

Contrast polarity and face recognition in the human fusiform gyrus

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Functional imaging has revealed face-responsive visual areas in the human fusiform gyrus, but their role in recognizing familiar individuals remains controversial. Face recognition is particularly impaired by reversing contrast polarity of the image, even though this preserves all edges and spatial frequencies. Here, combined influences of familiarity and priming on face processing were examined as contrast polarity was manipulated. Our fMRI results show that bilateral posterior areas in fusiform gyrus responded more strongly for faces with positive than with negative contrast polarity. An anterior, right-lateralized fusiform region is activated when a given face stimulus becomes recognizable as a well-known individual.

Humans are remarkably adept at recognizing individuals by their faces¹, an ability that may rely on specialized neural circuits. Findings from brain-damaged 'prosopagnosic' patients with deficient face processing²⁻⁷ as well as physiological data from nonhuman primates⁸ have now been supplemented by functional imaging. Certain ventral occipito-temporal areas of the human brain, centered around the fusiform gyrus, are shown by functional imaging to respond more strongly to faces than to other classes of visual stimuli¹¹⁻¹⁹. However, the functional significance of this remains unclear. In principle, the fusiform response to faces found in most studies might be driven simply by the spatial frequencies and/or edge arrangements that distinguish human faces from other stimuli (for instance, two eye-like blobs flanking a nose-like structure). Even a stronger fusiform response to upright rather than inverted faces¹⁸ might still involve differences in the spatial location of particular edges or of component spatial frequencies. It thus remains possible that the computational function of the fusiform is merely to extract particular edges or spatial frequencies, rather to subservise those computations that allow well-known faces to be recognized as individuals.

We sought to go beyond previous comparisons of faces to other objects, since such comparisons inevitably involve many uncontrolled differences in low-level stimulus properties, as noted above. Instead, by exploiting psychological constraints upon individual face recognition, we sought to determine whether the computational role of the fusiform gyrus is consistent with the requirements of such recognition. Psychological studies have shown that faces are particularly hard to recognize as known individuals when contrast polarity is reversed^{2,20-24}, as in photographic negatives (Fig. 1). The difficulty of recognizing negatives commonly has been attributed^{1,21,25} to disruption of 3D shape-

from-shading perception (because shadows become brighter regions in negatives, and so are misinterpreted). It might also be explained in terms of overlearned 2D representations for faces, provided these are contrast-polarity specific^{26,27}. On either account, the important point is that contrast-polarity reversal disrupts face recognition despite preserving all edges and spatial frequencies. While a negative may still be classified as a face, the image looks flat and impoverished in comparison with the corresponding positive, and, typically, the depicted individual can no longer be identified. The only circumstance in which negatives of faces become readily identifiable is where the corresponding positive image has been shown shortly before (as we demonstrate below). Most readers should be able to experience these phenomena by first inspecting Fig. 1 and then Fig. 2.

Here we exploit these psychological phenomena to test whether any regions in the fusiform respond to the contrast-polarity-specific structure that is evidently required for the recognition of well-known individuals. If so, three predictions can be made. First, the neural response in brain areas coding the required structure should be stronger to positive than to negative face images. Second, the preference for positives over negatives should be more pronounced for famous than for unknown faces in those brain areas responsible for recognizing well-known faces, since famous positives can yield identification of a well-known individual but unknown positives cannot. (Note that the brain regions involved in extracting face structure may not be identical to those that use this information for recognition; however, we sought to determine any fusiform involvement for both these predictions.) Our final prediction was that the negatives of famous faces should become more recognizable as well-known individuals, and thus induce a stronger neural response, following a 'priming' manip-

ulation where the corresponding positive is shown shortly before, which boosts recognition of famous negatives (as for the negative of Marilyn Monroe when viewing Fig. 2 after Fig. 1). Numerous psychological studies have shown that recognition of a well-known individual is facilitated by previous successful identification of that same face, but not by previous exposure in which the face was unidentified^{1,28–30}. Since faces of unknown people cannot yield identification even in positive form, the predicted increase in neural responses for primed negatives (that is, those previously seen in positive) versus unprimed negatives should be observed for famous but not for unknown faces.

