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External facial features modify the representation of internal facial features in the fusiform face area

Vadim Axelrod, Galit Yovel *

Department of Psychology, Tel Aviv University, Tel Aviv, 69987, Israel

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ABSTRACT

Most studies of face identity have excluded external facial features by either removing them or covering them with a hat. However, external facial features may modify the representation of internal facial features. Here we assessed whether the representation of face identity in the fusiform face area (FFA), which has been primarily studied for internal facial features, is modified by differences in external facial features. We presented faces in which external and internal facial features were manipulated independently. Our findings show that the FFA was sensitive to differences in external facial features, but this effect was significantly larger when the external and internal features were aligned than misaligned. We conclude that the FFA generates a holistic representation in which the internal and the external facial features are integrated. These results indicate that to better understand real-life face recognition both external and internal features should be included.

Introduction

The study of face recognition has been primarily focused on the representation of the internal facial features. The main reason external facial features are usually excluded is because it is believed that face recognition should primarily depend on the shape and configuration of the internal features rather than on external features such as hair that may dramatically vary when people get a hair cut, grow facial hair or put a hat on. Indeed, individuals who suffer from face recognition difficulties (i.e. prosopagnosia) report that they primarily rely on external facial features in order to recognize a person and when such information is missing or varied, they lose their ability to recognize the face. Accordingly, most studies of face recognition have presented faces in which the hair is excluded by either cropping the outline of the face (e.g., Goffaux and Rossion, 2007; Leopold et al., 2005; Robbins and McKone, 2003), putting a similar hat on all faces (e.g., Duchaine and Nakayama, 2006; Le Grand et al., 2001; Mondloch et al., 2002) or combining internal features of different faces with the same external features so discrimination depends only on the internal features (e.g., Yovel and Kanwisher, 2004; Yovel and Kanwisher, 2005).

Nevertheless, external features may modify the representation of the internal features. A striking demonstration of this effect was reported by Sinha and Poggio (1996, 2002), who presented two familiar faces that had the same internal features but each was combined with the external features of a different familiar face (e.g., the internal features of President Bill Clinton, with the external features of Clinton for one face and Vice-President Al Gore for the other face). In this *Clinton–Gore illusion* (and later *Bush–Cheney illusion*) they showed that the similar internal features appeared very different when each was combined with different external facial features. These findings imply that by excluding external facial features we lose important information about the way faces are represented in real life when both internal and external features are used for face recognition.

The primary focus on internal facial features has also been prevalent in functional MRI (fMRI) studies of face processing, particularly in studies that examined the representation of face identity. One of the most common paradigms that has been used to examine the representation of face identity is fMR-adaptation (Grill-Spector and Malach, 2001). In this paradigm the response of a given brain area to faces that differ in identity is compared to the response of similar faces. Because the fMRI response is reduced for repeated presentation of the same image, a brain area that shows release from adaptation to different faces, as reflected by a higher response to different than same stimuli, indicates that it is sensitive to the difference between the two images (Grill-Spector et al., 1999; but see, Sawamura et al., 2006). A consistent finding of fMR-adaptation of face identity studies is that the fusiform face area (FFA) is sensitive to face identity information (e.g., Ewbank and Andrews, 2008; Gilaie-Dotan and Malach, 2007; Mazard et al., 2006; Rotshtein et al., 2005; Yovel and Kanwisher, 2005). For example, in an elegant study Rotshtein et al. (2005) presented a morph sequence of two familiar faces and found an fMR-adaptation to two morphed faces that were perceived as two different identities but not for two faces of equal morph distance that were

* Corresponding author. Fax: +972 3 6409547.
E-mail address: galit@freud.tau.ac.il (G. Yovel).

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perceived to belong to the same identity (see also Gilaie-Dotan and Malach, 2007). These findings indicate that the higher fMRI response to different than same faces does not merely reflect differences in low level features, but the representation of identity of the face. In line with this idea, Yovel and Kanwisher (2005) have shown that fMR-adaptation to faces is abolished when the same faces are presented up-side down (inverted) (see also, Mazard et al., 2006).

