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The Anterior Temporal Face Area Contains Invariant Representations of Face Identity That Can Persist Despite the Loss of Right FFA and OFA

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Abstract

Macaque neurophysiology found image-invariant representations of face identity in a face-selective patch in anterior temporal cortex. A face-selective area in human anterior temporal lobe (fATL) has been reported, but has not been reliably identified, and its function and relationship with posterior face areas is poorly understood. Here, we used fMRI adaptation and neuropsychology to ask whether fATL contains image-invariant representations of face identity, and if so, whether these representations require normal functioning of fusiform face area (FFA) and occipital face area (OFA). We first used a dynamic localizer to demonstrate that 14 of 16 normal subjects exhibit a highly selective right fATL. Next, we found evidence that this area subserves image-invariant representation of identity: Right fATL showed repetition suppression to the same identity across different images, while other areas did not. Finally, to examine fATL's relationship with posterior areas, we used the same procedures with Galen, an acquired prosopagnosic who lost right FFA and OFA. Despite the absence of posterior face areas, Galen's right fATL preserved its face selectivity and showed repetition suppression comparable to that in controls. Our findings suggest that right fATL contains image-invariant face representations that can persist despite the absence of right FFA and OFA, but these representations are not sufficient for normal face recognition.

Key words: cognitive neuroscience, fMRI, fusiform face area, neuropsychology, occipital face area, prosopagnosia

Introduction

Humans are remarkably good at recognizing familiar faces across changes in size, luminance, viewpoint, position, and other physical properties. A fundamental question is how our visual system achieves invariant face recognition despite these changes (Rolls 2000; DiCarlo et al. 2012). Face processing is a promising area to investigate the cortical mechanisms underlying invariant recognition, because humans are remarkably good at recognizing familiar faces across retinal changes, and face processing involves a well-defined set of interconnected cortical areas that show a much stronger response to faces than to other objects (Tsao et al. 2008; Haxby and Gobbini 2011; Kanwisher and Barton 2011). Posterior face-selective areas include the occipital face area (OFA) in the inferior occipital gyrus (Gauthier et al. 2000), fusiform face area (FFA) in the lateral fusiform gyrus (Kanwisher et al. 1997), and a region in the posterior superior temporal sulcus (pSTS, Hoffman and Haxby 2000). More anterior face areas are found in anterior STS (Said et al. 2010; Pitcher et al. 2011), amygdala (Morris et al. 1996; Mende-Siedlecki et al. 2013), inferior frontal lobe (Nakamura et al. 1999), and anterior temporal lobe (fATL, also known as anterior temporal face patch, ATFP; Tsao et al. 2008; Pinsk et al. 2009; Rajimehr et al. 2009). A similar set of face-selective patches are also present in macaques, and single-cell recordings within the macaque patches suggest coding of a progressively more invariant representation in the face regions along the occipitotemporal axis, with the anterior medial

(AM) face patch containing neurons that respond to particular identities across different images (Freiwald and Tsao 2010).

Little is known about the cortical locus of invariant face representation in humans. The great majority of human imaging work has focused on the posterior face areas, leaving open the possibility that invariant representation occurs in the fATL, a possible homolog of macaque AM (Yovel and Freiwald 2013). Previous studies have found a face-selective response in the anterior temporal lobe, but fATL has been difficult to identify reliably (Rajimehr et al. 2009). This difficulty and the resulting paucity of studies of fATL may be due to signal drop-off in the anterior inferior portion of the temporal lobe induced by the susceptibility artifact near the ear canal (Ojemann et al. 1997; Devlin et al. 2000; Axelrod and Yovel 2013). In addition, the static images used in traditional localizer procedures often fail to effectively elicit activation in fATL. Dynamic stimuli elicit more reliable and robust face-selective activation than static stimuli (Fox et al. 2009; Pitcher et al. 2011), so here we first attempted to identify fATL and other face-selective areas using the dynamic localizer developed by Fox et al. (2009).

To investigate the cortical areas underlying invariant face processing, we examined the sensitivity of face-selective areas to identity information using an fMRI adaptation paradigm. fMRI adaptation, also known as fMRI repetition suppression, probes the representations of cortical areas by measuring and comparing the amount of repetition suppression across different conditions (Kourtzi and Grill-Spector 2005; Krekelberg et al. 2006). If an area is sensitive to face identity, for example, then the response to the repetition of 1 identity across different images should be weaker than that to 2 different identities because there is more overlap in neural response to the same pair than the different pair. Previous research using this method, however, has produced mixed findings about the functional roles of posterior face-selective areas. Some studies reported that repetition suppression in FFA persists despite physical differences between same identity images (Grill-Spector et al. 1999; Andrews and Ewbank 2004; Winston et al. 2004; Rotshtein et al. 2005; Ewbank and Andrews 2008). These studies, however, typically used block design (Grill-Spector et al. 1999; Andrews and Ewbank 2004; Ewbank and Andrews 2008; Furl et al. 2011), making the effect vulnerable to the confounding factor of expectation and repetition of the same image within a block. Consistent with this concern, other studies found release from adaptation in FFA when different images of the same identity were presented (Pourtois et al. 2005; Fang et al. 2007; Davies-Thompson et al. 2009; Xu et al. 2009; Ramon et al. 2010).

Image-specific coding in the OFA and FFA raises the question of whether invariant representations might be found in anterior areas such as fATL. Support for the importance of the anterior temporal lobe in face recognition comes from neuropsychological studies in which lesions to ATL lead to problems with famous face recognition, face imagery, configural face processing, or more general, person-based semantic dementia (Barton and Cherkasova 2003; Glosser et al. 2003; Williams et al. 2006; Gainotti 2007; Busigny et al. 2009). Multivariate analysis in normal subjects also suggests that fine-grained information is present in anterior temporal lobe (ATL, Kriegeskorte et al. 2007) or in both FFA and ATL (Nestor et al. 2011; Anzellotti et al. 2014). In addition, behavioral discrimination of faces was found to correlate better with activity in anterior temporal lobe than FFA (Nasr and Tootell 2012). Finally, as mentioned above, the macaque anterior face patch, which may be the homolog of human fATL, contains neurons that respond to particular identities across different views (Freiwald and Tsao 2010).

These findings lead to several questions concerning fATL and invariant face representation. First, what is the nature of face identity representation in fATL, and is it different from that in posterior face-selective areas? Secondly, what is the relationship between fATL and more posterior face-selective areas? Specifically, do face representations in fATL depend on the integrity of FFA and OFA? In spite of extensive research using fMRI adaptation, very few studies have examined the sensitivity to face identity in anterior areas using this paradigm. Rotshtein et al. (2005) found repetition suppression across different images of famous faces in the anterior temporal lobe, but their study did not localize fATL and the difference between the images in the same identity pairs was limited due to the use of morphed stimuli. To address which areas contain image-invariant face representations, our fMRI adaptation experiment used image pairs in the same trials that showed the same celebrity, but which differed in various ways including hairstyle, make-up, lighting, etc. Presentation of different images of the same person allowed us to investigate face processing rather than mere image processing, and familiar faces may generate more robust repetition suppression in fATL than unfamiliar faces (Burton 2013).

