = .08$, and no Glasses Identity × Location interaction.

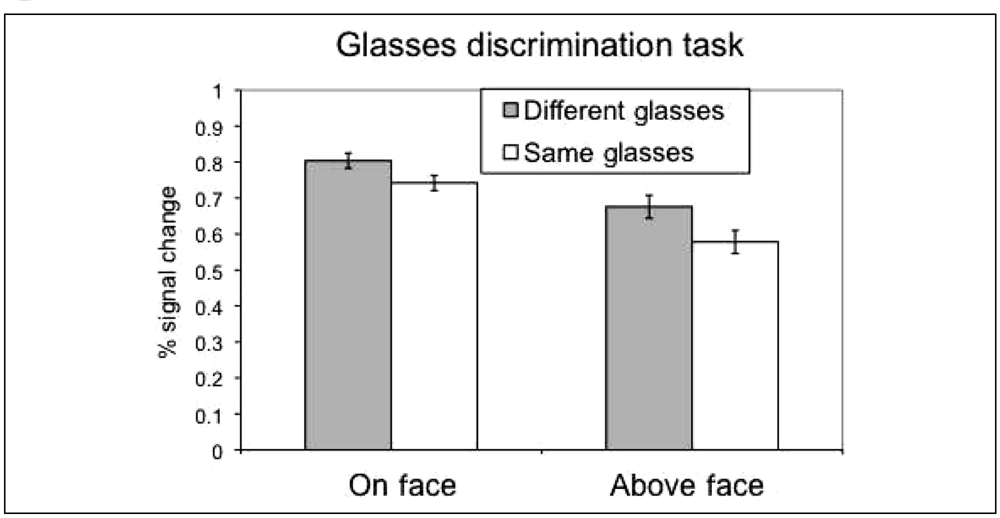


**Figure 4.** fMR adaptation in the FFA to glasses presented on the face or above the face during the glasses discrimination task (Experiment 2) revealed a significant higher response to different than same glasses in both locations (error bars represent the standard error of the difference between the responses to different and same glasses).

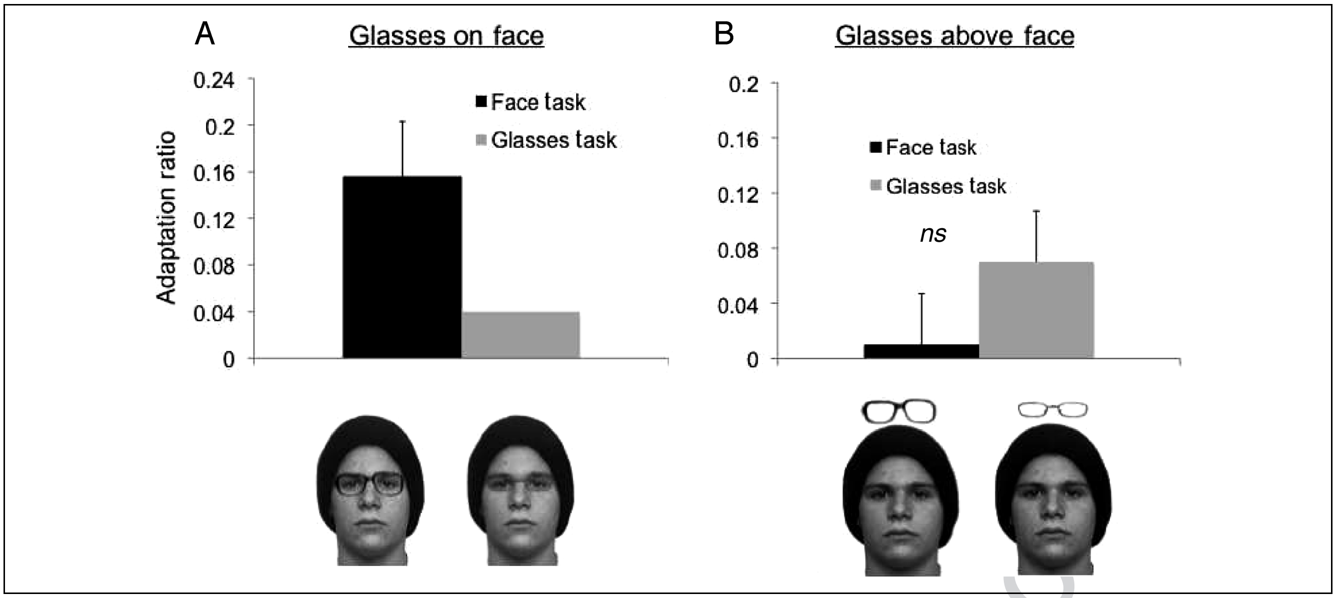


**Figure 5.** The effect of task and location on fMR adaptation to glasses in the FFA. The magnitude of adaptation effect for glasses is largest during a face-discrimination task than a glasses-discrimination task when glasses are presented on the face. There was no effect of task when glasses were presented above the face (error bars represent the standard error of the difference between adaptation scores of the two experiments).



