

Neural correlates of processing facial identity based on features versus their spacing

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Abstract

Adults' expertise in recognizing facial identity involves encoding subtle differences among faces in the shape of individual facial features (featural processing) and in the spacing among features (a type of configural processing called sensitivity to second-order relations). We used fMRI to investigate the neural mechanisms that differentiate these two types of processing. Participants made same/different judgments about pairs of faces that differed only in the shape of the eyes and mouth, with minimal differences in spacing (featural blocks), or pairs of faces that had identical features but differed in the positions of those features (spacing blocks). From a localizer scan with faces, objects, and houses, we identified regions with comparatively more activity for faces, including the fusiform face area (FFA) in the right fusiform gyrus, other extrastriate regions, and prefrontal cortices. Contrasts between the featural and spacing conditions revealed distributed patterns of activity differentiating the two conditions. A region of the right fusiform gyrus (near but not overlapping the localized FFA) showed greater activity during the spacing task, along with multiple areas of right frontal cortex, whereas left prefrontal activity increased for featural processing. These patterns of activity were not related to differences in performance between the two tasks. The results indicate that the processing of facial features is distinct from the processing of second-order relations in faces, and that these functions are mediated by separate and lateralized networks involving the right fusiform gyrus, although the FFA as defined from a localizer scan is not differentially involved.

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1. Introduction

Human adults are remarkably proficient at recognizing faces. One sign of their expertise is the ability to recognize thousands of individuals at a glance when faces are seen in their canonical upright orientation. This ability is impressive, given that all faces share the same first-order relations: they have the same arrangement of features with two eyes above a nose, which is above a mouth, all within an oval contour (reviewed in Maurer, Le Grand, & Mondloch, 2002). Apart from superficial and changeable cues

like hair color, adults use three types of information to individuate upright faces: the shape of the external contour (head shape, chin shape), the shape of individual internal features (shape of the eyes, eyebrows, nose, mouth), and the spacing of the internal features (distance between the eyes, distance between the eyes and mouth, etc.) (reviewed in Maurer et al., 2002).

Previous studies have identified a region of occipitotemporal cortex, in the fusiform gyrus, that responds more robustly to faces than to other types of visual stimuli (Downing, Chan, Peelen, Dobbs, & Kanwisher, 2006; Grill-Spector, Sayres, & Ress, 2006; Haxby et al., 1994; Kanwisher, McDermott, & Chun, 1997; Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000). This area is commonly known as the fusiform face area, or FFA, and faces often cause more activation of the right fusiform than the left. The magnitude of activity in FFA depends not only on the presence of face stimuli in the

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visual field, but also on whether attention is directed to the faces (O’Craven, Downing, & Kanwisher, 1999) and on the waxing and waning of conscious perception of a face in compound or ambiguous stimuli (Andrews, Schluppeck, Homfray, Matthews, & Blakemore, 2002; Tong, Nakayama, Vaughan, & Kanwisher, 1998).

There has been considerable debate as to the precise role of the FFA in face processing, including whether it is truly selective for faces or rather mediates the differentiation of objects with which one has developed an expertise (e.g., Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Grill-Spector, Knouf, & Kanwisher, 2004; Joseph & Gathers, 2002; Rhodes, Byatt, Michie, & Puce, 2004). Regardless of whether the processing in the FFA is specific to faces or generalizes to other objects of expertise, there remains the question of its specific role in face processing. Studies of individuals with prosopagnosia suggest that FFA activity might be necessary (Damasio, Damasio, & Van Hoesen, 1982), but not sufficient (Avidan, Hasson, Malach, & Behrmann, 2005; Hasson, Avidan, Deouell, Bentin, & Malach, 2003; Rossion et al., 2003), for face identification, and that activity in other occipital regions also may be critical (see also Clarke, Lindemann, Maeder, Borruat, & Assal, 1997; Evans, Hegg, Antoun, & Hodges, 1995; Haxby et al., 2001; Ishai, Schmidt, & Boesiger, 2005). That has led some investigators to conclude that the FFA is specialized only for face detection (detecting that a face is present based on its first-order relations of two eyes above a nose, which is above a mouth), and hence for activating other areas that decode the specifics of the face, including its identity. Recent evidence that activation does not attenuate for upright faces if the identity of the whole face or a constituent part is altered on each trial has led others to speculate that neurons in the FFA represent faces holistically (Schiltz & Rossion, 2006) and/or engage in the more specific processing necessary to identify an individual face (Mazard, Schiltz, & Rossion, 2006).