Because most fMRI studies of face identity have focused on the representation of internal facial features, we do not know yet whether external features may influence the representation of the internal features in the FFA. In a recent study, Betts and Wilson (2009) have used fMR-adaptation to examine cross adaptation between internal and external features and concluded that they are represented independently. This study, however, did not directly examine whether the identity of the external feature may modify the identity of the internal features as was demonstrated in behavioral studies (Patterson and Baddeley, 1977; Sinha and Poggio, 1996, 2002).

Taken together, results so far have shown that the FFA is sensitive to the identity of internal facial features. The goal of the current study was to examine whether the representation of internal features is influenced by the identity of external facial features. To test this effect we examined the response of the FFA to three types of different and same identity pairs of faces: a pair in which the hair is covered with a similar hat, a pair without a hat, a pair in which one face had a hat on and the other did not (see Fig. 1A). In Experiment 1 we asked whether the FFA is sensitive to differences in external facial features. If the representation of face identity in the FFA is invariant to changes in external features, we expect to reveal higher response to different faces than same faces that differ in external features (Fig. 1B, left). If the FFA is not invariant to external features such as hat/hair, it will show release from adaptation to same faces that differ in external features (Fig. 1B, right).

Experiment 1

Material and methods

Subjects

Ten healthy volunteers (age: 19–30, all right handed, 7 females) participated in Experiment 1. All subjects gave informed consent to participate in the study, which was approved by the ethics committee of the Tel Aviv Sourasky Medical Center.

Stimuli. All face and object stimuli were grayscale. Functional localizer images were miscellaneous photographs of faces and objects; scrambled objects were a random mixture of pixels of the object image category. In the fMR-adaptation experiment face stimuli were photographs of twelve different male faces with and without a hat drawn from the Harvard Face Database, with permission and consent. The faces subtended 4.5° in width and 6.8° in height.

Apparatus. MRI data was collected in a 3 T MRI scanner. Echo planar imaging sequence was used to collect fMRI data with TR = 1.5 s, TE = 35 ms, flip angle: 90°, 22 slices per TR, slice thickness: 4 mm no gap, matrix 64 × 64, FOV 256 mm. The slices were aligned in parallel to the temporal lobe and covered the entire occipital and temporal lobes but did not include the superior parietal and frontal cortex.

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 the subjects' eyes.

Functional localizer sessions

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 min. Each localizer scan consisted of 4 blocks for each category and 5 blocks of a baseline fixation point. In order to ensure general vigilance, subjects were instructed to press a response box button, whenever two identical images appeared consecutively (1-back task). Subjects were presented with 2 localizer scans.

fMR-adaptation sessions

We used a rapid event-related design with 8 conditions, 6 face conditions and 2 object conditions. Each trial consisted of four images. The face conditions included either faces with a hat, faces without a hat or pairs of faces in which one had a hat and the other did not. On each trial the four faces were either of same identity or were

