Individual faces elicit distinct response patterns in human anterior temporal cortex

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Visual face identification requires distinguishing between thousands of faces we know. This computational feat involves a network of brain regions including the fusiform face area (FFA) and anterior inferotemporal cortex (aIT), whose roles in the process are not well understood. Here, we provide the first demonstration that it is possible to discriminate cortical response patterns elicited by individual face images with high-resolution functional magnetic resonance imaging (fMRI). Response patterns elicited by the face images were distinct in aIT but not in the FFA. Individual-level face information is likely to be present in both regions, but our data suggest that it is more pronounced in aIT. One interpretation is that the FFA detects faces and engages aIT for identification.

fMRI | information-based | population code

When we perceive a familiar face, we usually effortlessly recognize its identity. Identification requires distinguishing between thousands of faces we know. A puzzle to both brain and computer scientists, this computational feat involves a network of brain regions (1) including the fusiform face area (FFA) (2, 3) and anterior inferotemporal cortex (aIT) (4). There is a wealth of evidence for an involvement in face identification of both the FFA (1, 5–18) and aIT (4, 16, 19–26).

The FFA responds vigorously whenever a face is perceived (2, 3, 27). This implies that the FFA distinguishes faces from objects of other categories and suggests the function of face detection (27, 28). An additional role for the FFA in face identification has been suggested by three lines of evidence: (*i*) Lesions in the region of the FFA are frequently associated with deficits at recognizing individual faces (prosopagnosia) (6, 9, 10). (*ii*) The FFA response level covaries with behavioral performance at identification (11). (*iii*) The FFA responds more strongly to a sequence of different individuals than to the same face presented repeatedly (8, 12–17).

For aIT as well, human lesion and neuroimaging studies suggest a role in face identification. Neuroimaging studies (4, 22–24, 26) found anterior temporal activation during face recognition with the activity predictive of performance (22). Lesion studies (19, 20, 25) suggest that right anterior temporal cortex is involved in face identification. In monkey electrophysiology, in fact, face-identity effects appear stronger in anterior than in posterior inferotemporal cortex (29–31).

These lines of evidence suggest an involvement of both the FFA and aIT in face identification. A region representing faces at the individual level should distinguish individual faces by its activity pattern. However, it has never been directly demonstrated that either the FFA or aIT responds with distinct activity patterns to different individual faces.

We therefore investigated response patterns elicited by two face images by means of high-resolution functional magnetic resonance imaging (fMRI) at 3 Tesla (voxels: $2 \times 2 \times 2$ mm^3). We asked whether response patterns associated with the faces are statistically distinct. This would mean that the activity patterns allow the decoding from the fMRI signals (32–42) of the perceived individual.

The decision to use only two particular face images involves a trade-off. The disadvantage consists in the fact that any two face images necessarily differ along many dimensions. We are, thus, throwing a wide net: effects are expected in any brain region that represents at least one of the dimensions distinguishing the face images. Although these regions should include the putative individual-face representation, interpretation will be difficult if several regions are found to distinguish the faces.

The advantage of using only two face images consists in the fact that we do not need to average response patterns elicited by different images. For each image, averaging responses to its repeated presentation yields a sufficiently stable response pattern, which can be regarded as an estimate of the response on a single perceptual trial. In contrast, previous studies using large numbers of images needed to average response patterns elicited by different images, usually from the same category. Such average response patterns are hard to interpret, because it is unclear whether they actually arise on any single trial of perception.

The faces (one male, one female; Fig. 1) were presented in the same size, view, and lighting. Because of this matching of the two images and because faces in general are similar in their overall shape, the two face images are by many measures (e.g., spatial image correlation) much more similar than the images conventionally contrasted in object-vision neuroimaging. This raises the question whether fMRI will have sufficient resolution and sensitivity to detect any effect at all.

To be able to replicate previously described face-category effects (2), we included two house images (43) in the experiment as control stimuli. To minimize low-level confounds, we processed the four images to have identical histograms and, thus, identical light and spatial-signal energy. Subjects were presented with the images in a rapid event-related design, in which they performed an anomaly-detection task, requiring them to pay close attention to each repeated presentation of an image [Fig. 1; and see supporting information (SI) Figs. 4 and 5 for behavioral performance during fMRI].