One candidate cue for processing identity is the spacing of internal facial features, a specific type of configural processing that is called sensitivity to second-order relations (reviewed in Maurer et al., 2002). Adults use this cue effectively to discriminate upright but not inverted faces, and, with most stimulus sets, this degradation with inversion is far greater for spacing changes than for featural changes (Freire, Lee, & Symons, 2000; Leder & Bruce, 1998; Leder & Carbon, 2006; Malcolm, Leung, & Barton, 2005; Mondloch, Le Grand, & Maurer, 2002; Rhodes, Hayward, & Winkler, 2006; but see Riesenhuber, Jarudi, Gilad, & Sinha, 2004; Sekuler, Gaspar, Gold, & Bennett, 2004; Yovel & Kanwisher, 2004, 2005). Likewise, adults’ ability to recognize that a face has been distorted decreases significantly as the face is rotated away from upright when the distortion alters the spacing of features in unnatural ways, but is not impaired when the distortion alters the features (blackened teeth or white pupils) (Collishaw & Hole, 2000; Murray, Yong, & Rhodes, 2000). This behavioral evidence on inversion suggests that separate processes may underlie the perceptual analysis of a face stimulus depending on whether the coding reflects variations in facial features or variations in their spacing. Similarly, the filtering of face images to remove the low spatial frequencies, on which adults rely in poor light or at a distance, degrades adults’ sensitivity

to differences in the spacing of the eyes but has no impact on their sensitivity to featural differences (Goffaux, Hault, Michel, Vuong, & Rossion, 2005). The separability of processing based on features versus their spacing is further supported by evidence of differential rates of development (Mondloch et al., 2002) and evidence of differential impairment for features versus spacing in adults with Williams Syndrome, in children with a history of early visual deprivation from congenital cataract, and in some adults with prosopagnosia (Barton, Press, Keenan, & O’Connor, 2002; de Gelder & Rouw, 2000; Karmiloff-Smith et al., 2004; Le Grand et al., 2006; Le Grand, Mondloch, Maurer, & Brent, 2001; Le Grand, Mondloch, Maurer, & Brent, 2003).

Little is known about the brain areas involved in the processing of features versus second-order relations. In the only direct study,¹ Yovel and Kanwisher (2004) concentrated on the FFA and contrasted responses to faces and houses with featural or spacing changes. They found more activity in the fusiform face area in face blocks than in house blocks, regardless of whether the faces and houses differed in features or spacing, a pattern that suggests that the fusiform face area is not differentially involved in the two types of processing.

That conclusion is consistent with the results for inversion on FFA activity. In contrast to large behavioral effects of face inversion on the processing of second-order relations, most neuroimaging studies indicate that, on initial presentation, FFA activity is similar for upright and inverted photographs of faces (Aguirre, Singh, & D’Esposito, 1999; Epstein, Higgins, Parker, Aguirre, & Cooperman, 2006; Haxby et al., 1999; Kanwisher, Tong, & Nakayama, 1998; Mazard et al., 2006; Schiltz & Rossion, 2006; but see Yovel & Kanwisher, 2004, 2005). The lack of a consistent neural inversion effect when a face is first presented suggests that activity in the FFA is not tied specifically to the processing of second-order relations. On the other hand, the fact that brain areas outside the FFA respond differently to upright and inverted faces suggests that the processing of second-order relations may be widely distributed. For example, activity is greater in the right superior temporal sulcus (STS) for upright than for inverted faces (Leube et al., 2003; Yovel & Kanwisher, 2005), but activity is greater for inverted than for upright faces in areas of occipital cortex that typically respond more to non-face objects, such as houses (Aguirre et al., 1999; Epstein et al., 2006; Haxby et al., 1999; Kanwisher et al., 1998; Yovel & Kanwisher, 2005).

In the present study, we used functional magnetic resonance imaging (fMRI) to investigate the neural correlates of processing of facial identity based on features versus their spacing. We took an approach similar to Yovel and Kanwisher with two important differences. First, we used stimuli that kept spacing differences within natural limits. In the study by Yovel and Kanwisher (2004), the faces for the spacing trials had eyes that had been

¹ A PET study (Rossion et al., 2000) contrasted two conditions named similarly to ours, but an examination of the methods indicates that the investigators studied something entirely different. Both conditions (named whole-face and part-based) involved featural changes and neither used manipulations of the spacing of the features. The conditions differed in whether or not holistic processing would interfere with correct performance.