Our study used two-tone red/green pictures of faces, like those created by Andy Warhol (Figs. 1 and 2). The faces were either of well-known (famous) individuals, or unknown people, and in either case could be presented as positive or negative two-tones (shadows appeared as dark red in the positives and as light green in the negatives; to hold overall luminance constant throughout and thus eliminate low-level differences between positives and negatives, the total areas of dark red and light green were equal in each picture; see Methods). These four types of stimuli were presented in a blocked factorial fMRI design, with blocks of faces separated by baseline periods of fixation. For half the blocks ('unprimed'), the particular face pictures shown had not been seen in previous blocks. For the other blocks ('primed'), the particular face pictures had appeared before, but with the reverse contrast polarity. Comparing these blocks allowed determination of any effects of previous exposure to the stimuli on fMRI activations.

We sought to measure the spontaneous brain activity produced when the various types of faces were seen while avoiding possible contamination from differences in task complexity between conditions. Accordingly, we chose a task designed to be neutral with respect to the various types of face; this required only that the stream of faces be monitored for the occasional presentation of a checkerboard probe.

RESULTS

Reaction times (RTs) for pressing a button in response to the checkerboards did not differ between any of the conditions, averaging 404 ± 17 ms (s.e.).

As would be expected, all face pictures strongly activated the ventral visual pathway, including areas of the fusiform gyrus associated with responses to faces in prior fMRI studies^{14–18}, with respect to the fixation baseline (Fig. 3). This extensive activation exceeded a corrected significance threshold of 0.0001 and was highly consistent across subjects. Given the aims of the study, our subsequent analyses used this comparison as a mask, to restrict further interrogation of the data to visually responsive brain areas driven when monitoring the face stimuli. Note that this 'mask' is not overly restrictive, as it incorporates the entire ventral stream of visual processing, from early occipital areas through to inferotemporal cortex. Although first tested in a fixed effect model, all activations were subsequently assessed in a random effect model and found to be significant across subjects (see Methods).

Our first prediction of a stronger response for positive than for negative two-tones was confirmed by enhanced activation in bilateral posterior fusiform gyri (Fig. 4). This activation was more extensive in the left hemisphere (as discussed later), peaking in the posterior border of the fusiform gyrus and extending anteriorly. In the right hemisphere, activation peaked in the lateral border of the fusiform gyrus. Note that stronger responses for positives than negatives could not result from edge or spatial-frequency differences or differences in overall brightness between the stimuli, since these were equivalent for positive and negative

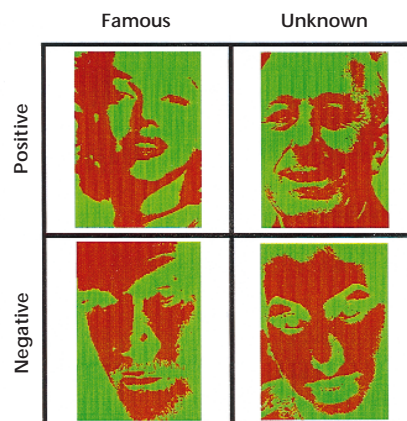


Fig. 1. Four example face stimuli, each illustrating one condition. Note that the negatives yield flatter, impoverished percepts. The famous negative should be unrecognizable despite depicting a well-known individual, whereas the famous positive should be easy to recognize.

images. Note that, unlike previous studies that compared faces with very different classes of objects^{11–17,19}, the present study compared only face-like stimuli. Thus, the critical psychological difference responsible for the activation was presumably the richer percept of structure for positive versus negative faces.