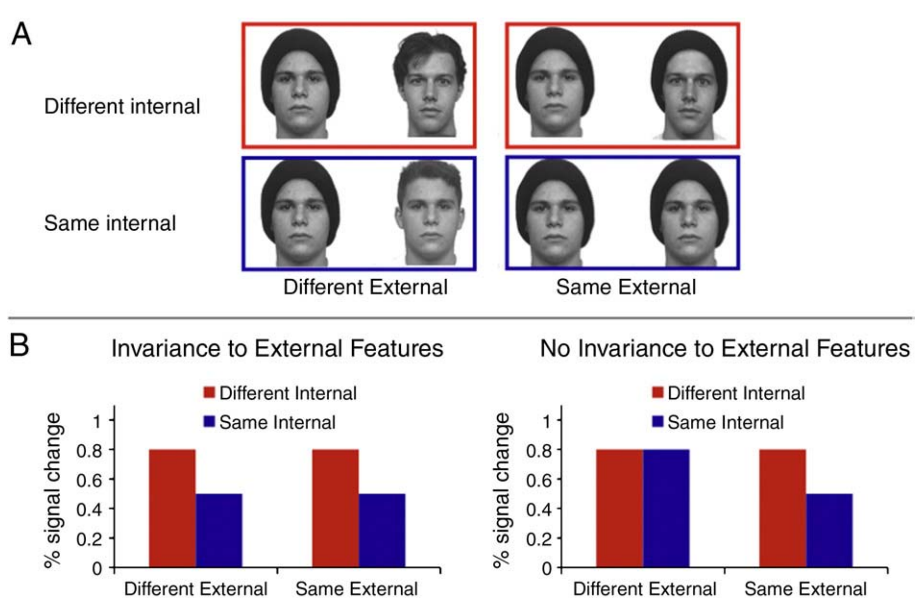

Fig. 1. Predicted FFA responses to same or different faces that differ or share the same external features shown above. If the FFA is invariant to changes in external features it will show a similar adaptation effect (higher response to different than same identity faces) when external features are the same or different (left side graph). If the FFA is sensitive to external features it will show release from adaptation to same identity faces that differ in external features (right side graph).

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composed of two pairs of different identity faces (see Fig. 1A, which presents one pair of each face condition). The other two conditions presented different objects (cars, chairs) to assure that the face-selective ROIs selected based on the localizer scan are indeed face-selective also for the fMR-adaptation scans (i.e., higher response to face stimuli than non-face stimuli). Exposure duration was 0.3 s and inter-stimulus-interval (ISI) was 0.2 s. The inter trial interval was 1 s. The total length of each trial was 3 s: $(0.3\ s+0.2\ s)\times 4+1\ s$. Each scan included 12 repetitions for each condition and 24 null events presented in a pseudo-randomized order (http://surfer.nmr.mgh.harvard.edu/optseq/), which allowed the deconvolution of fMRI signal time locked to the rapidly presented stimuli. The stimuli were projected on the screen with 30 pixel location jitter in order to prevent discrimination based on apparent motion. Subjects were asked to press one key on trials when faces were of same identity and a different key when faces were different in identity. Each experiment consisted of six sessions. Each scanning session included 240 TRs and lasted 6:12 min.

At the beginning of the experiment (during the anatomical scans), a familiarization session was presented. The 12 different face identities were presented sequentially in pairs of same identity-different external feature stimuli. The two faces in each pair were presented side by side, so subjects could learn how each face looks with and without the hat. Subjects were told that they should passively view these faces that will be later presented in the sequential presentation matching task. Each pair was presented for 5 s. The session lasted 5 min, which included 5 cycles of the 12 identities.

Data analysis. Functional MRI 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 presented during a blank screen and discarded from the analysis. Data were preprocessed using time slice correction, realignment, normalization to a standard template [Montreal Neurological Institute (MNI), voxel size $3\times 3\times 3$], and spatially smooth with an $8\times 8\times 8$ mm full-width at half-maximum (FWHM) Gaussian kernel. GLM was conducted for the functional scans for each participant by modeling the observed event-related BOLD signal according to the regressors. Data from the functional localizer was used to define face-selective areas. The time-courses of the fMR-adaptation task were extracted for the right and left FFA.

Functional localizer

The face-selective region in the fusiform gyrus (FFA) was defined according to the contrast faces>objects ($p<.00001$, uncorrected). We focused on the FFA because previous studies have shown that other regions in the ventral visual cortex showed no (e.g., STS) or weak (i.e. OFA, LOC) sensitivity to face identity (Grill-Spector et al., 2004; Rotshtein et al., 2005; Yovel and Kanwisher, 2005).

fMR-adaptation experiment

The time-courses of BOLD response were extracted for each of the 8 conditions within the face-selective ROIs. Peak values (around 6 s from stimulus onset) were used as dependent measures for fMR-adaptation calculation. For all subjects the FFA response was higher for the faces than the non-face conditions of the fMR-adaptation task.

Results and discussion

Behavioral results

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

Functional MRI results

Fig. 2 presents the averaged BOLD signal change in FFA across 10 subjects. Since there was no significant interaction between hemispheres and the other conditions, the data was averaged across hemispheres, using a weighted average based on the volume of the right and left FFA.