Results

Conventional Activation-Based Analysis. Conventional univariate mapping analysis of our data yielded the category effects expected on the basis of the literature. Face-category activation (faces–houses) was very strong in the right and left fusiform gyrus, revealing the FFA (SI Fig. 6*a*, single subject; SI Fig. 7, Talairach-space group map). Weaker face-category activation was found in right and left aIT in the group analysis (SI Fig. 7). Single-subject and group mapping analyses also revealed the parahippocampal place area (43).

Responses to single images from the same category have not previously been contrasted with fMRI. Contrasting the two faces in

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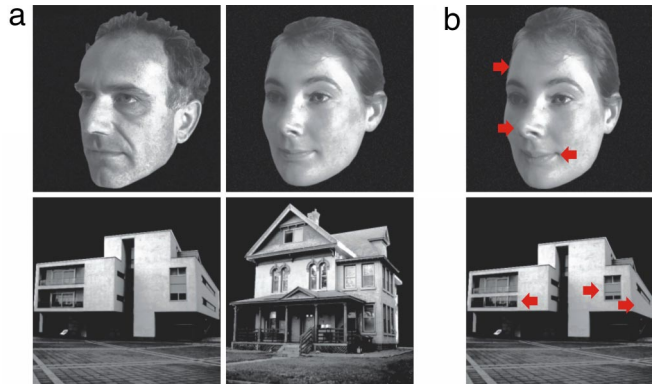

Fig. 1. Stimuli and anomaly-detection task. (*a*) The four particular images whose inferotemporal response patterns are investigated in this study. Each image was processed to have a precisely uniform histogram. The images were presented sequentially while subjects fixated a central cross (not shown). Subjects performed an anomaly-detection task: ≈12% of the images were subtle variations (*b*) of the four originals (*a*), in which the global shape of the object as well as details had been slightly distorted (red arrows). Anomalies were unpredictable because several anomalous versions were used for each original. The task required subjects to attend to each image presentation even after many repetitions and allowed us to monitor attentive viewing.

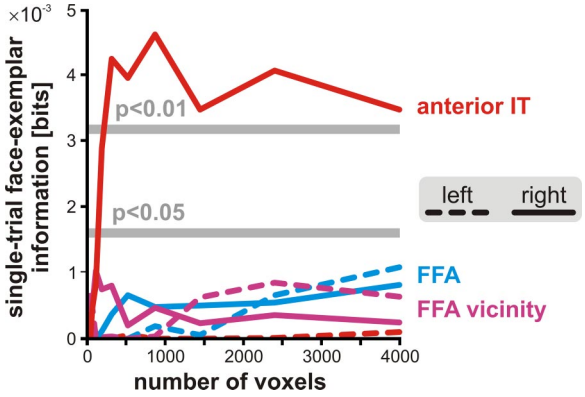

Fig. 2. Face-exemplar information as a function of region size. When we define the FFA by the category contrast (SI Fig. 6) and vary the threshold to select between 10 and 4,000 contiguous voxels, significant face-exemplar information is not found at any threshold (blue dashed line, left FFA; blue solid line, right FFA). When we define the ''FFA vicinity'' as the 4,000 cortical voxels in a sphere centered on the FFA in each subject and hemisphere (SI Fig. 6) and select the *n* voxels containing most face-exemplar information on independent data, significant face-exemplar information is not found for any threshold (magenta dashed line, left FFA vicinity; magenta solid line, right FFA vicinity). When we define aIT in each subject and hemisphere as the 4,000 most anterior voxels in temporal cortex and, again, select the *n* voxels containing most face-exemplar information on independent data, no significant face-exemplar information is found for the left hemisphere (red dashed line). However, robust face-exemplar information is found in right aIT (red solid line) The figure shows group results for regions of interest defined in each individual subject. Independent data were used for (*i*) defining the regions and voxel weights and (*ii*) testing the multivariate effects and estimating face-exemplar information.

a conventional univariate mapping analysis did not yield significant effects either in single subjects or at the group level for either unsmoothed or smoothed (6-mm full-width at half-maximum) data. Contrasting the two houses did reveal effects in early visual areas. This is plausible, given that the two house images have very different distributions of low-level features, whereas the two faces are very similar in terms of low-level image features. (For further activation-based control analyses, see *SI Text*, *Results of Control Analyses*.)