Our second prediction was that, for those brain areas involved in recognition of well-known individuals from facial structure, the preference for positives over negatives should be stronger with famous faces, as only these can yield identification of well-known individuals. This was tested by the interaction between positive versus negative, and famous versus unknown. Stronger activation focused in the right mid-fusiform gyrus was found for famous positive faces (Fig. 5). For positive versus negative famous faces, this region showed a simple effect in addition to the interaction (maximum at $x = +32$, $y = -36$, $z = -18$; $p < 0.005$), but no such simple effect was observed for unknown faces. (The slight trend for the opposite pattern with unknown faces did not approach

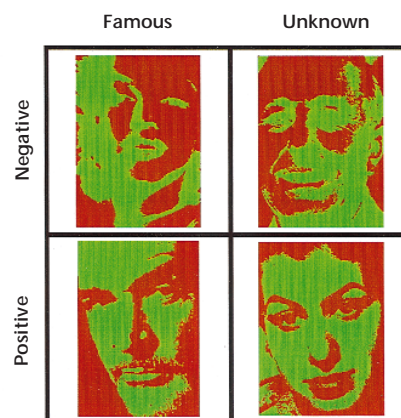


Fig. 2. The same four faces as in Fig. 1 with reversed contrast polarity. Comparing the faces in Fig. 1 to those in this figure shows that each picture yields an impoverished percept when in negative rather than positive. However, note that famous negatives become easier to recognize once the positive has been seen (for example, Marilyn Monroe becomes recognizable in this figure only after seeing Fig. 1, indicating a priming effect from previous recognition).

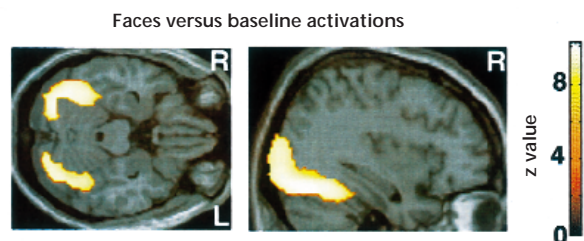


Fig. 3. Activation for all face conditions versus the fixation baseline. Coronal and sagittal sections are shown. Activated voxels passed $p < 0.0001$ corrected in the group analysis and were found in every subject.

significance.) There was no such activation in the left hemisphere. Thus, the right mid-fusiform region is sensitive to whether a positive face is recognizable as a well-known individual. This region lies anterior to the bilateral fusiform areas that were activated by positives versus negatives, regardless of familiarity (compare Figs. 4 and 5); indeed, no voxel in those more posterior areas showed any tendency toward the interaction found in the more anterior right region (all $p > 0.5$), and the z-scores for this interaction differed significantly ($p < 0.001$) between the right mid-fusiform region and its strongest value for posterior areas ($z = 2.95$ versus -0.16). Note that, in contrast to previous imaging studies on the recognition of known faces^{19,31–33}, the observed significant interaction in the right mid-fusiform area rules out influence from spurious differences in spatial frequencies or edge layout between the famous versus unknown face stimuli. The positive and negative of each stimulus share these low-level features, yet the right mid-fusiform response was only greater for famous faces among the positives and not for famous versus unknown faces among the negatives (Fig. 5). Thus, increased activation in the right mid-fusiform in response to famous positive faces seems to result specifically from recognition of well-known individuals, and not from spurious differences in the low-level features of famous versus unknown people.

Our final analysis addressed priming effects (influences of previous exposure) arising when a particular face that had appeared in one block subsequently reappeared in a later block, but now with the reverse contrast polarity. Recall that previous experience with a positive face should facilitate subsequent identification of its negative, but that this phenomenon can only apply for famous faces, as only these correspond to well-known and identifiable individuals. In a separate behavioral study with the same stimuli that were used in our imaging study (see Methods), we confirmed that previous exposure to famous positives affected subsequent explicit recognition of their negatives. We found that whereas famous positives were recognized more often than 'unprimed' famous negatives (69% versus 17%, $p < 0.0001$), previous experience with famous positives significantly increased the rate of subsequent recognition for their negatives (45% if the positive had been seen, versus 17%, $p < 0.001$).