A 2-way ANOVA with Identity (same-different) and External Feature (Hat, Hair, Hat–Hair) as repeated measures revealed a significant interaction between Identity and External feature $F(2,8)=21.305$, $p<.001$; $\eta^2=0.842$, which reflects a different pattern of fMR-adaptation to face identity according to the external feature manipulation (see Fig. 2B). For faces that shared the same external features (Hat or Hair) we found a higher response to different than to same faces ($t(9)=7.81$, $p<0.001$ for Hat and $t(9)=2.34$, $p<0.044$ for Hair). These results replicate previous studies that reported fMR-adaptation to faces that share the same external features in the FFA. The critical condition for our experiment was when faces shared the same internal features but differ in external features. Results demonstrate a total release from adaptation for the same identity faces that differ in external features. The higher response to same than for different faces was not significant $t(9)=2.06$, $p=0.07$.

These results indicate that the FFA is not invariant to external features. Further analysis for same identity conditions only reveals a significantly higher response to same faces that differ in external features than same faces that shared the same external features (Hat–Hair vs. Hat: $t(9)=13.860$, $p<0.001$; Hat–Hair vs. Hair: $t(9)=5.54$, $p<0.001$). Those results clearly demonstrate a strong release from adaptation to external features, despite the fact face identity remained constant.

Our findings replicate previous reports that show a higher response to different than same identity faces that share the same external features. The novel question of the current experiment was whether the representation of face identity in the FFA is invariant to external features. Our findings show that the FFA is not invariant to changes in external features. The response to same faces that differ in external features did not differ from the response to different faces, and was significantly higher than the response to same faces that had the same external features (Fig. 2). Two possible explanations may account for these findings: According to the first hypothesis the FFA is sensitive to the difference between hair and hat per se. These findings are consistent with a recent report, which reveals fMR-adaptation to external facial features alone (Andrews et al., 2010; Betts and Wilson, 2009). Another possibility is that the external features modified the identity of the internal facial features, and the release from adaptation also reflects the effect of external features on the representation of internal features, rather than sensitivity to external features per se. Experiment 2 was designed to decide between these two alternatives.

Experiment 2

To explore whether the FFA is sensitive to differences in external features per se or to their influence on the representation of the internal features, we used the same images presented in Experiment 1 but we misaligned the external and internal features (see Fig. 3A). Such stimulus manipulation has been used in the past to examine the interactive effect

Table 1
Experiment 1: Behavioral performance of face discrimination task for *aligned* face stimuli measured in the scanner. The first value is the percentage of correct responses; the value in brackets is the average reaction time calculated from fMRI event onset.

	Same external (cap)	Same external (hair)	Different external (cap–hair)
Same identity	98% (2.21 s)	98% (2.16 s)	95% (2.24 s)
Different identity	98% (2.16 s)	98% (2.12 s)	96% (2.12 s)

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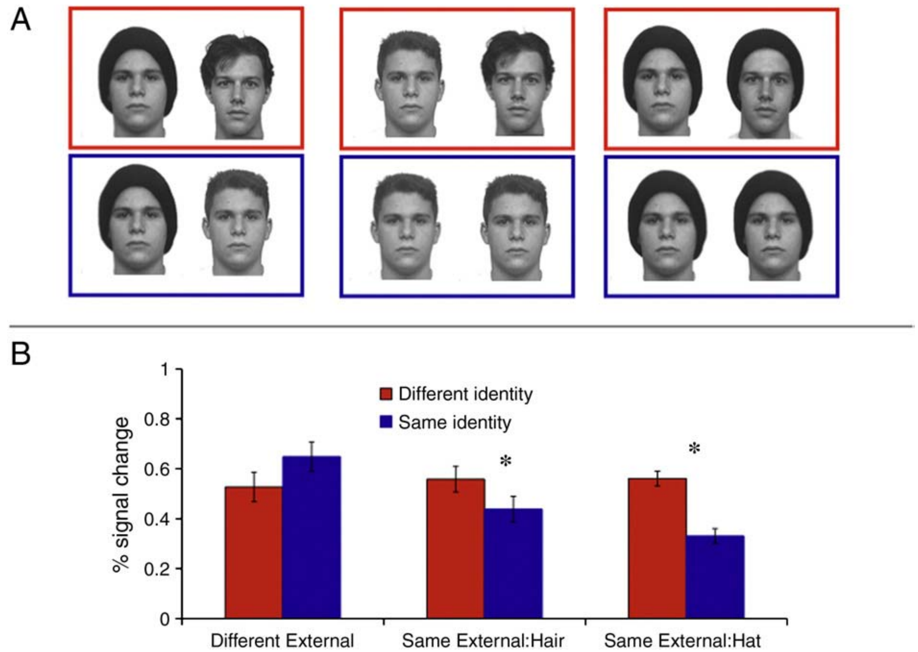