Finally, in contrast to the face-selective areas that showed a higher response when glasses were on the face than above the face, a main effect of location OFA, $F(1, 5) = 12.96$, $p < .02$, and FFA, $F(1, 7) = 19.680$, $p < .003$, the LOC showed similar response to glasses regardless of their location, $F(1, 7) = 0.106$, $p = .755$.

Results so far demonstrate that the FFA shows adaptation to glasses during a glasses discrimination task. Is this effect as large as the effect we found during a face discrimination task (Experiment 1)? To compare the magnitude of adaptation effects across the two experiments, we calculated an adaptation index score (Different − Same) / (Different + Same). Adaptation for glasses presented on the face was significantly larger when subjects discriminated faces than when they discriminated glasses, $t(15) = 3.053$, $p = .008$ (Figure 5A). There was no effect of task when glasses were presented above the face, $t(15) = 1.55$, $p = .14$ (Figure 5B). A two-way mixed ANOVA with glasses location (on face, above) as a within-subjects factor and task (face task, glasses task) as a between-subject factor revealed a significant Glasses Location × Task interaction, $F(1, 15) = 8.429$, $p = .011$. Importantly, a similar analysis for the OFA and LOC revealed no significant interaction Glasses Location × Task interaction for the OFA, $F(1, 12) = 3.1$, $p = .11$, and LOC, $F(1, 12) = 2.1$, $p = .17$. In both areas, the largest adaptation effect was found for glasses presented on top of the face during a glasses discrimination task and therefore a larger sensitivity to glasses per se rather than to their effect on the representation of face identity. Overall, these findings suggest that fMR adaptation to glasses presented on the face but not above the face reflects the sensitivity of the FFA to the modified representation of face identity because of changes in glasses identity rather than a foveal bias.

Given the strong effect glasses have on the representation of faces and the fact that glasses are an object that is strongly associated with faces, it was important to verify that glasses alone are not generating a strong response in the FFA than other nonface stimuli, as is the case for other isolated facial features such as eyes (Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000). In addition, we wanted to assess the extent to which the FFA may be more sensitive to the identity of glasses than the identity of other object stimuli. To that effect, we measured the overall response and the adaptation to glasses and another nonface stimuli, chairs. As shown in Figure 6, the response of the FFA to glasses did not differ significantly from the response to chairs, $t(7) = 0.863$, $p = .417$. Notably, the response of the FFA to glasses and chairs was half the size the response to faces (Figure 7).

Examination of fMR adaptation to glasses and chairs revealed no significant difference between the response to different and same glasses, $t(7) = 0.713$, $p = .499$, and no significant difference between the responses to different than same chairs, $t(7) = 1.031$, $p = .337$. The absence of adaptation to glasses presented alone may be inconsistent with the significant adaptation to glasses presented above the face. Interestingly, however, a direct comparison of the magnitude of fMR adaptation to glasses presented alone with fMR adaptation to glasses presented above the face using a two-way ANOVA with glasses presentation type (above face, alone) and glasses identity (different, same) as repeated measures revealed no significant adaptation to Glasses Identity, $F(1, 7) = 2.42$, $p = .164$, and no Adaptation × Presentation Type interaction, $F(1, 7) = 0.129$, $p = .344$. These findings suggest that the adaptation effect to glasses during a glasses discrimination task is not a robust effect. The higher fMR response to glasses presented