Neuroimaging studies of normal subjects, however, cannot determine whether a particular area is necessary for normal functioning of other areas or normal behavioral performance (Price et al. 2003). A powerful means to address this issue comes from brain-damaged individuals with lesions to parts of the face network (Schiltz et al. 2006; Steeves et al. 2009). To investigate the relationship between fATL and posterior areas, we performed the same localizer and fMRI adaptation experiment with Galen, an individual with acquired prosopagnosia who lost his right FFA and right OFA due to brain surgery (Susilo et al. 2013). Galen allowed us to examine whether fATL can preserve its face selectivity and retain its representations despite the loss of FFA and OFA. A simple hierarchical model (OFA → FFA → fATL) of the face network would predict that a lesion to posterior areas would disrupt the operation of fATL.

Materials and Methods

Neurologically Intact Subjects

Sixteen neurologically intact subjects (aged 18–22, 9 females) and Galen participated in the experiments. All subjects were screened for MRI scanning and provided informed written consent in accordance with the protocols approved by the Committee for the Protection of Human Subjects of Dartmouth College. They were either paid or received course credit for their participation.

Galen's Case History and Description

Galen is a right-handed male physician who was 30-year-old when he participated in this study. He was first reported in Susilo et al. (2013), but here we provide a more complete description of his case history. Galen underwent surgery to excise an arteriovenous malformation in the right occipitotemporal lobe in 2004, after which he noted face recognition problems. Since then Galen has had difficulties in recognizing faces, especially famous faces and people who look similar and/or are related (e.g., members of a family with similar sex and age). He reports using non-face cues such as voice, gait, and context to identify people. Galen is clearly intelligent and accomplished. He majored in English before attending medical school, and he is currently a physician at a Veterans Administration Hospital. Galen had no

other visual complaints except a temporary left superior quadrantanopia that lasted for several months after the surgery.

Galen's performance on a variety of behavioral tests is shown in Supplementary Fig. 3. On tests of face memory, Galen was impaired on the Cambridge Face Memory Test (Duchaine and Nakayama 2006), a famous face test (Duchaine and Nakayama 2005), and an old–new face discrimination test (Duchaine and Nakayama 2005). Although severely impaired with face identity, his performances on these tests were above chance. His ability to perceptually discriminate faces with minimal memory demands, as assessed with the Cambridge Face Perception Test (Duchaine et al. 2007), was in the lower end of the normal range, and he was impaired on 2 other face perception tests: The Queen Square Identity Matching Test (Garrido et al. 2009) and a face shape matching task (Pitcher et al. 2009). These results suggest that Galen's face-processing problems involve both perception and memory.

Galen showed normal performance on the Cambridge Car Memory Test (Dennett et al. 2012), the Abstract Art Memory Test (Wilmer et al. 2010), and the Verbal Paired-Associates Memory Test (Woolley et al. 2008; Supplementary Fig. 3). Galen also scored normally with 8 tests measuring body perception or body memory (Susilo et al. 2014) and showed normal-sized body inversion effects in a task designed to place similar demands on face and body processing (Susilo et al. 2013). In terms of low-level visual abilities, Galen performed normally when discriminating stimuli that differed along 6 basic visual attributes (circle size, oval length, line length, line angle, dots distance, and spatial frequency).

Lesion Site

High-resolution MR images of Galen's brain (Fig. 1A) showed a lesion extending from the middle occipital lobe to the lateral parahippocampal gyrus in the right hemisphere, encompassing a large part of his right occipitotemporal lobe and the fusiform gyrus. A small lesion was also present in the right cerebellum.

Stimuli and Experimental Design

In Experiment 1, we first used a dynamic localizer (Fox et al. 2009) to identify face-selective areas in our normal subjects (Fig. 2A). Next, using event-related fMRI adaptation, we examined which area(s) contain(s) invariant representations of face identity. In Experiment 2, we performed the same experiments with Galen using procedures identical to those in Experiment 1. Galen's results were then compared with those of the normal subjects in Experiment 1 to examine the effect of his lesion on the face selectivity and repetition suppression of other face-selective areas.

Localizer Experiment

The stimuli in the localizer experiment were video clips of 3 visual categories: faces, objects, and scrambled objects [created by scrambling the video clips of objects spatially into 24 × 16 grids; see Fox et al. (2009) for more details]. All stimuli were grayscale and were approximately 18.5° × 12.3° of visual angle.

Each subject completed 3 localizer runs. Each run comprised 9 blocks of 12-s video clips interleaved with 12-s fixation blocks (Fig. 2A). Faces, objects, and scrambled objects were presented 3 times within each run in a quasi-random order across runs. Within each block, subjects passively viewed 6 video clips [1500 ms per clip, with a 500-ms interstimulus interval (ISI)] randomly selected from 60 video clips of each category. Stimuli were presented using Superlab 4.5.3 (http://www.superlab.com/, last accessed December 2, 2014) and presented to the subject via a Panasonic DT-4000U DLP projector (resolution: 1024 × 768; refresh rate: 60 Hz) at the rear of the scanner.

fMRI Adaptation Experiment

In the fMRI adaptation experiment, face images of well-known celebrities were used as stimuli. To control for the effect of age
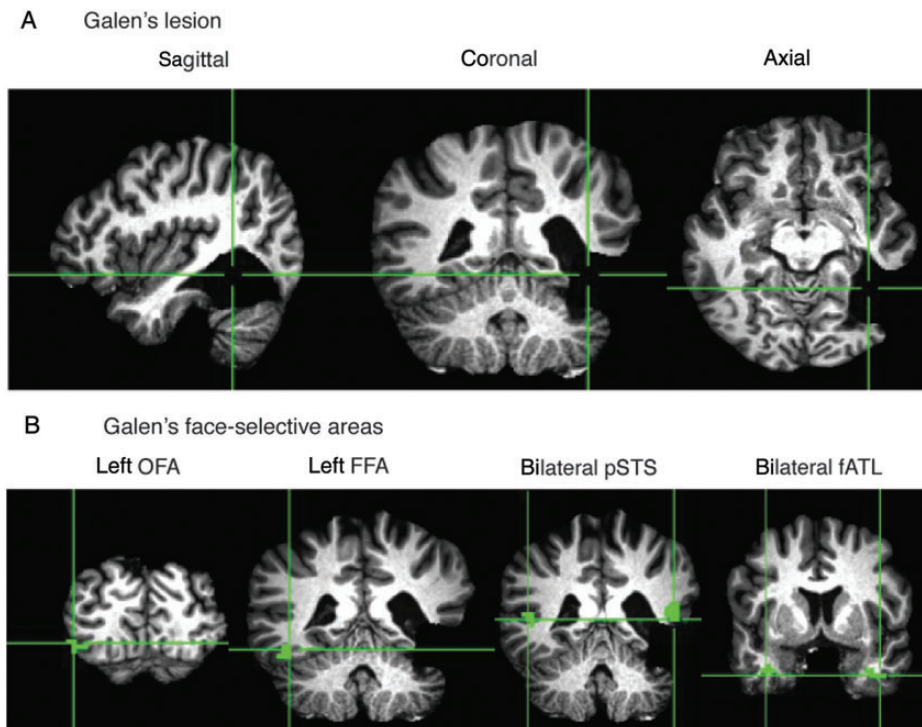