Fig. 2. The FFA response to same and different identity faces that differ in external features or share the same external features (hair or hat), show that the FFA is sensitive to differences in external features. Error bars indicate the standard error of the difference between different and same conditions.

of the identity of the upper and lower half of faces in the Composite Face Task (Robbins and McKone, 2007; Schiltz and Rossion, 2006; Young et al., 1987). Recognition of half of the face was much better when the two different identity halves were misaligned than aligned. These findings suggest that the two halves are fused together and each influences the representation of identity of the other. We used the same rational to assess the influence of the external on the internal features. Our proposition was as follows: if the release from adaptation to different external features that we found in Experiment 1 is solely due to the sensitivity of the FFA to external features, we will find the same release from adaptation to different external faces for the misaligned faces. If the effect that we found in Experiment 1 also reflects the influence of the external features on the internal features, we will find a smaller release from adaptation for the misaligned faces than the aligned faces that differ in external features but share the same internal features.

Material and methods

Subjects

Eight subjects participated in Experiment 2 (age: 19–32, 5 females). All subjects signed a consent form that was approved by the ethics committee of the Tel Aviv Sourasky Medical Center.

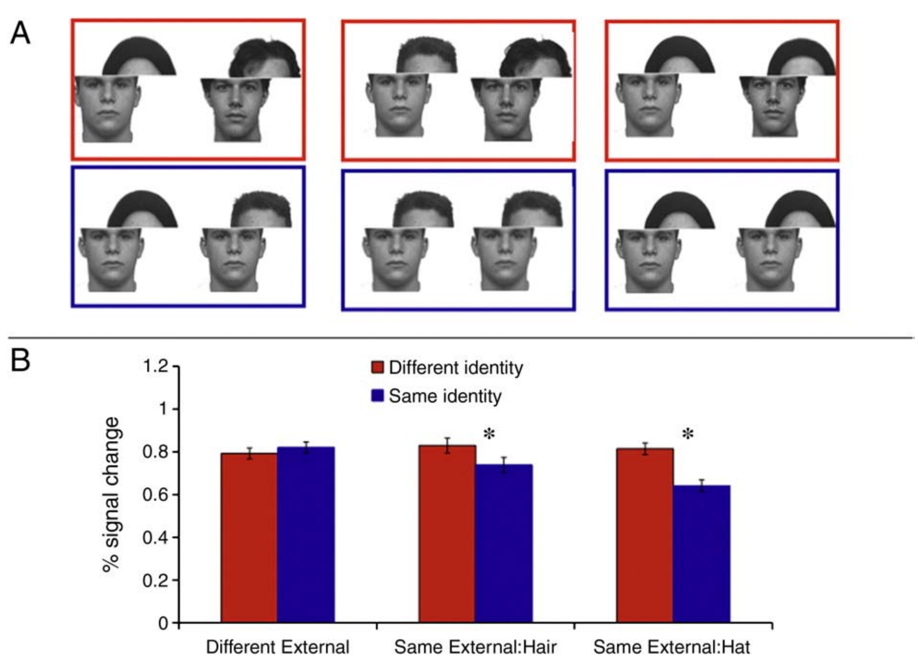

Fig. 3. The FFA response to same and different identity faces that differ in external features or share the same external features (hair or hat) in which the external and internal features are misaligned. The FFA is sensitive to differences in external features even when they are misaligned. Error bars indicate the standard error of the difference between different and same conditions.