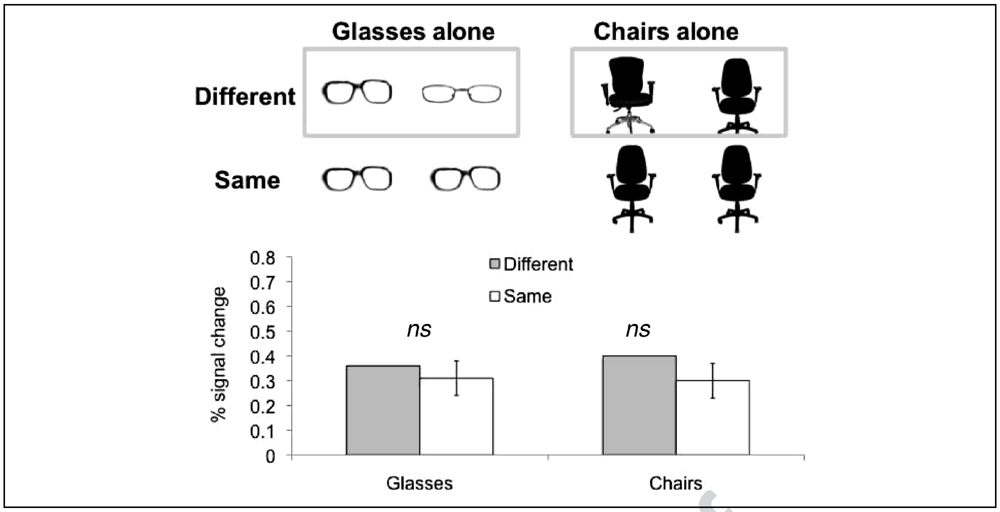


**Figure 6.** The response of the FFA to nonpreferred stimuli presented alone. No difference between the overall level of response of the FFA to glasses and chairs. The difference between the responses to different and same glasses and chair stimuli was not significant (error bars represent the standard error of the difference between the responses to different and same stimuli).

simultaneously with faces than for glasses presented alone, $F(1, 7) = 173.18, p < .0001$, probably improved the signal-to-noise ratio in the former case and was more sensitive to reveal small adaptation effects, which were absent for the low fMRI response of the FFA to nonface stimuli.

Taken together, our findings show that the FFA showed the greatest sensitivity to glasses when they were presented on the face during a face discrimination task but a much smaller or a nonsignificant effect in all other conditions.

## GENERAL DISCUSSION

fMRI studies have revealed several category-selective brain areas, which show a much stronger response to one object category (preferred) relative to all other categories (nonpreferred). Contrary to most previous fMRI studies that presented isolated images of each of these categories, here we examined the representation of a more complex stimulus, which includes both preferred and nonpreferred stimuli, in a category-selective brain region. Our findings clearly show that the identity of nonpreferred stimuli may modify the representation of preferred stimuli. Remarkably, we found the largest release from adaptation to different glasses when they were presented on the face during a face discrimination task rather than during a glasses discrimination task. Task demands did not influence the magnitude of adaptation to glasses presented above the face (Figure 5). These findings imply that the FFA is sensitive to the effect of glasses on the representation of face identity rather than to the identity of glasses per se. Previous studies have indicated that the FFA generates a holistic representation of faces (McKone & Yovel,