Figure 1. (A) The axial, coronal, and sagittal view of Galen's lesion. (B) The coronal view of Galen's face-selective areas.
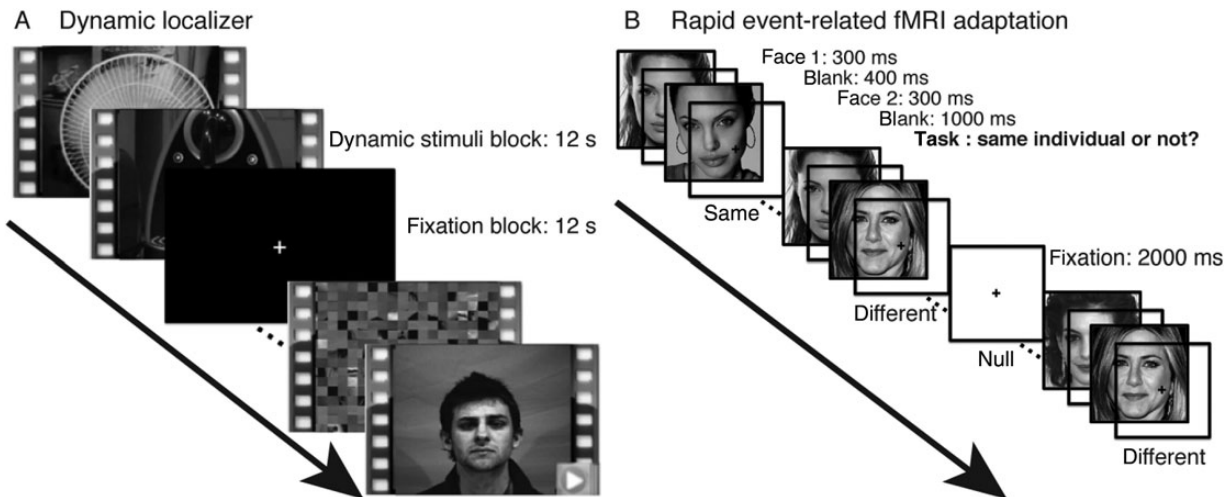
Figure 2. Example stimuli and procedures of the experiments. (A) In the localizer experiment, 3 categories were presented: faces, objects, and scrambled objects. (B) In the fMRI adaptation experiment, pairs of celebrity faces were presented in rapid succession. The first and second images in a pair were always different, but could show the same person or different people. Subjects indicated whether the identities in a pair were the same or different.

and sex, all the celebrities were young women. For each celebrity, we selected 2 frontal-view face images with neutral expression and direct gaze. The 2 images differed from each other in various ways including hairstyle, make-up, lighting, etc. Faces were cropped to show only the neck and head to reduce the potential influence from body or poses. All images were grayscale, with luminance and contrast normalized using the SHINE toolbox (Willenbockel et al. 2010) in Matlab. Stimuli were presented in the center of the display and subtended approximately 7.7° × 7.7° of visual angle. The stimuli were presented using the Psychtoolbox (Brainard 1997; Pelli 1997) in Matlab.

We used a rapid event-related design (Fig. 2B). Each subject completed 6 runs. In each trial, the first stimulus was 1 of the 27 celebrity identities and was presented for 300 ms. After a 400-ms ISI, the second stimulus was presented for 300 ms and followed by a 1000-ms fixation to separate the trials. In the "same" condition, the second stimulus was a different face image of the same identity. In the "different" condition, the second stimulus was an image of another identity (see Supplementary Fig. 1 for a complete set of stimuli). The subjects were not able to predict the trial type based on the first image, reducing the potential influence from the expectation toward the stimuli type (Summerfield et al. 2008). The sequence of the experimental conditions was predefined using a de Bruijn sequence to reduce the carry-over effects (Aguirre et al. 2011), yielding 81 trials in total in each run including the "null" trials (2000-ms fixation).

MRI Acquisition

Subjects were scanned on a 3.0-T Phillips MR scanner (Philips Medical Systems, WA, USA) with a SENSE (SENSitivity Encoding) 32-channel head coil. At the beginning of the scan, an anatomical volume was acquired using a high-resolution 3D magnetization-prepared rapid gradient-echo sequence (220 slices, field of view = 240 mm, acquisition matrix = 256 × 256, voxel size = 1 × 0.94 × 0.94 mm).

Functional images were collected using echo-planar functional images (time to repeat = 2000 ms, time echo = 35 ms, flip angle = 90°, voxel size = 3 × 3 × 3 mm). Each volume consisted of 36 interleaved 3-mm thick slices with 0-mm interslice gap. The slice volume was adjusted to cover most of the brain including the entire

temporal lobe. Previous studies found that the location and extent of susceptibility effects are influenced by the slice orientation and phase-encoding direction (Ogawa and Lee, 1990; Ojemann et al. 1997). In our study, we adopted oblique slice orientation aligned with each subject's anterior commissure–posterior commissure (AC–PC) line, because it produces fewer susceptibility artifacts than the commonly used traverse orientation (Ojemann et al. 1997) and at the same time provides better coverage of the brain, enabling us to examine the face network in the whole brain. The phase-encoding direction (anterior–posterior) was chosen to move the signal loss away from the more anterior part of the brain.

fMRI Data Analysis

Imaging data were analyzed using the AFNI software package (Cox 1996). Before statistical analysis, the first 2 volumes of each run were discarded to allow for magnetic saturation effects and each volume was registered to the third volume of the first run. The echo planar imaging data were warped to align with the anatomical data and transformed to a standard space in the Talairach template (Talairach and Tournoux 1988). Each volume was blurred with a 4-mm FWHM (full width at half maximum) Gaussian kernel. Time series of each run were scaled by the mean of the baseline before passing onto the deconvolution analysis. Detrending and motion correction were carried out by including trends and head motion as regressors in the regression model. Time points with excessive motion (>0.3 mm) were removed from the regression matrix before the regression was performed.

In the localizer experiment, a general linear model procedure was used for region of interest (ROI) analysis. Face-sensitive areas were localized using a "faces > objects" contrast with a statistical threshold of $P < 0.0001$ (uncorrected) except that we used a threshold of $P < 0.001$ to localize fATL. This compares favorably with other papers that investigated fATL (Rajimehr et al 2009; Nasr and Tootell 2012; Axelrod and Yovel 2013). We localized the object-selective areas using an "objects > scrambled objects" contrast with a threshold of $P < 10^{-8}$ (uncorrected). Time courses from each ROI were extracted and further analyzed.