Stimuli

Face images from Experiment 1 were modified by misaligning top part of the face, which contain either hat or hair, and the bottom part which contained the internal facial features (Fig. 3A).

Procedure

All experimental procedures and data analysis were similar to those used in Experiment 1.

Results and discussion

Behavioral results

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

Functional MRI results

Fig. 3B presents the percent signal change of the peak response of the FFA for each condition averaged across 8 subjects. Because there was no significant interaction between hemispheres and any of the other factors, the data were collapsed across hemispheres.

A 2-way ANOVA Identity (same-different) × External Feature (Hat, Hair, Hat–Hair) revealed significant main effects for Identity $F(2,7) = 27.63$, $p < .001$; $\eta^2 = 0.798$, significant main effects for External Feature $F(2,7) = 5.68$, $p < .041$; $\eta^2 = 0.654$, and significant interaction between identity and external feature $F(2,7) = 15.93$, $p < .0.004$; $\eta^2 = 0.842$.

Paired *t*-tests revealed a significantly higher response to different identity than same identity faces when external features were similar ($t(7) = 6.35$, $p < 0.001$ for Hat and $t(7) = 2.611$, $p < 0.035$ for Hair), but not when external features were different ($t(7) = -1.082$, $p < 0.315$). Furthermore, analysis of same faces only revealed a higher response when external features were different than when they were similar (Hat–Hair vs. Hat: $t(7) = 9.175$, $p < 0.001$; Hat–Hair vs. Hair: $t(7) = 4.083$, $p < 0.005$). Thus, similar to Experiment 1, we found release from adaptation to external features, which indicates that the FFA is sensitive to differences in external features.

Our next question was whether the magnitude of the effect for external features was similar for aligned and misaligned faces. Release from adaptation to external features when they are aligned with the internal features (Exp 1) may reflect both sensitivity to external features per se, as well as the effect of the external features on the perceived identity of the face. In that case, we expect that the magnitude of the adaptation effect for external features (i.e. the difference between the response to different relative to same external features for same identity faces) will be larger for aligned than misaligned faces. To assess this hypothesis we compared the magnitude of release from adaptation to external features for aligned and misaligned same identity faces only. For each subject we computed two adaptation ratio indices, one in which we compared different external features (Hat–Hair condition) to same external features that shared the same hat (Hat condition): Hat Ratio = (Different Hat–Hair − Same Hat) / (Different Hat–Hair + Same Hat); the second in which we compared the different external feature condition (Hat–Hair) to the same external feature condition same hair: Hair Ratio = (Different Hat–Hair − Same Hair) / (Different Hat–Hair + Same Hair). The magnitude of release from adaptation to different external features was significantly larger for aligned than misaligned faces (Fig. 4) both when the same external feature was Hair $t(16) = 2.7$ $p < .02$ and when same external feature was a Hat $t(16) = 3.5$, $p < .005$. These findings are consistent with the idea that the FFA is sensitive to the external features per se, but further shows that it is also sensitive to their effect on the perceived identity of the internal features.

Table 2
Experiment 1: Behavioral performance of face discrimination task for *misaligned* face stimuli measured in the scanner. The first value is the percentage of correct responses; the value in the brackets is the average reaction time calculated from fMRI event onset.

	Same external (cap)	Same external (hair)	Different external (cap–hair)
Same identity	98% (2.07 s)	98% (2.11 s)	98% (2.09 s)
Different identity	98% (1.96 s)	98% (2.00 s)	99% (2.00 s)

General discussion

The goal of this experiment was to assess whether the representation of face identity in the FFA is modified by changes in external features. In the first experiment we presented faces of same or different identity that either shared the same external features or differed in external features. We found that the FFA was sensitive to different external features, showing release from adaptation for same faces that differ in external features. These findings are consistent with recent reports, which showed that the FFA represents information about external facial features (Andrews et al., 2010; Betts and Wilson, 2009). These findings however cannot tell whether the sensitivity of the FFA to external facial features reflects, at least to some extent, the effect of the external features on the representation of the internal features rather than sensitivity to external features per se. In order to answer this question, in Experiment 2 we misaligned the external and internal features (Fig. 3A). When the external and internal features are misaligned, the FFA still shows sensitivity to the external features, but it was significantly smaller than the effect that we found when the external and internal features were aligned (Fig. 4). These findings suggest that the FFA is not only sensitive to external features but is also sensitive to their influence on the representation of internal facial features.