This behavioral study confirms that previous exposure to famous positives can make otherwise unrecognizable famous negatives identifiable for the first time. Accordingly, we examined the fMRI data from the famous-face blocks for any simple effect showing greater activation for primed famous negatives (previously seen as positive) than unprimed famous negatives (not previously seen). This revealed bilateral fusiform activations for primed famous negatives (Fig. 6). The right-

hemisphere activation peaked at the lateral border of the fusiform gyrus, and extended into midfusiform gyrus (thus overlapping with the activations in both Figs. 4 and 5). The left hemisphere activation peaked more posteriorly in the fusiform (overlapping with the activation in Fig. 4). Thus, previous viewing of positives enhanced fusiform activation in response to the very same negatives of famous faces; this fits with our behavioral finding that exposure to positives makes famous negatives more identifiable.

The fMRI data from the faces of unknown people provide a control to test whether the influence from prior exposure on the fusiform activation for famous faces was merely due to the repetition of low-level features shared by positives and negatives, rather than the proposed influence upon identification of well-known individuals. Repetition of spatial frequencies and edges arises for negatives of unknown people that have previously been seen as positives, just as for famous faces, but in this case cannot enable identification of a well-known individual. A significant interaction between primed versus unprimed, and famous versus unknown negative faces, was found for the activated regions ($p < 0.0001$ for the left hemisphere, $p < 0.0004$ for the right, at the maxima for the simple effect of priming with famous negatives; Fig. 6). Whereas previous exposure to positives of famous negatives led to increased activation for those negatives, such previous exposure had the opposite effect for unknown faces, leading to reduced activation. Indeed, the maxima for the simple effect of priming with the famous negatives also show a simple effect for unknown faces, but in the opposite direction ($p < 0.004$ for the left hemisphere; $p < 0.05$ for the right).

DISCUSSION

Our first finding, namely bilateral enhancement of posterior fusiform activation for positives versus negatives of the same two-tone faces (Fig. 4), implies that the activated regions are sensi-

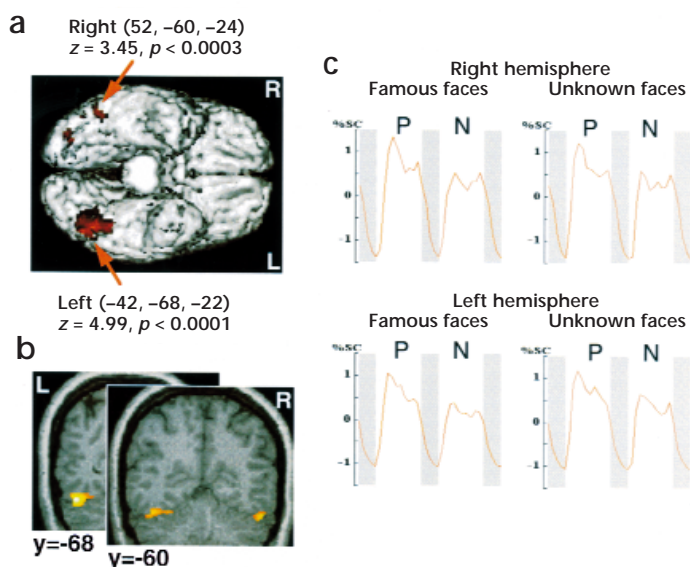


Fig. 4. Activations for the main effect of positive versus negative face stimuli, pooling over fame. (a) Activations superimposed on the ventral surface of a T1-weighted template; the regions of local maxima are marked with arrows, and corresponding Talairach coordinates indicated together with z and p values. (b) Coronal sections through these maxima. (c) Averaged timecourses of activity in the maxima, shown for illustrative purposes; these give the percent signal change relative to the overall mean activity at each voxel for the four conditions (gray bands represent fixation-baseline periods; P, positives; N, negatives). Upper graphs for the right hemisphere, lower for the left.