To evaluate the face selectivity of these areas, we localized ROIs based on the 2 odd runs and measured the face selectivity of each ROI based on the remaining run. We extracted the

response of each face-selective area to compare their responses to faces, objects, and scrambled objects (Fig. 3). To compare the selectivity of right fATL to other areas, the selectivity of each ROI was calculated for each subject (if present) and compared using a within-subject *t*-test. For each test, if a particular area or right fATL was absent for some subjects, the data of those subjects were not included in the statistical analysis. Multiple comparisons were accounted for by calculating Bonferroni-corrected alpha.

For the fMRI adaptation experiment, preprocessing procedures were identical to those used for the localizer experiment. Instead of using canonical hemodynamic response function models which assume the shape of the hemodynamic response, we used a finite impulse response model (Glover 1999; Ollinger et al. 2001) for our rapid event-related design. Each stimulus was modeled by a set of 7 tent functions ("mini-boxcars," Goutte et al. 2000; Henson et al. 2001) expanding from the onset of the event out to 14 s with 2-s bins. The peristimulus time courses were deconvolved and beta weights were assigned to each temporal point. The peak β was used as the response estimate for each condition. A group comparison was run on the responses of the 2 experimental conditions in each ROI to evaluate the adaptation effect.

A temporal signal-to-noise ratio (TSNR) was computed for each voxel by dividing the mean signal by the standard deviation of signal time course after detrending. The TSNR of all subjects including Galen were averaged to create the TSNR map (Supplementary Fig. 2).
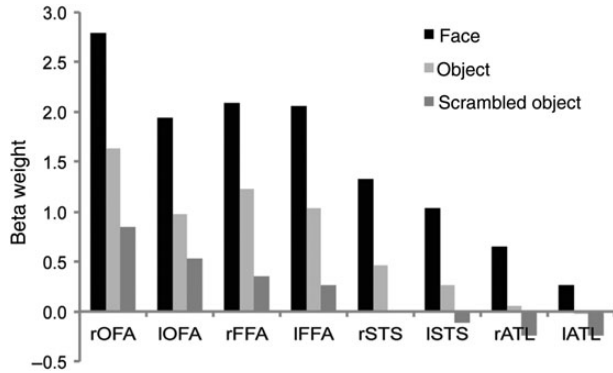

Figure 3. Response profiles of face-selective areas in normal subjects in the localizer experiment. The y-axis shows the average response magnitude of each area to faces, objects, and scrambled objects in the localizer experiment.

Results

Experiment 1: Face-Selective Areas and Image-Invariant Representation

Localizer Experiment

In the localizer experiment, 3 categories of stimuli (faces, objects, and scrambled objects) were presented. Face-selective areas were localized using a "faces > objects" contrast and the object-selective areas using an "objects > scrambled objects" contrast. Significant face-selective responses were present in areas corresponding to bilateral OFA, FFA, and pSTS ($P < 0.0001$, uncorrected). We also found a face-selective response in right fATL ($P < 0.001$, uncorrected, Talairach coordinates: -38 ± 6, 3 ± 7, -33 ± 4; mean cluster size: 26 voxels) in 14 of 16 subjects. The location of right fATL was similar to those reported in other studies, and the threshold we used compares favorably with other papers that investigated fATL (Rajimehr et al. 2009; Nasr and Tootell 2012; Rossion et al. 2012; Axelrod and Yovel 2013). Left fATL was identified in less than half of the subjects and excluded in subsequent analyses. Significantly stronger activation to objects than faces was observed in the bilateral occipital lobe, which we defined as lateral occipital complex (LOC, $P < 10^{-8}$, uncorrected). Table 1 summarizes the Talairach coordinates of the ROIs, their mean cluster size, and the number of normal subjects showing each ROI.

To examine the face selectivity of the face areas while avoiding non-independent-selective analysis (Kriegeskorte et al. 2009), we used the odd runs (first and third) to localize the face-selective areas and found we could still reliably localize most of the areas (left OFA 10/16; right OFA 8/16; left FFA 12/16; right FFA 12/16; left STS 12/16; right STS 13/16; left fATL 10/16; and right fATL 10/16). We then extracted the response from the remaining run to compare the selectivity profiles in the face-selective areas. Like previous studies (Kanwisher et al. 1997; Pitcher et al. 2011), the response to faces in OFA and FFA was 2–3 times the response to objects. Bilateral pSTS and right fATL showed even higher selectivity due to their smaller response to objects and scrambled objects. We calculated a selectivity index "$[\beta(\text{face}) - \beta(\text{object})]/[\beta(\text{face}) + \beta(\text{object})]$" to evaluate and compare their selectivity to faces (Tsao et al. 2008). The selectivity index of right fATL is significantly higher than bilateral FFA [left FFA: $t_{(8)} = 3.03$, $P = 0.008$; right FFA: $t_{(8)} = 2.96$, $P = 0.008$, Bonferroni-corrected alpha = 0.008]. The comparison with bilateral OFA and right STS revealed significant difference but not after Bonferroni correction [left OFA: $t_{(6)} = 2.16$, $P = 0.03$; right OFA: $t_{(5)} = 1.95$, $P = 0.05$; right STS: $t_{(8)} = 2.40$, $P = 0.021$].

Table 1 Talairach coordinates and cluster size of functionally defined ROI in normal subjects and acquired prosopagnosic Galen

Area	Normal subjects			Galen	
	Number	Size (voxels)	Coordinates	Size (voxels)	Coordinates
lOFA	12/16	44 ± 25	38 ± 6, 81 ± 6, -10 ± 2	12	40, 82, -10
rOFA	9/16	55 ± 47	-39 ± 8, 78 ± 5, -10 ± 4	Lesioned	
lFFA	16/16	31 ± 24	41 ± 4, 47 ± 9, -17 ± 3	6	48, 42, -15
rFFA	16/16	35 ± 24	-42 ± 4, 46 ± 3, -18 ± 4	Lesioned	
lpSTS	14/16	48 ± 47	56 ± 6, 44 ± 10, 9 ± 5	18	49, 37, 2
rpSTS	15/16	51 ± 35	-54 ± 6, 45 ± 8, 7 ± 3	67	-59, 49, 11
lfATL	7/16	16 ± 5	40 ± 7, 2 ± 5, -28 ± 4	28	33, -6, -29
rfATL	14/16	26 ± 12	-38 ± 6, 3 ± 7, -33 ± 4	10	-32, 4, -31
lLOC	15/16	63 ± 38	41 ± 7, 76 ± 5, 0 ± 7	81	58, 64, -1
rLOC	14/16	49 ± 28	-44 ± 4, 76 ± 6, -1 ± 7	Lesioned	

Note: The number of normal subjects who showed significant face-selective activation for each area is also listed.