Information-Based Activity-Pattern Analysis. The signature of a distributed face-exemplar representation would be a subtle difference between the fine-grained regional response patterns elicited by the two face images—despite their visual similarity. Because univariate mapping is not sensitive to subtle response-pattern differences, we performed an information-based multivariate analysis, which is designed for this type of effect (44, 45). A significant multivariate difference between the response patterns elicited by the two faces in a given region of interest (ROI) would indicate the presence of face-exemplar information. The information estimate (in bits) reflects how accurately the face exemplar could be decoded from the ROI's multivariate response on a single trial (main results in Fig. 2, see *Methods*, SI Fig. 8 and *SI Text*). Independent data were used for (*i*) defining the regions and voxel weights and (*ii*) testing the multivariate effects and estimating face-exemplar information. All pattern-information analyses were performed on unsmoothed data.

Is There Face-Exemplar Information in the FFA? The FFA was defined by the category contrast (faces–houses) in each individual subject (false-discovery rate, $q < 0.05$). No significant face-exemplar information was found in the FFA in any subject ($P > 0.05$). To maximize statistical power, we combined the data from the individually defined FFAs in a fixed-effects group analysis (see *Methods*). The FFA face-exemplar information was insignificant ($P > 0.05$) in the group analysis as well.

Could the threshold used to define the FFA have excluded face-exemplar voxels at the fringe of the region? To include more voxels at the fringe of the FFA, we systematically varied the threshold of the category contrast to select a contiguous set of 10–4,000 voxels in each subject. Although the resulting extended "FFA" at 4,000 voxels is a huge region reaching far into occipital and anterior temporal cortices, this did not reveal any significant face-exemplar information in either hemisphere (Fig. 2, blue lines, multivariate fixed-effects group analysis, $P > 0.05$).

Could the conventional definition of the FFA by the category contrast have entailed a bias against inclusion of voxels carrying face-exemplar information? Face-exemplar voxels excluded by the conventional definition of the FFA might nevertheless belong to the same functional unit. Another possibility is that the use of a different reference category (e.g., objects instead of houses) would change the precise ROI for the FFA and reveal face-exemplar information. A third possibility is that the face exemplar is encoded in a more widely distributed fashion in the FFA and its vicinity.

To exclude all three possibilities, we asked whether there is face-exemplar information in the vicinity of the FFA (including the FFA itself). To find face-exemplar information, we searched for it in each subject separately using a multivariate searchlight (44): For each voxel, we selected the 3-mm-radius spherical neighborhood (comprising 19 voxels) and computed the Mahalanobis distance reflecting the difference between the activity patterns elicited by the two faces. The Mahalanobis distance for each voxel's spherical neighborhood was entered in a descriptive map called the "face-exemplar information map." This information-based map (as well as the activation-based map used to define the FFA) was based on half the data (data set A) of each subject. Statistical tests and information estimates were based on independent data (the other half: data set B).

The "FFA vicinity" was then defined, for each subject and hemisphere, as 4,000 cortical voxels within a sphere centered on (and including) the FFA (SI Fig. 6 *c* and *d*, magenta). For each subject and hemisphere, the FFA vicinity was tested for face-exemplar information by the following procedure for $n = 10$ to $n = 4{,}000$ voxels: (*i*) Select the *n* voxels (of the 4,000) with the greatest values in the face-exemplar information map. (*ii*) Perform a multivariate fixed-effects group analysis on this voxel set using independent data (see *Methods*). Fig. 2 shows the results. Face-exemplar

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information remains insignificant in the FFA vicinity of either hemisphere (magenta), independent of the number of voxels included.

Is There Face-Exemplar Information in aIT? Analogously to the FFA vicinity, we defined aIT in each subject and hemisphere as the 4,000 most anterior voxels in temporal cortex within our inferotemporal imaging slab (SI Fig. 6 *c* and *d*, red). We then tested aIT in exactly the same way as the FFA vicinity: we selected between 10 and 4,000 voxels with the greatest values in the face-exemplar information map in each subject and performed the same multivariate group test on independent data.