tive to the contrast-polarity-specific structure critical for face recognition¹. These fusiform areas are evidently driven more strongly by structurally richer face percepts, in agreement with evidence from monkey single-cell recordings³⁴. Our data further show that the right midfusiform gyrus region is specifically sensitive to the recognition of a face as a well-known individual, as demonstrated by the interaction between fame and contrast polarity (Fig. 5). Recall that none of these effects can be attributed to any influence from spurious differences in spatial frequencies or edge layout between the particular famous and unknown positive and negative faces that were used, since these low-level features are held constant across the reversal of contrast polarity. In this respect, our experiment differs from a recent study¹⁹ that also used both famous and unknown faces, but employed written names for the comparison conditions.

The activation specific to the positives of famous faces was more anterior than that found for the overall comparison of positive versus negative faces (compare Figs. 5 and 4, noting the absence of the interaction pattern of Fig. 5 in posterior fusiform regions in Fig. 4). The main effect of positive versus negative includes activation by unknown positive faces, and thus emphasizes only the structurally richer face percept for positives, rather than processes related to the recognition of well-known faces as isolated by the interaction. Consequently, our results provide direct evidence to support previous proposals^{35–38} that posterior regions of the fusiform are primarily concerned with encoding the structure of faces, whereas more anterior regions are involved in contacting long-term representations of well-known faces. Furthermore, the contrasting laterality of these activations (compare Figs. 4 and 5) offers a resolution to previous discrepancies concerning possible hemispheric asymmetries in the lesions that produce various forms of prosopagnosia^{2–7}.

Specifically, bilateral posterior fusiform activation accompanying richer structural percepts (positives versus negatives) is consistent with a role for both hemispheres in the structural encoding of faces. This activation appeared somewhat more extensive in the left hemisphere (Fig. 4a; perhaps because of the two-tone stimulus format³⁹), although it should be noted that the percent signal change was the same or larger in the right (Fig. 4c). By contrast, the midfusiform activation that we associate with recognition of well-known individuals was exclusively right lateralized (Fig. 5). This difference accords with clinical dissociations between apperceptive versus associative prosopagnosia^{2–7,36}, and with several previous claims for hemisphere

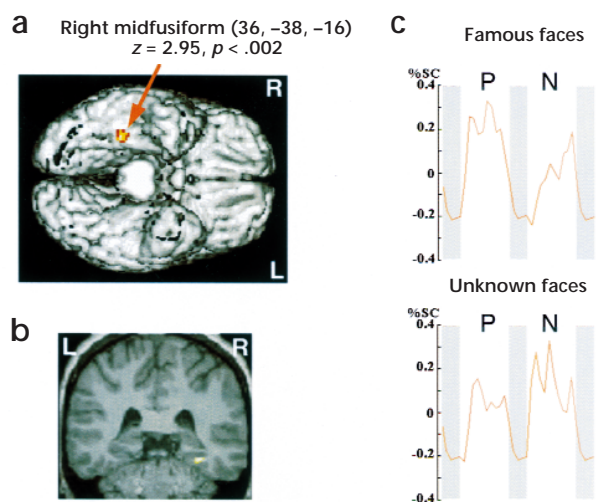
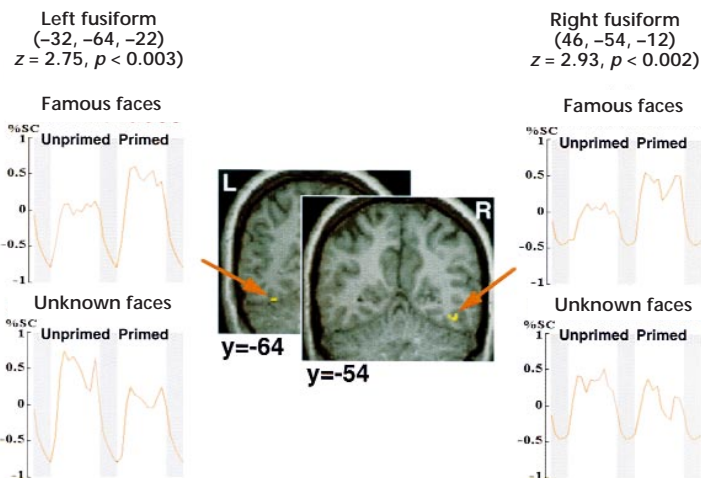