Given the potential for signal drop-off in anterior temporal cortex, we averaged the TSNR of all the subjects to evaluate the quality of the signal in the ATL (Simmons et al. 2010; Von Der Heide et al. 2013). The resulting map (see Supplementary Fig. 2 in Supplementary Material) shows that the TSNR in the fATL region was lower than posterior ROIs, probably due to the susceptibility-induced loss of signal. We calculated that a TSNR value above 29 is considered good given the time points per condition in our experiment ($N = 162$, effect size = 1%, $P = 0.05$, Murphy et al. 2007). However, in the area around the fATL ROI, the TSNR was still above 100, enabling the detection of changes in blood oxygen level-dependent signal across conditions.

fMRI Adaptation Experiment

In the scanner, subjects pressed 1 of 2 response buttons to indicate whether the 2 images in a pair were the same identity or not. No feedback was provided. One subject's behavioral performance was not included due to a technical problem. A-prime (A'), an unbiased measure of discrimination that ranges from 0.5 to 1.0 (Pollack and Norman 1964), was computed to estimate accuracy.

The average A' in the discrimination task was 0.84 (SD = 0.03), indicating that subjects could discriminate between same and different pairs in most trials. In the debriefing after the scan, all subjects reported that they were familiar with all of the celebrities presented in the experiment.

For the imaging results, we first evaluated the repetition suppression effect in each ROI, including right fATL, left/right OFA, left/right FFA, left/right pSTS, and also left/right LOC. Left fATL was not analyzed, because it was localized in less than half of the subjects. To compare the repetition suppression magnitude across different areas and subjects, an adaptation index was calculated for each subject as the difference between the peak beta weights (β) in the "same" and "different" conditions divided by their sum "[peak β (different) – peak β (same)]/[peak β (different) + peak β (same)]." ANOVA analysis of the repetition suppression indices revealed a significant effect of area ($F = 3.219$, $P = 0.002$). To investigate this effect, we compared the fMRI responses in the "same" and "different" conditions in each area. Figure 4 shows that right fATL was the only area exhibiting significant repetition suppression to the same face identity ($t = -3.33$,
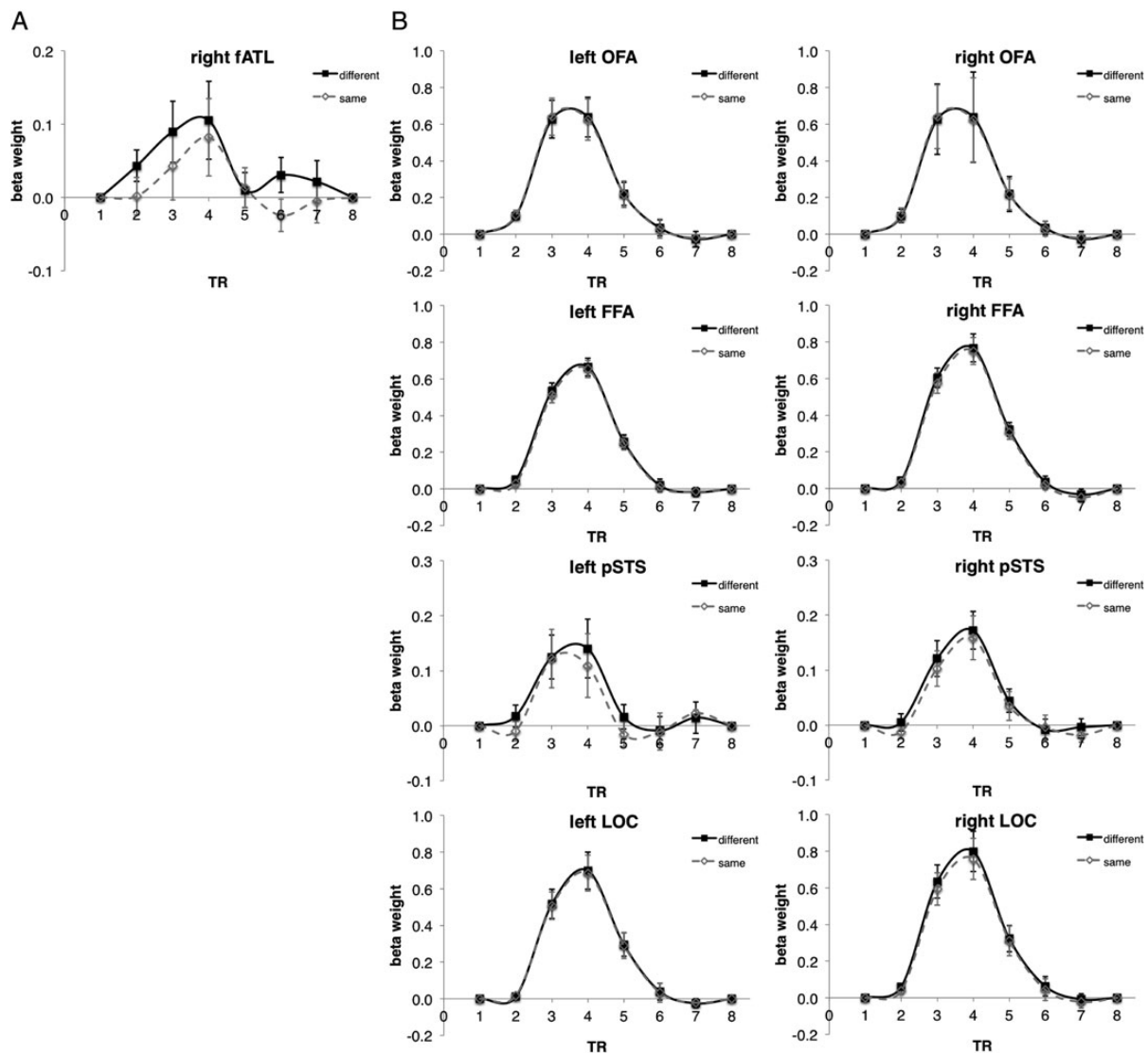

Figure 4. The estimated response time course to the same identity (dashed line) and different identities (solid line) in right fATL (A) and other ROIs (B) in normal subjects.

$P = 0.003$, Bonferroni-corrected alpha = 0.006). Significant repetition suppression was observed in the left fATL localized in the controls, but not after Bonferroni correction ($t_{(7)} = 2.86$, $P = 0.012$). The response to the "same" and "different" conditions in other ROIs was not significantly different.

To check that the repetition suppression found was not merely a result of a difference in image statistics for the same and different identity condition, we performed an additional analysis to evaluate the correlation between image-level similarity and response measure. We calculated the Euclidean distance of the pixel values between each image pair and then correlated the Euclidean distance of the image pair and right fATL response across all trials in each individual. Correlation results were averaged across individuals (mean = 0.004, SD = 0.06) and no significance was found ($t_{(12)} = 0.26$, $P = 0.799$). Moreover, there was no significant correlation between the 2 measures within the same condition [mean = 0.01, SD = 0.08, $t_{(12)} = -0.38$, $P = 0.707$] or different condition [mean = 0.02, SD = 0.07, $t_{(12)} = 0.90$, $P = 0.384$].