Fig. 2 shows the results. In left aIT (red dashed line), face-exemplar information remains insignificant, independent of the number of voxels included. In right aIT, by contrast, face-exemplar information becomes highly significant ($P < 0.01$) when more than approximately 200 voxels are included.

Finding Face-Exemplar Information by Searchlight Mapping. To address more broadly whether face-exemplar information is present in any region within our fMRI slab, we performed a group-statistical information-based brain mapping (44) with randomization inference. We first computed face-exemplar information maps with a 3-mm-radius searchlight in each subject separately, as above, but using all data. These maps were transformed into Talairach space and subjected to group-statistical inference (see *Methods*).

This method provides an alternative perspective, (*i*) because it is not restricted to predefined regions of interest and (*ii*) because informative regions need to correspond in Talairach space to be sensitively detected [although their intrinsic pattern representations can be unique to each individual subject (45)]. Despite these differences to the ROI-based analysis, results were consistent: Face-exemplar information was found only in right aIT (global maximum of the group-statistical map shown in Fig. 3 and SI Fig. 9*b*, Talairach coordinates of centroid: 38, 2, −38, $P < 0.0001$ at peak voxel).

Summary of Results. Information-based multivariate ROI and mapping analyses indicate that right aIT responds with a distinct activity pattern to each of the faces. We found no evidence of face-exemplar information in any other region within our temporal-occipital imaging slab in either the information-based searchlight mapping or the multivariate ROI analyses performed on the FFA and its vicinity.

Discussion

Individual-Face Information Is Unlikely to Be Completely Absent in the FFA. At face value, our findings could be taken to suggest that the FFA is invariant to differences between faces. However, given the evidence from previous studies (1, 5–18, 51), we do not believe that the FFA is cleanly invariant to face identity.

We have made every effort to optimize sensitivity to fine-scale effects and go beyond previous work by combining high-resolution fMRI and information-based multivariate analysis of local response patterns. Nevertheless, the use of blood oxygen-level dependent (BOLD) fMRI with isotropic 2-mm-width voxels limits the neuronal activity pattern differences we are capable of detecting. Undetected information could reside in the fine-grained activity patterns beyond the limits imposed by voxel size and hemodynamics. Alternatively, face-exemplar information could be encoded in the temporal activity pattern, to which our statistical model here is insensitive. Our results therefore clearly do not imply the absence of face-exemplar information in the FFA or elsewhere in the brain.[§]

[§]The absence of an effect (however small) can never be statistically demonstrated. This is a general limitation in science, but particularly severe here, because each fMRI voxel reflects the activity of hundreds of thousands of neurons pooled across seconds.