Fig. 5. Activation produced by the interaction between fame and contrast polarity (specifically, voxels with a larger positive versus negative difference for famous than unknown faces). **(a)** Activation superimposed on the ventral surface of a T1-weighted template; arrow marks the maximum. **(b)** Coronal section through the maximum. **(c)** Averaged time courses for the activated cluster, illustrating percent signal change for the four conditions.

specialization in face recognition (ref. 33, for instance).

We did not compare the neural response for faces against other classes of objects in this study, as our aim was to go beyond such comparisons (which are confounded by many low-level stimulus properties) to characterize the general computational role of the fusiform gyrus. However, it is of interest to compare the activations found here with those obtained in the many previous studies that contrasted faces with other classes of objects^{11–17}. There is good overlap between the posterior fusiform activations found here for positive versus negative faces (which we associate with structural encoding; Fig. 4) and previous comparisons of faces versus objects^{11–17}. By contrast, the right midfusiform activation revealed by the interaction between contrast polarity and fame (which we associate with recognition of well-known individuals) lies anterior to typical face-versus-object activations. This makes sense, given that previous face-object

Fig. 6. The effect of previous exposure to the corresponding positive on the fMRI response to famous face negatives. In the center, coronal sections are shown through maximal activations for the contrast of primed versus unprimed famous negatives, in the left hemisphere (more posterior section) and right hemisphere. The upper graphs on the left and right show averaged timecourses for the maxima, showing mean corrected percent signal change for the primed and unprimed conditions for the famous negatives. The lower two graphs plot the time course of mean corrected percent signal change at these same maxima for the primed and unprimed conditions with the unknown negatives. Note that the maxima for the simple effect of priming with the famous negatives also show an interaction between priming and fame, with simple effects in opposite directions for famous versus unknown faces.



comparisons typically used faces of unknown people. Moreover, it accords with proposals that more anterior regions use the output of posterior structural encoding for recognition of known individuals^{35–38}.

Because our study did not use object conditions analogous to the face conditions, it remains unknown whether similar activations could have been found with objects. However, psychological studies show that object recognition is much less impaired by contrast-polarity reversal than is face recognition⁴⁰, presumably because the latter relies more on shape-from-shading and/or contrast-polarity-specific representations for within-category individuation^{22,25,41}. Indeed, any apparent face specificity in the fusiform may arise precisely because individuation of faces makes particular demands upon such processes.

Could any of our results be explained by differential attention during the various face conditions? Performance in the checkerboard detection task did not differ between conditions. Moreover, any attentional account would have to explain the anatomical specificity of our activations (that is, bilateral posterior fusiform activation for faces with a richer structural percept, and right midfusiform activation specifically for identifiable well-known faces). Any proposal that subjects attended more to the structure of the faces in the former case, but to their identity in the latter, would be equivalent to our own explanation of the functional role of activated regions. Similarly, eye movements do not provide a plausible alternative account for our data. Subjects were instructed to fixate the central dot throughout. Moreover, eye movements during free viewing of faces by normal observers follow the same stereotypic pattern for familiar and unfamiliar faces⁴², and we know of no evidence that they could differ within the relatively short exposure durations used here. Finally, differences in eye movements between conditions should have differentially activated eye-movement-related structures and early retinotopic visual areas, but no such activations were found.