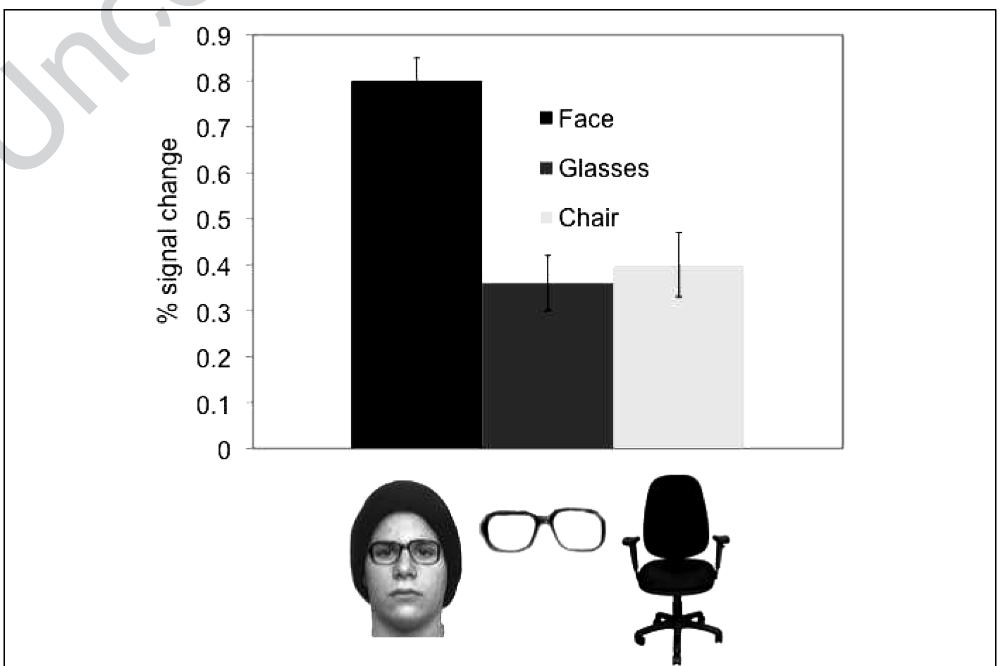


**Figure 7.** The overall response of the FFA across different and same trials of faces, glasses, and chairs shows that the FFA response to glasses is similar to chairs and much lower than the response to faces.

2009; Kanwisher & Yovel, 2006; Schiltz & Rossion, 2006). These studies have focused on the holistic representation of the internal facial features. Our study shows that the holistic representation of faces in the FFA may also include nonfacial stimuli that interact with the representation of the internal facial features.

The maximal adaptation effect to glasses presented on the face during a face discrimination task was unique to the FFA. Examination of the response of the OFA and the object general LOC revealed no significant effect of task on the magnitude of adaptation to glasses presented on the face. In contrast to the FFA, the OFA and the LOC were similarly sensitive to the identity of glasses regardless of their location relative to the face and whether subjects discriminated glasses or faces.

Interestingly, our behavioral findings show that subjects correctly matched identical faces that differ in glasses as same faces. These findings are inconsistent with the release from adaptation that we found for same faces that differ in glasses in the FFA and suggest that the representation that determined behavior is different from the representation that is generated by the FFA. Before the experiment, our subjects were familiarized with the appearance of the same face with different glasses (see Methods). We therefore suggest that the representation of the FFA may reflect the appearance of the face image rather than the knowledge that subjects had about the similarity of two same faces that differ in glasses. Such knowledge, which is based on prior familiarization with the faces and is reflected in behavioral performance, may be represented in more anterior areas such as the anterior temporal cortex or the frontal lobes that have been shown to be involved in face recognition (Avidan & Behrmann, 2009; Kriegeskorte, Formisano, Sorger, & Goebel, 2007).

### Effects of Attention on fMR adaptation

Previous studies that examined the effect of task/attention demands on the magnitude of adaptation reported a stronger adaptation effect to attended than nonattended features. For example, Yi et al. (2006) showed adaptation to faces in the FFA and to houses in the parahippocampal place area (PPA), when these stimuli were attended but not when they were unattended (see also Murray & Wojciulik, 2004). Attention effects also yielded better discrimination performance in a multivoxel pattern analysis study (Reddy & Kanwisher, 2007). Our findings actually showed the opposite effect. Adaptation to glasses in the FFA was much stronger when glasses where unattended during a face discrimination task than when glasses where attended during the glasses discrimination task. A possible explanation for the discrepancy is that in the studies of Yi et al. and Reddy and Kanwisher (2007), the stimuli were presented either as overlapped transparent images or side by side, respectively, so the representations of the two categories were independent. Our stimuli included a combined image in which the representation of the two categories may interact. The opposite effect of attention that we reveal further strengthens our conclusion that the FFA was sensitive to the effect of the glasses on the identity of the faces rather than sensitivity to the glasses themselves.

### The Representation of Nonpreferred Stimuli in the FFA

The fact that glasses are objects that are primarily associated with faces may raise the question of whether they are treated by the FFA as nonpreferred stimuli or as a facial feature such as eyes. It was therefore important to assess whether the FFA response to glasses is different from the response to other nonface objects that are not associated with faces. A comparison between the response to glasses and the chairs showed that the FFA response to glasses does not differ from the response to chairs and both were much lower than the response to faces (Figure 7). Tong et al. (2000) have shown that the response of the FFA to isolated eyes was significantly higher than the response to nonpreferred, house stimuli. Our findings therefore suggest that unlike isolated eyes, which generate a large response in the FFA, isolated glasses are not processed as a facial feature by the FFA but as any other nonface object.