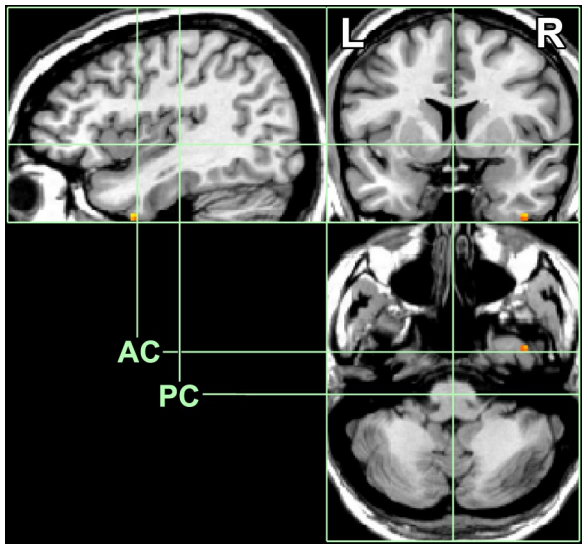

Fig. 3. Peak of distributed face-exemplar information in aIT. We used information-based functional brain mapping (44) to determine where locally distributed face-exemplar information was greatest within our occipitotemporal fMRI slab. The only region found was in right aIT (Talairach coordinates of centroid 38, 2, −38). The full information-based Talairach-space group map is shown in SI Fig. 9*b*. A single subject's map and the event-related spatial response patterns in the anterior face-exemplar region are shown in SI Fig. 11. The group map was thresholded to highlight voxels with $P < 0.001$, uncorrected (orange-yellow). The peak voxel had $P < 0.0001$ (yellow). Information-based mapping was performed in each subject by using a 3-mm-radius spherical information searchlight (44) (see *Methods*, SI Fig. 8*b*, and SI Text: *Information-Based Group Mapping in Talairach Space*); thus, each highlighted voxel indicates face-exemplar information distributed within a more extended local neighborhood (volume highlighted: 8 voxels = 64 mm^3, volume contributing information: 56 voxels = 448 mm^3). Single-subject information-based maps were transformed into Talairach space and averaged across subjects. Statistical inference was performed at each voxel by a randomization test involving random relabeling of the face trials. The background shows the MNI template brain transformed into Talairach space. Green boxes indicate the cuboid subvolumes of Talairach space. Anterior commissure (AC) and posterior commissure (PC) are indicated. The right hemisphere is on the right side in the coronal and axial slices.

Our findings do suggest that any face-identity effect is much weaker than the category effect in the FFA.

Individual-Face Information Appears Most Pronounced in the aIT. That fMRI could detect face-exemplar information in aIT, but not in the FFA or its vicinity, suggests that individual-level face information is, by at least one measure, more pronounced in aIT than in the FFA and its vicinity. The FFA and other regions are likely to contain face-exemplar information as well, at lower levels. In particular, the face images must have elicited subtly different activity patterns in early visual cortex with its retinotopic maps of low-level features. Because the faces were matched in size, view, lighting, and histogram, neither information-based mapping nor ROI analysis revealed a face-exemplar effect in early visual cortex, although all other pairs of stimuli could be distinguished (see SI Fig. 10 and *SI Text*, *Results of Control Analyses*). That our methods revealed the face-exemplar information in aIT, but not early visual cortex, suggests that the subtle differences in the early visual representation are magnified in ventral-stream processing to yield a much larger, and thus detectible, difference in aIT. The sensitivity of fMRI to the difference in aIT indicates that there are massive neuronal face-exemplar effects in that region. This suggests a functional role of this region in distinguishing individual faces (SI Fig. 11).

Low-Level Confounds Cannot Account for the aIT Face-Exemplar Effect. The absence of significant face-exemplar information in the early visual fMRI patterns (see SI Fig. 10 and *SI Text*, *Results of*

Control Analyses) suggests that the faces were appropriately matched for our purposes. This is plausible for a number of reasons. (*i*) Faces, in general, are similar in feature set and global configuration. One consequence of this is a similar spatial frequency spectrum. (*ii*) In addition, the faces were matched in size, view, and lighting, which yielded similar retinotopic images. (*iii*) Furthermore, we matched the image histograms. As a consequence, our stimuli also had identical light and spatial-signal energy. The two face images were, thus, much better matched for low-level confounds than can be achieved, for example, when a set of face images is contrasted against a set of other object images to localize face-sensitive regions including the FFA.

Both the FFA and aIT May Be Necessary for Face Identification. Our findings may appear at odds with the studies suggesting a role for the FFA in face identification (1, 5–18). However, the contrasting evidence can be reconciled: the FFA may detect faces (2, 3, 27, 28), engage aIT to identify them (4, 16, 19–26), and subsequently receive feedback from aIT. In this view, face identification requires both regions, and the activity of both should predict success and failure of the process. This would explain why (*i*) lesions in the region of the FFA are associated with deficits at recognizing individual faces (6, 9, 10) and why (*ii*) the FFA response level reflects behavioral performance at identification (11).

The face-processing stages of detection and identification have been associated with the successive components M100 and M170 in a magnetoencephalography study (46). Having detected a face, the FFA may not only trigger identification in aIT but, more generally, engage specialized nodes of the core and extended face network (1, 5) for detailed analysis, including analysis of facial expression in STS (7).