Our final result, concerning the effects of previous exposure to positives (priming) upon the neural responses to corresponding negatives (Fig. 6), provides further evidence on the relationship between fusiform activity and recognition of well-known individuals. We found increased fusiform responses to the very same famous negative stimuli if they had previously been seen as positives; this previous exposure also renders these faces identifiable. The qualitative difference between the effects of such prior exposure for known versus unknown faces (see Fig. 6) confirms that the priming effect for famous negatives is not merely due to the repetition of low-level features, but instead to the face becoming identifiable as a well-known individual.

The generic term 'priming' has been used in past work to encompass numerous influences from prior experience^{28–30,43–49}. Broadly speaking, these fall into two distinct classes. In one case, repeating a stimulus merely increases the efficiency (or speed) with which information is extracted, but does not qualitatively change this information. This 'passive' behavioral consequence of stimulus repetition has been consistently associated with an attenuated neural response^{43–47}, as illustrated here by the primed negatives of unknown faces. In the other case, prior exposure alters information extracted from the primed stimulus, as when a degraded or ambiguous stimulus such as a famous negative becomes identifiable only when primed by its positive. This more 'active' consequence of priming may increase neural activation, presumably because additional computations can be performed (in accord with the now successful recognition). Only two previous studies have observed increased activation with priming^{48,49}; just as for the famous negatives here, interpretation of

degraded or ambiguous stimuli in these studies changed after priming. Within the same experiment, our study found that the two possible effects of priming—passive versus active—have qualitatively different neural consequences. Contrast between passive repetition effects and active priming effects has long been central to psychology^{1,50}; our findings suggest that it may prove equally fruitful in imaging research. Finally, note that the priming effect for famous faces (Fig. 6) activated voxels that overlapped not only with the activations associated with recognition of well-known individuals in our initial analyses (right midfusiform; Fig. 5), but also with those associated with structural encoding (bilateral posterior fusiform; Fig. 4). This may arise because once a well-known individual has been recognized from a negative (for instance, Marilyn Monroe in Fig. 2), the structure in the image receives a richer internal representation.

As with most other imaging studies of priming, the present design does not separate possible influences of explicit versus implicit memory when measuring the effects of prior exposure (for instance, whether subjects attempted to recall famous individuals encountered earlier in the experiment). This should be an interesting topic for future research. Our study bears some similarities to a previous PET investigation on the priming of degraded pictures⁴⁸, but differs in numerous important respects. That previous study presented unrecognizable two-tones that were perceived as more meaningful following exposure to a grayscale version of the image, and found stronger fusiform activations after this exposure. This accords with our own finding that, accompanying psychological changes as a function of prior experience, fusiform activations for a given stimulus also change. However, note that positive stimuli were not compared with negative as here, nor famous with unknown stimuli, and so none of the present conclusions could have been drawn from that study⁴⁸. Moreover, identification as a function of previous exposures was not separated from the more passive consequences of stimulus repetition. This was achieved here by comparing effects of previous exposure to positives on recognition of famous versus unknown negative faces.

In conclusion, our results establish that the computational function of the fusiform gyrus goes well beyond the mere extraction of edges and spatial frequencies. Bilateral posterior regions in the fusiform gyrus respond to the contrast-polarity-specific structure normally required for the recognition of well-known individuals from their faces. A more anterior region in the right mid-fusiform is activated when such recognition takes place.

METHODS

Subjects. Written, informed consent was given by 8 right-handed volunteer subjects (5 male) aged 20–30. The study was approved by the National Hospital for Neurology and Neurosurgery Ethics Committee.

Stimuli. We used 40 famous faces (including well-known politicians and movie stars, 15 female) and 40 unknown faces matched for sex, approximate age and image size. Each image was cropped to contain an equal number of red and green pixels, giving an equivalent amount of each color in a positive and its negative. Visual angles subtended by the stimuli were 12 degrees vertically, and 5.5–4 degrees horizontally; the average sizes (and variances) for famous and for unknown faces were equivalent.