Experiment 2: Galen

Localizer Experiment

The procedures and analysis were identical to those run with normal subjects. The results of the localizer experiment showed that Galen's right FFA, right OFA, and right LOC were missing due to his lesion. In contrast, left OFA, left FFA, and bilateral pSTS were all present (Fig. 1B). Talairach coordinates and the cluster sizes of his functionally defined ROIs are listed together with those of the normal subjects in Table 1. Importantly, using a similar approach to localize and evaluate the selectivity of face-selective areas, Galen's right fATL also showed a face-selective response (faces: 0.29, objects: −0.08, scrambled objects: −0.16; Fig. 5). For comparisons between Galen and controls, we used a t-test modified for single-case analyses (Crawford and Howell 1998). The face selectivity index of his right fATL was comparable to the right fATLs in the normal subjects ($t = 0.566$, $P = 0.296$). The absolute response amplitude of Galen's right fATL (0.30) was smaller than most of the normal subjects (M = 0.67, SD = 0.56), but the difference was not significant ($t = -0.64$, $P = 0.269$). Like normal subjects, Galen's right fATL responded little to non-face stimuli (Fig. 5).

fMRI Adaptation Experiment

To assess whether Galen's behavioral performance and his repetition suppression were abnormal compared with the subjects in Experiment 1, we again used the t-test modified for single-case analysis (Crawford and Howell 1998). As can be seen in Fig. 6, Galen's performance (A′ = 0.66) was out of the normal range and significantly worse than the control group ($t = -6.06$, $P < 0.001$), although it was above chance.

Like controls, Galen's right fATL showed a weaker response to same pairs than different pairs ($P = 0.031$; Fig. 7). We compared Galen's repetition suppression to the controls in 2 ways. In addition to the adaptation index used in Experiment 1, we simply calculated the amount of repetition suppression by measuring the difference of peak beta weights across conditions [peak β (different) − peak β (same)]. Figure 8 plots both of these measures for Galen and each normal subject in right fATL. The absolute size of Galen's repetition suppression in this area (repetition suppression = 0.04) was comparable to that of controls (repetition suppression: M = 0.06; SD = 0.07; $t = -0.335$, $P = 0.372$) as was his adaptation index (Galen: 0.41; controls: M = 0.27; SD = 0.29; $t = 0.492$, $P = 0.316$). The responses in the same and the different conditions in Galen's right fATL were also comparable to the controls (same: $t = 0.05$, $P = 0.482$; different: $t = -0.149$, $P = 0.442$). Because we did not find an effect in areas other than right fATL in normal subjects in Experiment 1, one approach to analyzing the repetition suppression in these other areas in Galen is to correct for multiple comparisons. If we correct for multiple comparisons (Bonferroni-corrected alpha = 0.007), he did not show repetition suppression in other ROIs. However, because we did not correct for multiple comparisons when analyzing his right fATL repetition suppression, we also present results for these areas uncorrected (left fATL: $P = 0.029$; left FFA: $P = 0.862$; left pSTS: $P = 0.055$; right pSTS: $P = 0.053$; left OFA: $P = 0.760$; left LOC: $P = 0.768$).

Discussion

The present study investigates the cortical mechanisms of invariant face recognition, specifically the nature of face representation in the human anterior temporal face area (fATL). We first used a dynamic localizer to identify right fATL in 14 of our 16 normal subjects and in Galen, an acquired prosopagnosic who lost right FFA and right OFA. Right fATL was more face-selective than FFA and OFA, with little to no response to non-face categories. We then examined fMRI adaptation in normal subjects and in Galen to address 2 issues: (1) Whether the right fATL represents face identity invariantly and (2) whether right fATL can retain its representation in the absence of right FFA and right OFA.
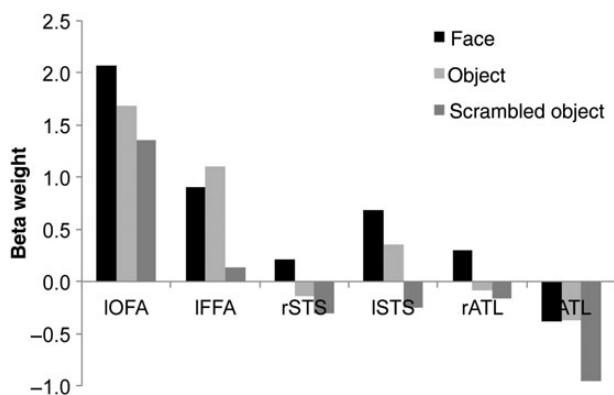

Figure 5. Response profiles of Galen's spared face-selective areas in the localizer experiment. The y-axis shows the response magnitude of different areas to faces, objects, and scrambled objects.
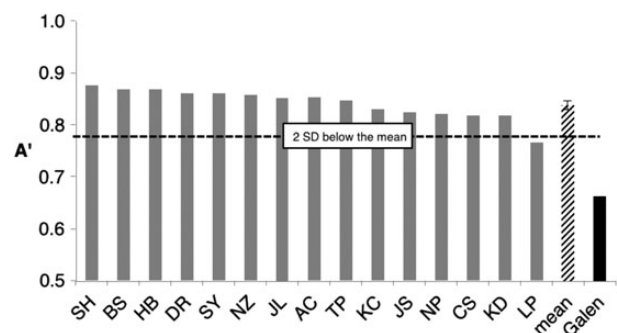