Our interpretation is also consistent with the third line of evidence for a role for the FFA in identification, namely that (*iii*) the FFA responds more strongly to a sequence of different individuals than to the same face image presented repeatedly (8, 12–17). The greater response to face-identity change than face-identity repetition is usually taken to indicate neuronal information about face identity. This interpretation is based on the idea of "fMRI release from adaptation" (47), which is expected to occur if each identity drives a different set of FFA neurons. If each set of neurons representing a face drove each of our voxels approximately equally, we might well have failed to detect the information, because our approach of direct measurement and analysis of the response patterns is limited by fMRI spatial resolution. The fMRI adaptation technique, by contrast, is not limited by the fMRI resolution. The presence of some amount of individual face information in the FFA appears likely and would be consistent with our interpretation here.

However, the interpretation of the fMRI adaptation results requires some caution (48, 49), because release-from-adaptation effects can carry over from a region A to another region B, even if the projection pools responses so that the selectivity causing the release in A is not present in B. For example, release from adaptation in a low-level region could carry over to the FFA, even if the projection pools responses so that the low-level selectivity is lost in the FFA. Similarly an aIT release from adaptation upon identity change as previously reported (16) could carry over to the FFA as an unspecific activation, even if identity could not be decoded from FFA neuronal responses. More generally, a change of perceived face identity is likely to trigger an attentional response entailing widespread activation. All affected regions (either within the face network or beyond it) would then exhibit a release-from-adaptation effect. Furthermore, if exact-image repetition defines the baseline (as in most cases, but see refs. 12, 15, and 16), it is unclear whether the release from adaptation is caused by face-identity change or low-level feature change.

From a computational perspective, face detection is a difficult task, particularly for cluttered scenes, and might well merit a dedicated functional region. There is no strong theoretical reason to believe that detection and identification must be colocalized. In fact, the representational basis functions optimal for face detection are very different from those optimal for distinguishing individuals. In a simple template-matching framework, detection would require something like an average-face template, whereas identification would require multiple templates sensitive to the subtle differences between faces.

Our Findings Are Consistent with a Wide Range of Monkey and Human Studies. ***Monkey electrophysiology, neuroimaging, and lesion studies.*** Our aIT finding is consistent with monkey cell recordings, where face-specific responses are found in many locations, but identity-specificity is strongest in the anterior temporal cortex (29–31). The monkey aIT representation has recently been described as a norm-based code for individual faces (50). Another recent study (51) investigated single-cell responses in the monkey middle face patch, which might be the homologue of the human FFA (52). These authors show that cell responses in the monkey middle face patch contain both face-category and face-identity information. However, category information is more pronounced, and identity information becomes available at a greater latency. An earlier monkey study (53) showed that bilateral ablation of the monkey STS (including the region of the middle face patch) does not entail face-identification deficits, suggesting that the middle face patch might not be the main locus of face identification.

All these results are consistent with the interpretation that the middle face patch detects faces, engages aIT to individuate them, and then receives feedback from aIT. It is unclear, however, how closely the human FFA resembles the monkey middle face patch at the level of single-cell responses.

Human electrophysiology and neuroimaging. An early study using positron emission tomography (PET) describes bilateral anterior temporal activation associated with performance of a face-identity task (4). Bilateral anterior temporal lobe exhibits a reduced response to repeated presentations of familiar faces (24). Right temporal polar cortex, in particular, has been found to be active during face perception and recognition (with its activity predictive of performance) (22), during discrimination of familiar and unfamiliar faces (23), and during the naming of faces (54). The latter study suggests that the right temporal pole serves a face-specific function, whereas the left temporal pole is domain-generally involved in naming unique entities (54). These human imaging studies all used PET.

Using fMRI, right anterior temporal cortex has also been found active during face-from-name retrieval (26), but the region is superior to ours. Some fMRI studies may have missed aIT effects, because aIT is often affected by a large fMRI-signal dropout (55, 56) caused by heterogeneous magnetic susceptibility of the local anatomy. This would explain why studies employing PET (4, 22–24, 54) or higher-resolution fMRI (16) [which is less affected by the dropout (55)] more consistently report anterior temporal activity related to face recognition. For example, there is fMRI-adaptation evidence (16) for an involvement of both the FFA and bilateral aIT in face-identity representation. This study used 2-mm slices (1-mm gap) with $3 \times 3\text{-mm}^2$ in-plane voxel size.