The influence of external features on the identity of internal features is consistent with the holistic nature of the representation of the face. For example, in the composite face effect, the identity of one half of the face may modify the identity of the other half of the face (Le Grand et al., 2004; Young et al., 1987). Evidence for a composite face effect in the FFA was recently reported by Schiltz and Rossion (2006) who also applied an fMR-adaptation design and found that the FFA showed release from adaptation to two identical half faces that were combined with two different half faces. This fMR composite effect was found for upright but not for inverted faces, which is consistent with behavioral findings that show a composite effect for upright but not for inverted faces. Furthermore, in a recent study we also showed that external features such as glasses may modify the representation of the internal features (Axelrod and Yovel, in press). Thus, even non-face object stimuli can influence the representation of internal facial features when they are combined with them to generate a coherent facial image of both external and internal features.

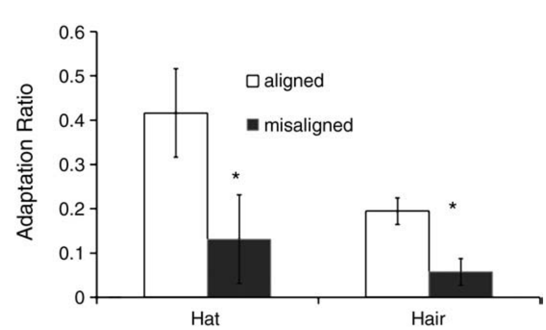

Fig. 4. A comparison of the magnitude of the release from adaptation (adaptation ratio) to the external features for aligned and misaligned faces. Release from adaptation is significantly larger for aligned than misaligned faces, indicating that external features modify the representation of internal features in the fusiform face area. Error bars indicate the standard error of the adaptation ratio.

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Consistent with the influence of the external facial features on the representation of the internal facial features that we revealed in the FFA, previous behavioral studies that examined the effect of external features on recognition of internal features have reported that subjects tend to make more recognition errors when the same face is presented with different hairstyles (Patterson and Baddeley, 1977). In our study, behavioral performance for data collected in the scanner was at ceiling level for all conditions. The high performance for the same identity faces that differ in external features can be attributed to the pre-scan familiarization session during which subjects were presented with the faces and their appearance with and without the hat. The original goal of this familiarization session was to maximize the chances of revealing invariance to external features in the FFA, if such an effect indeed exists. The fact that performance level was at ceiling limits our ability to draw any conclusions about the relationship between performance level and the response of the FFA in our study.

What is then the nature of the representation of face identity in the FFA? Data from multiple studies have suggested that the FFA is sensitive to face identity but is not invariant to changes in view or lighting. Our study shows that the FFA is sensitive also to change in external features of the face. Interestingly, however, the FFA is also sensitive to the effect of the external features on the representation of the internal features. These findings therefore provide further support to the notion that FFA generates a holistic representation of a face but this holistic representation is not limited to the internal features but includes also the external features. Nonetheless, our data also show that the FFA is sensitive to differences in external features per se. These findings are consistent with recent reports that revealed release from adaptation to external facial features presented alone (Andrews et al., 2010; Betts and Wilson, 2009). These findings imply that external features may be also represented independently from the internal features in the FFA. Importantly, however, the larger release from adaptation that we revealed in the FFA when external features were aligned than misaligned, clearly suggest that in addition to possible independent representations, external and internal features also interact.

In summary, our study examined whether the representation of face identity in the FFA is influenced by modification of external features. We revealed that the FFA generates a holistic representation of a face, which includes both the internal and external facial features. We therefore suggest that the many previous studies of face identity processing that excluded the hair have overlooked an important aspect of face identity processing, one that incorporates information from both external and internal features. Although the need to exclude external features in certain type of face recognition tasks is unavoidable, to better understand how faces are processed in a real-life situation, both internal and external features should be included.

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