Figure 6. Behavioral results of Galen (in black) and individual controls (in gray) on the same-different task done during the fMRI adaptation experiment. A-prime (A′) is an unbiased measure of discrimination to estimate accuracy (Pollack and Norman 1964). Chance performance is 0.5. The error bar on the control mean column displays standard error.
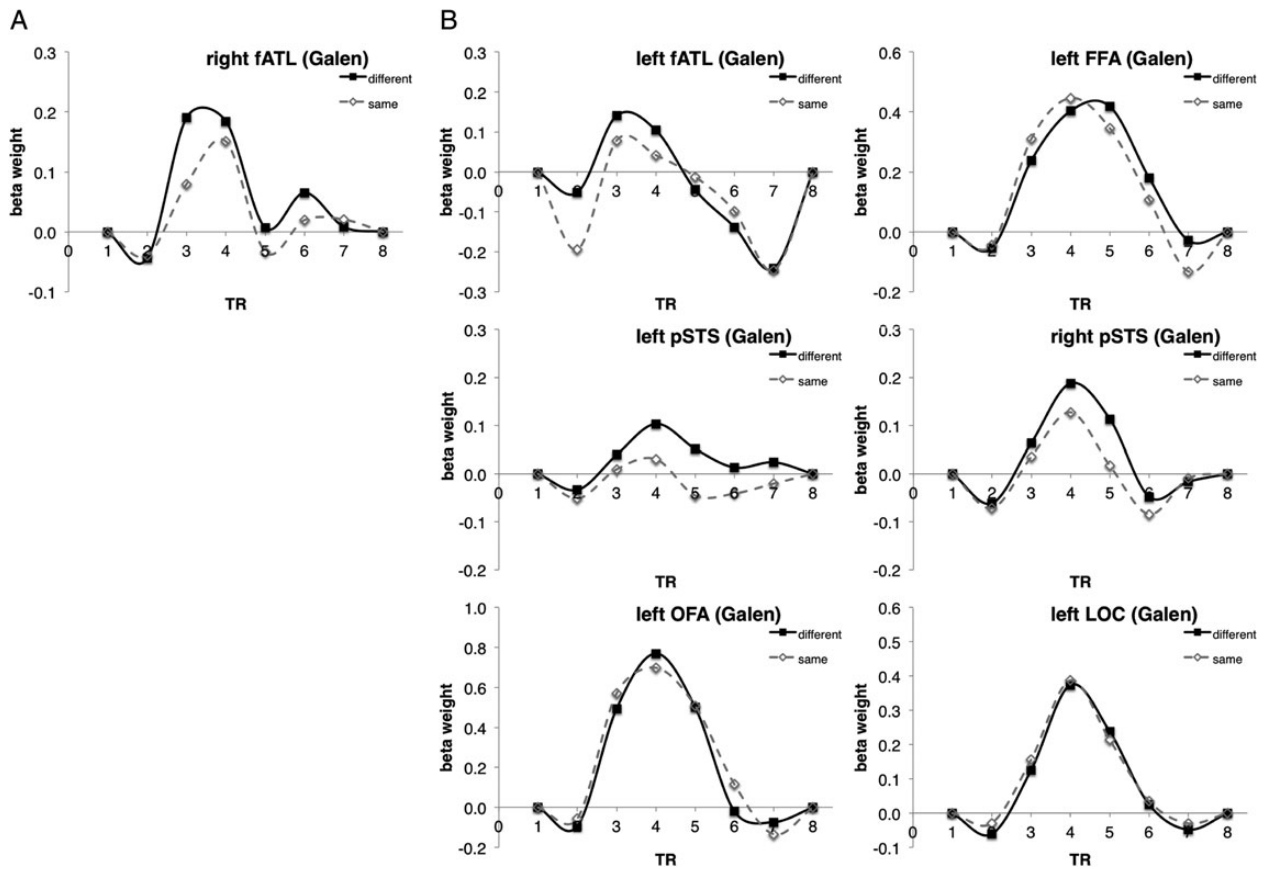
Figure 7. The estimated response time course to the same identity (dashed line) and different identities (solid line) in Galen's right fATL (*A*) and other ROIs (*B*).
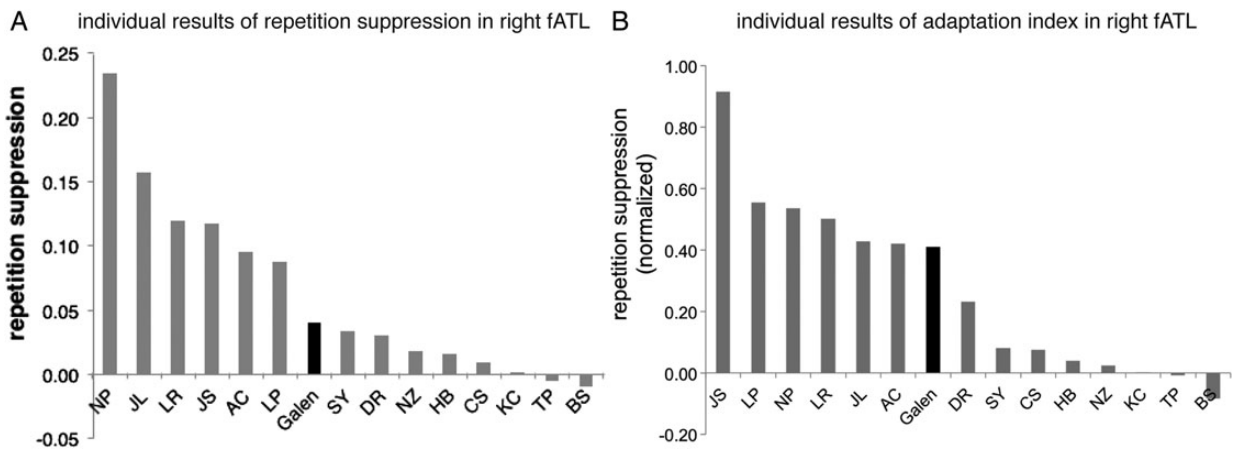

Figure 8. Individual repetition suppression results in the right fATL. The amount of repetition suppression (*A*) is calculated as "peak β (different) – peak β (same)." An adaptation index (*B*) is also calculated as "[peak β (different) – peak β (same)]/[peak β (different) + peak β (same)]." The repetition suppression of Galen's right fATL (in black) is well within the normal range when compared with normal subjects (in gray).

The results from the normal subjects indicate that invariant face identity representation occurs in the right fATL but not in the other face areas we examined, including right FFA. Right fATL was present in Galen, the acquired prosopagnosic missing his right FFA and right OFA. More surprisingly, his right fATL showed repetition suppression to different images of the same identity comparable to controls.

Taken together, our results indicate (1) a highly face-selective area can be reliably localized in the right anterior temporal lobe in normal subjects, (2) the right fATL contains invariant representations of face identity, (3) this area can preserve its face-selectivity and its invariant representation despite the loss of the right FFA and right OFA, and (4) normal repetition suppression in the right ATL is not sufficient for face recognition.

Implications of the Results From Normal Subjects

The Role of fATL in the Face Processing Network

The human face-processing system is believed to represent faces in a series of stages (Bruce and Young 1986; Haxby and Gobbini 2011). Our fMRI adaptation results revealed that only one face-selective area showed repetition suppression to the same identity across different images, namely right fATL. Our findings are consistent with anatomical logic as well as results involving a variety of methods that indicate that more anterior face areas contribute to more abstract processing of face identity. For example, an event-related potential study showed that different images of the same identity elicit repetition suppression in the N250 component but not in the N170 component, and the N250 component originates from more anterior regions than the N170 (Schweinberger et al. 2002). Other fMRI studies suggested that face viewpoint is represented in a more mirror-symmetric manner as it progresses from posterior to anterior face areas (Axelrod and Yovel 2012; Kietzmann et al. 2012). Lesions causing prosopagnosia in more posterior areas are likely to result in face perception deficits, whereas more anterior lesions tend to leave perception intact but produce problems with configural processing or face memory (Williams et al. 2006; Barton 2008; Gainotti and Marra 2011, but see Busigny et al. 2014). Our results also fit with macaque data showing that, along the ventral pathway, the representation of faces changes from view-specific to mirror-symmetrical and reaches full invariance in AM, the most anterior face patch (Freiwald and Tsao 2010). Finally, the presence of image-invariant representations in human right fATL and its location at the anterior end of the temporal lobe provides support for the possibility that human fATL and macaque AM are homologous areas (Tsao et al. 2008; Freiwald and Tsao 2010; Yovel and Freiwald 2013).