Our findings show that the FFA was sensitive to the identity of glasses during a glasses discrimination task when glasses were presented simultaneously with faces (Figure 4) but not when they were presented alone (Figure 6). Previous studies that have employed the fMR-adaptation paradigm reported mixed results. For example, Avidan, Hasson, Hendler, Zohary, and Malach (2002) reported fMR adaptation to the nonpreferred houses and cars in the face-selective FFA (see also, Ewbank, Schluppeck, & Andrews, 2005) and to faces in the scene-selective PPA. In contrast, Yi et al. (2006) found no adaptation to the nonpreferred houses in the FFA and no adaptation to faces in the PPA (see also, Henson & Mouchlianitis, 2007). An inherent problem in the study of nonpreferred stimuli is the fact that they elicit, by definition, low responses in category-selective regions. Thus, any null effects that are found for nonpreferred stimuli may reflect the low signal-to-noise ratio of this weak signal rather than the true representation of nonpreferred stimuli (e.g., Grill-Spector et al., 2004). Indeed, our findings revealed significant adaptation to glasses only when they were presented simultaneously with faces but not when presented alone. Although the mean response to different glasses was higher than to identical glasses presented alone (Figure 6), the low fMRI signal generated for glasses presented alone was much more variable. Thus, the stronger fMRI signal to glasses that are presented simultaneously with faces may increase the signal-to-noise ratio and provide a more sensitive way to assess the representation to nonpreferred signal in a category-selective area. This procedure may be a useful tool to study the representation of nonpreferred stimuli, not only for fMR-adaptation designs but also for MVPA split-half correlation analysis (Haxby et al., 2001), studies that examine correlations of region activation with success in recognition (Grill-Spector et al., 2004; Grill-Spector, Kushnir, Hendler, & Malach, 2000) as well as examination of the response of single neurons to nonpreferred objects.

The stronger response to glasses presented with faces than alone may be consistent with reports of single cell recording in inferotemporal cortex that revealed an intermediate response to simultaneous presentation of preferred and nonpreferred stimuli, which was lower than the response to preferred stimuli alone but higher than the response to nonpreferred stimuli alone (e.g., Zoccolan, Cox, & DiCarlo, 2005). These studies have focused on the reduced response to the simultaneous presentation of pairs of stimuli (i.e., effect of clutter) relative to preferred stimulus alone. Here we highlight the other side of the possibly same effect—the increase in response to the nonpreferred stimuli by simultaneous presentation with the irrelevant preferred stimulus and its potential benefit to the study of the representation of nonpreferred responses.

Recent studies have suggested that adaptation to nonpreferred stimuli in the FFA may be mediated by “hot spots” of non-face-selective areas within the FFA that cannot be detected with standard resolution fMRI (but see, Baker, Hutchison, & Kanwisher, 2007; Grill-Spector, Sayres, & Ress, 2006). Although we cannot completely deny the possible contribution of such glasses-selective areas, if they indeed exist (Tsao, Freiwald, Tootell, & Livingstone, 2006), to the adaptation effect we found for glasses (Figure 4), the maximal fMR adaptation to glasses during a face discrimination task (Figure 5) cannot be solely mediated by such glasses-selective “hot spots” but more likely to be mediated by face-selective areas that are sensitive to the modified representation of faces generated by the different glasses. Having said that, it is noteworthy that neural selectivity cannot be directly inferred from patterns of fMR adaptation. Recent single-neuron recording studies in monkeys have pointed out that in contrast to inferences made in earlier fMR-adaptation studies about the representation of information at the neuronal level (e.g., Grill-Spector, Kourtzi, & Kanwisher, 2001), the pattern that is revealed with fMR adaptation does not necessarily reflect the representation of a single neuron (Bartels, Logothetis, & Moutoussis, 2008; Sawamura et al., 2006). Nevertheless, fMR adaptation provides complementary information to electrophysiology about processing at a larger scale that may not be detected at the local level of single unit (Bartels et al., 2008).

In summary, our study examined the effect of nonpreferred stimuli (glasses) on the representation of preferred stimuli (faces) in a category-selective brain region (FFA). Our results suggest that the identity of nonpreferred stimuli (glasses) significantly modified the representation of preferred stimuli (faces). Given that the visual system is commonly exposed to simultaneous presentation of stimuli from various categories, the future investigation of whether where and under what conditions the representations of these different categories influence each other in object-category-selective cortex is critical for understanding how the visual system represents natural, complex visual scenes.


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Reprint requests should be sent to Galit Yovel, Department of Psychology, Tel Aviv University, Tel Aviv, Israel, or via e-mail: galit@freud.tau.ac.il.




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