Our findings are also consistent with three related studies describing intracranial electrophysiological recordings in human patients exposed to face stimuli (57–59). The authors describe a human "anterior face area" located in the right hemisphere and giving rise to the face-specific AP350 potential (57), which is shown to be reduced on repetitions of the same face (59). This response reduction on repetition is consistent with an identity representation in right aIT. A reduction on repetition was not found in the earlier face-specific N200 originating in more posterior ventral cortex (59).

Acquired prosopagnosia. Prosopagnosia is the inability to recognize individual faces. This disorder can be acquired by brain damage. In particular, it can be caused by lesions in the general region of the FFA (6, 9, 10). Damage to the FFA in these cases may impair

engagement of aIT for identification. Prosopagnosia can also occur in the presence of a face-selectively responding FFA (17, 60), demonstrating that other face-specific regions besides the FFA are needed for identification. In the patient in question (PS) (17, 60), the FFA responses to sequences of faces of different identity appear altered (17), which could be caused by altered input or feedback to the FFA. Prosopagnosia can also be caused by anterior temporal lesions (19, 20, 25). Lesions in the right temporal polar cortex can impair face identification (19). Right anterior temporal atrophy is frequently associated with progressive prosopagnosia (20). Gainotti *et al.* (25) describe a patient with a right anterior temporal focal atrophy associated with impaired identification of familiar people from their faces or voices. The authors suggest that the impairment may be caused by damage to face-recognition units (61) in the right anterior temporal cortex.

Congenital prosopagnosia. Prosopagnosia can also be congenital in the absence of any apparent brain damage (62). Like acquired prosopagnosics, congenital prosopagnosics can detect faces (63) and often exhibit intact FFA activity (64, 65). However, they cannot identify faces, and there is evidence of decreased cortical volume in the right anterior temporal cortex (62, 66).

What Is the Nature of the Human aIT Face Representation? The presence of face-exemplar information in aIT suggests that aIT contains a population code representing the subtle differences between individual faces. However, many questions remain.

What face properties are represented in the aIT? First, individual faces in general and our stimuli in particular differ along many dimensions. There is an extended literature addressing face-space dimensions (67, 68) including gender, age, attractiveness, overall configuration, local features and skin texture. The relative importance of these dimensions in the aIT face representation needs to be elucidated.

How does aIT face representation relate to memory? Anterior temporal activity has been found to be greater for familiar than unfamiliar faces and has therefore been associated with access to memory about people (1, 5, 24) (see also refs. 69 and 70). In our study, faces were perceptually familiar to the subjects from a task training immediately preceding the experiment, but subjects did not have any conceptual knowledge (e.g., names, biographical information) about the individuals. A perceptual representation of face identity in interaction with medial temporal memory regions might be expected to show greater activity for familiar faces. Feedback from memory could provide *a priori* information serving to stabilize the activity pattern representing the individual, thus reducing perceptual noise. As a consequence, familiar faces may elicit more distinct individual-face representations. This would be consistent with a report of an aIT face-identity-change effect correlated with face familiarity (16) (see also ref. 71). Clearly memory and perception depend on each other; in fact, it is difficult to draw a bold line between them (72). Another possibility, then, is that the aIT face representation itself contains long-term memory traces. For example, the basis patterns of the representation (or the attractors of its dynamics) may correspond to known faces. Haxby *et al.* (1, 5) suggest that anterior temporal cortex contains representations of person identity, name, and biographical information (see also refs. 73 and 74).

Is the right aIT representation face-specific or domain-general? The anterior temporal cortex is thought to represent complex feature conjunctions suited for fine-grained discriminations (75–77), including the discrimination between individual faces. The right aIT representation did not distinguish the houses—despite their greater visual dissimilarity (SI Figs. 9*c* and 10). It thus does not appear to be completely domain-general. Previous studies suggest that right anterior temporal cortex processes face information (22, 23, 26, 54, 57, 59). However, the region could, for example, distinguish animate objects in general. Establishing face-specificity [as has been done for the FFA (11, 28, 78, 79) (but see refs. 80 and 81)] will require testing with exemplars from a range of different categories.

Methods

In this section, we give only an abbreviated methods description. Details on subjects, stimuli, task, design, and analysis are in *SI Text*.