The Face Selectivity of fATL

The comparison between the face selectivity of fATL and more posterior face areas reveals another interesting characteristic of fATL. The fATL appears more face-selective than OFA and FFA, with little to no response to objects and scrambled objects. This finding is in line with previous studies in human and macaques, showing that face selectivity is greater in more anterior areas (Tsao et al. 2008; Bell et al. 2009; Yovel and Freiwald 2013). Greater face selectivity might be closely related to sensitivity to specific identities. When neurons in a region respond to relatively simple face features such as eyes or aspect ratio (Freiwald et al. 2009), it is likely that some non-face stimuli will contain similar features. In contrast, high-level areas like fATL that respond in a more face-selective manner may do so, because few non-face stimuli have the necessary combination of features to drive neurons in such areas.

The Function of fATL

Our study with normal subjects found that right fATL shows repetition suppression to face identity across different images. This repetition suppression appears to result from image-invariant representation rather than more image-based representation, because we used face images that differ from each other in many ways, and our image-based analysis found no correlation between the fMRI response and image similarity. Moreover, if the fATL response reflected image-level adaptation, we would have expected repetition suppression in other face-selective areas such as OFA or FFA and possibly in bilateral LOC, but these other areas did not show such effects. Our findings suggest that fATL is crucial to individual face recognition, particularly for

familiar faces (Gobbini and Haxby 2007; Von Der Heide et al. 2013), and indicate that fATL may be one cortical locus of invariant representations of face identity. Given the importance of image-invariant representation for face recognition, ATL may deserve a more prominent role in models of face recognition, as suggested in another model of face processing (Rossion 2008; Collins and Olson 2014).

Although our study focuses on the contribution of fATL to face processing, it is possible that its function is not limited to face recognition. fATL may serve as a complex hub of person information with multiple functions such as processing or retrieving facial information, person knowledge, social knowledge, and emotions (Olson et al. 2007; Ross and Olson 2010; Simmons et al. 2010). For example, fact learning about a person activates anterior temporal lobe more than a control task when the presentation involves only names and sentences (Simmons et al. 2010). It will be valuable for future work investigating fATL to assess its response to social stimuli other than faces.

Repetition Suppression in OFA and FFA

In contrast to several fMRI adaptation studies (Winston et al. 2004; Schiltz et al. 2006; Steeves et al. 2009), we found no repetition suppression to face identity in posterior face-selective areas such as FFA and OFA. A likely explanation for this difference is that these previous studies used the same image in the same identity condition (Schiltz et al. 2006; Avidan and Behrmann 2009; Steeves et al. 2009), whereas we used different images of the same identity. If this account is correct, previous repetition suppression effects in posterior face areas do not reflect identity-level adaptation but rather image-level adaptation or view-specific adaptation (Freiwald and Tsao 2010). Indeed, a number of studies showed that repetition suppression in FFA did not generalize across views, suggesting the representation in FFA is not image-invariant (Eger et al. 2005; Pourtois et al. 2005; Davies-Thompson et al. 2009; Fang et al. 2007). One study, however, found that FFA showed comparable repetition suppression to different images of the same identity (Rotshtein et al. 2005), although another study failed to find this effect (Ramon et al. 2010). In any case, these 2 studies used morphed stimuli, whereas our study used natural images that varied in many aspects (hairstyle, expression, lighting etc.). The greater differences between our face images may have lessened the possibility of image-based adaptation and thus required a more abstract representation of face identity to generate repetition suppression.

Implications From Galen's Results

The Organization of Face-Selective Areas

Our lesion study offers a unique and critical insight into the face-processing network in humans. Although leading models of face processing have not made explicit predictions about the effect of posterior lesions on the functioning of more anterior areas (Haxby et al. 2000; Haxby and Gobbini 2011; Kanwisher and Barton 2011), we expected that the loss of Galen's right FFA and OFA might lead to abnormal face selectivity and disrupted face representations in fATL. However, Galen's right fATL continued to exhibit a face-selective response. More surprisingly, the repetition suppression to face identity across different images in this area was comparable to that shown by controls, suggesting that Galen's right fATL continues to represent facial identity in the absence of right FFA and right OFA. This finding is similar to a prosopagnosia patient with bilateral posterior lesions who showed face-selective activation in anterior regions associated

with face processing and a greater response to familiar than unfamiliar faces (Valdés-Sosa et al. 2011).

How can the right fATL continue to represent face identity invariantly in the absence of right FFA and right OFA? One possibility is that Galen's fATL builds its representation based on input from the remaining network in his face-processing pathways. For example, Galen's left fATL also showed repetition suppression that was close to significant ($P = 0.029$, Bonferroni-corrected alpha = 0.007), and so may be representing faces in an image-invariant manner. These representations may have been conveyed through interhemispheric connections to the right fATL (Davies-Thompson and Andrews 2012). Right hemisphere face-responsive areas such as amygdala, precuneus, medial prefrontal cortex, or inferior frontal gyrus may also provide input to right fATL (Simmons et al. 2010). Galen's repetition suppression results suggest that his bilateral pSTS may also represent face identity information. A previous study found significant functional connectivity between pSTS and anterior temporal lobe (Simmons et al. 2010), which might provide a pathway for information about individuals to reach fATL. pSTS is typically thought to be responsible for processing dynamic or changeable facial information such as face expression or gaze (Hoffman and Haxby 2000). Although we used faces with neutral expressions, the photographs of the celebrities may still contain subtle but idiosyncratic expression information, which might have contributed to Galen's identity processing. It is also possible that Galen's face-processing network has undergone reorganization in the 8 years since his surgery. For example, pSTS or other face-selective areas that do not typically represent face identity might now represent identity and have contributed to the representation in fATL. Reorganization in areas concerned with visual recognition has been suggested by a prosopagnosia patient with massive lesions in bilateral fusiform-temporal pathways (Valdés-Sosa et al. 2011) and an object agnosia patient with a lesion to his lateral fusiform gyrus (Konen et al. 2011). To explore these possibilities, future studies could compare the structural and functional connectivity of fATL with other areas in Galen and normal subjects.

Invariant Face Representation in Right fATL and Face Recognition Ability

Galen's repetition suppression in right fATL indicates that right fATL continues to represent face identity in an image-invariant manner despite the loss of right posterior face-selective areas. However, despite the normal repetition suppression, Galen was significantly impaired with the behavioral task and has deficits with face recognition in daily life. This combination of results indicates that the presence of repetition suppression in right fATL is not sufficient for normal face discrimination. Additional areas such as right FFA and right OFA seem necessary for normal behavioral performance.

It is notable that despite his prosopagnosia, Galen's behavioral performance on the task in the scanner and several other face recognition tasks (see Galen's case history and description) are above chance. It may be that the representations in his right fATL contribute to this residual performance. The results from Galen are similar in some respects to prosopagnosic cases who fail to overtly recognize faces yet show physiological or behavioral evidence of recognition (Tranel and Damasio 1985; de Haan et al. 1987; Renault et al. 1989; Barton et al. 2001; Valdes-Sosa et al. 2011). Although our experiment and tasks were not designed to investigate covert face processing, Galen's normal repetition suppression in right fATL coupled with poor behavioral discrimination suggests that this area is a potential neural locus of covert recognition in prosopagnosia.

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