Procedure. Each 41-second stimulation block of a particular experimental condition comprised a succession of 40 600-ms face presentations separated by 330 ms intervals (the first 10 faces were each different, the next 10 were the same faces in a different order, and so on). Note that the term 'face recognition' in this paper refers to identification of a well-known individual by his/her face, not to detecting

repetition of a particular face within a block; the latter applied equally for all the different stimulus types we compared. The subsequent block showed 10 different faces, also four times each, and so on. During the face blocks, the task was to fixate a central white point within the stream of successive faces and to indicate detection of a red-green checkerboard within this stream (four per block) by pressing a button with the right hand. This was implemented to ensure visual monitoring of stimuli with a task that was neutral with respect to familiarity and contrast polarity.

Each subject saw a total of 16 face blocks, since the 4 face conditions (famous positive, unknown positive, famous negative, unknown negative) were presented 4 times to each subject. Each condition appeared once in the first four blocks, with order counterbalanced over subjects. The next four blocks each showed the same face stimuli, except that contrast polarity was now reversed, changing the order of conditions accordingly. The subsequent four blocks had new face stimuli (with the reverse order of conditions to the first four), and the last four blocks repeated these with reverse contrast. Hence, blocks 1–4 and 9–12 presented unprimed faces and blocks 5–8 and 13–16 presented primed faces. Which particular faces were primed and which were unprimed was counterbalanced across subjects. Fixation-baseline periods of 20.5 s intervened between successive face-blocks. During these, the central white fixation point appeared on a blank screen, flickering at the same pace as it did when accompanying the faces in the experimental blocks (600 ms on, 330 ms off).

A Siemens VISION system at 2T acquired both T1 structural and gradient EPI T2* BOLD-contrast images of the entire brain volume (48 transverse, ascending slices, $3 \times 3 \times 3$ mm; TR = 4.1 s; TE = 40 ms). A total of 251 functional images were acquired per subject, and the first 6 discarded to eliminate magnetic saturation effects. This left 10 volumes per face block, and 5 volumes per baseline period. Image processing and statistical analyses used SPM97d (<http://www.fil.ion.ucl.ac.uk/spm>). The imaging time series was realigned, spatially normalized to the stereotaxic space of Talairach and Tournoux and smoothed with a Gaussian kernel of 10 mm, full width, half maximum.

For the separately conducted behavioral study, the same 40 famous faces as in the fMRI experiment were presented. However, the order and timing of presentation differed because of the requirement to measure explicit recognition. Twelve new subjects judged whether each face depicted a famous person or not; their button press response removed the face stimulus. Following an affirmative response, they had to name the person or give an appropriate semantic description (if they recognized the person but forgot the name). In practice, faces judged as famous were always correctly named and/or described. The task was first performed on 20 of the famous faces, half positive and half negative, in random order. Subsequently, the same faces appeared but now in reverse contrast polarity, to assess whether previously seeing a positive would prime recognition of its negative. The final two blocks repeated this with the 20 remaining famous faces.

Statistical analyses. fMRI data analysis modeled the different conditions (positive and negative famous versus unknown faces, primed or unprimed, plus baseline) as box-car functions convolved with a hemodynamic response function. Specific effects were tested by applying appropriate linear contrasts to the parameter estimates for each condition, resulting in a *t*-statistic for each voxel. When transformed to *z*-statistics, these provide statistical parametric maps. We performed a group analysis involving all subjects, where we first compared all the face blocks to the baseline, at $p < 0.0001$ corrected. Subsequent orthogonal analyses were then restricted to the visually responsive areas revealed by this contrast (masking procedure in SPM). Furthermore, as tests performed in SPM97d rely on a fixed-effect model, we performed a conjunction analysis that discards voxels yielding significant subject-by-contrast interactions. Thus, no reported activations differed significantly between subjects. Subsequently, a random effect model was developed as an extension to SPM97d (to be released in SPM99), and we verified that all reported effects were significant across subjects ($p < 0.01$). Finally, note that all the activations are in the fusiform gyrus, known *a priori* to be associated with face processing.

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