Design and fMRI Measurements. We used a rapid event-related design with a basic trial duration of 3 s (minimal stimulus–onset asynchrony), corresponding to two functional volumes (volume acquired every 1,500 ms). Each image was presented for 400 ms. We measured 15 transversal functional slices (including early visual regions as well as the entire ventral visual stream) with a Siemens Magnetom Trio scanner (3 Tesla). Voxels were isotropic: $(2\ mm)^3$.

Statistical Analysis. ***Significance testing of activity-pattern effects.*** We used a standard univariate *t* test to determine whether two images elicit distinct response patterns in an ROI (Fig. 2). The *t* test is performed after projecting the data onto a multivariate discriminant dimension determined with independent data (SI Fig. 8*a*). This univariate *t* test on the multivariate discriminant constitutes a multivariate test of response-pattern difference. Compared with classical multivariate tests, this test has the advantage of not requiring the assumption of multivariate normal errors; univariate normality (as is commonly assumed in univariate fMRI analysis) suffices.

For each subject, two data sets (A and B) of the same experiment are used in the analysis. Set A is used to form a subject-specific hypothesis regarding (*i*) the precise ROI discriminating the images and (*ii*) the multivariate dimension discriminating the images. Set B is then used to test this hypothesis.

For example, to test for a face-exemplar effect in a given ROI, we first determine the response patterns elicited by the faces in data set A by using standard linear modeling. We then determine the weighting of the voxels that best discriminates the two faces in set A (face-exemplar discriminant). This weighting is closely related to the *t* map for the contrast between the two faces (but normalized by error variance instead of standard error, equivalent to a Fisher discriminant with diagonal covariance). If the contrast pattern represents an actual difference between the response patterns elicited by the two face images in the ROI, it should replicate in data set B. We therefore compute a weighted sum of the ROI time courses in data set B using the weights determined from set A. This yields a single time course (the discriminant time course), which can be subjected to a *t* test as commonly used in fMRI analysis. We use this approach to perform a fixed-effects group analysis, using prewhitening to account for temporally autocorrelated errors.

Information estimates. As a measure of the amount of information a region contains about which of two images is being perceived, we estimate the mutual information between the stimulus and the multivariate response it elicits on a single trial. For the two faces, one bit of single-trial face-exemplar information (Fig. 2) would imply that a single trial's fMRI response pattern (20 s of fMRI data acquired after a single 400-ms presentation of a face image) always suffices to determine, with perfect certainty, which of the two faces was shown. We apply this measure to all pairs of the four image conditions and refer to it as the single-trial pair-wise condition information. Because fMRI measurement is noisy and limited in resolution and because our estimate depends on assumptions (see *SI Text*), the pair-wise condition information is an estimate of a lower bound on the actual information present in the region.

Information-based mapping. Face-exemplar information was mapped by information-based functional brain mapping (44, 45). This method scans the imaged volume with a spherical searchlight to find regions whose response pattern distinguishes the faces (SI Fig. 8*b*). More precisely, we used a spherical searchlight of 3-mm radius to highlight 19 voxels [size: $(2\ mm)^3$] at a time. This searchlight was centered at each imaged voxel in turn, highlighting overlapping spherical sets of voxels. Using the linear model, we estimate the response patterns associated with the two faces within the searchlight and compute the Mahalanobis distance as a multivariate contrast statistic. The Mahalanobis distance is recorded in a statistical map at the voxel at the center of the searchlight. This method yields a continuous map indicating the evidence for face-exemplar information in the local neighborhood of each voxel.

For the ROI-based analysis of face-exemplar information in the FFA and aIT (SI Fig. 6 and Fig. 2), we performed a descriptive information-based mapping for each subject separately using only data set A. The resulting face-exemplar information map served to define the ROI at a given number of voxels (see SI Fig. 6 and *SI Text*). Independent data (data set B) was then used to perform statistical inference for the ROI by means of the pattern-discriminant *t* test described above.

In addition, we also performed an information-based group mapping in Talairach space (Fig. 3 and SI Fig. 9*b*) using all data. Here, we used a randomization scheme involving permutation of the condition labels for statistical inference

(details in *SI Text*). All information-based mapping analyses were performed with custom software developed in Matlab.

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