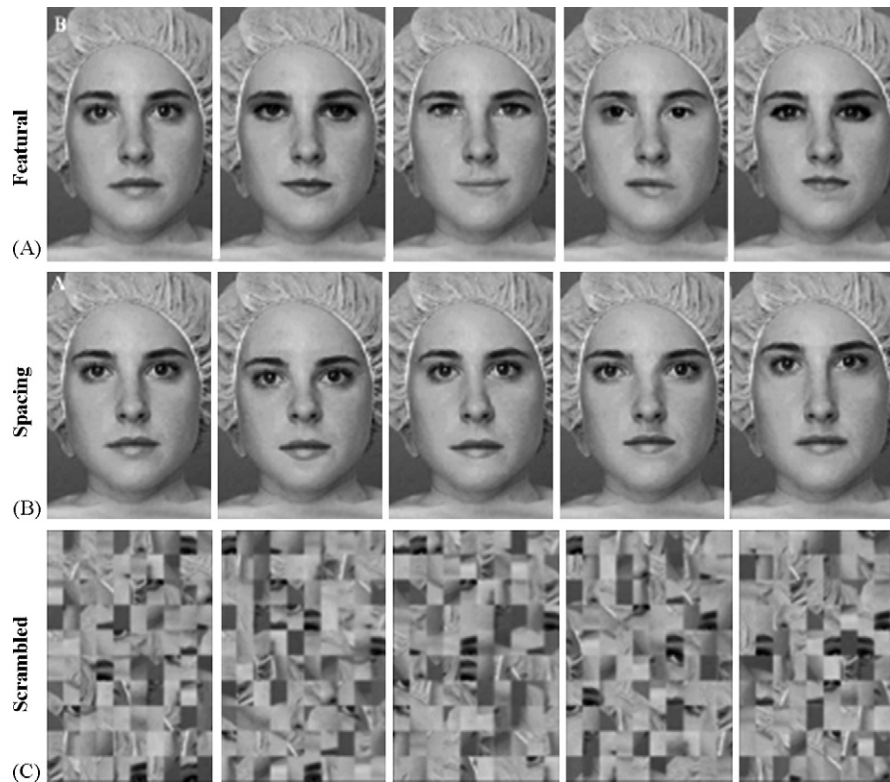


Fig. 1. The five exemplars used for each stimulus set. (A) In the featural set, the sisters differ from Jane (the leftmost face) in the shape of the eyes and mouth. (B) In the spacing set, the sisters differ from Jane in the relative location of the eyes and mouth. (C) For the scrambled baseline, images were created by cutting the Jane stimuli into sections and assembling them randomly.

moved beyond natural limits, presumably in order to equate adults' accuracy in discriminating between upright face pairs differing in spacing with their accuracy for featural changes.² Our measurements of the images provided by Yovel indicate that "Alfred's" eyes were moved in or out by up to 4.4 standard deviations (S.D.s) from the mean inter-pupillary distance measured in a representative sample of adult Caucasian faces reported in Farkas (1981). Changes of this magnitude make the faces look distorted and unnatural. As well, the mouth was moved not only up or down but also laterally by a small amount in some of the stimuli, so that differences in spacing also included differences in symmetry. Perhaps as a result of the asymmetries and/or the unnaturally large spacing changes, Yovel and Kanwisher (2004) found an unusual effect of inversion on behavioral performance:

² Studies keeping spacing changes within natural limits and interchanging features that are of similar size, as is true of the task used in the current study, have found that adults are slightly but significantly more accurate at discriminating the featural differences than the spacing differences (Freire et al., 2000; Gilchrist & McKone, 2003; Goffaux et al., 2005; Le Grand and Maurer, 2003; Mondloch et al., 2002). Accuracy varies depending on the particular featural swap (i.e., which eyes and which mouths are compared on different trials), but comparisons across 58 different feature swaps indicate that accuracy is usually high ($\geq 90\%$ for 86% of the pairings) with the swaps used in the current experiment being of a typical difficulty level (Mondloch & Maurer, unpublished data). Further research of this type is needed to determine whether there is a true difference in the efficiency with which adults process the two types of information in the natural distribution of differences among individuals.

inversion caused a larger drop in accuracy for their featural set than for their spacing set, which is the opposite pattern from what is usually reported.

In contrast, we adapted a task (Mondloch et al., 2002) that differentiates the processing of face identity based on features versus their second-order relations and for which there are extensive behavioral data (Karmiloff-Smith et al., 2004; Le Grand & Maurer, 2003; Le Grand, Maurer, et al., 2003; Le Grand et al., 2001; Le Grand, Mondloch, et al., 2003; Mondloch, Dobson, Parson, & Maurer, 2004; Mondloch et al., 2002). The task requires the observer to make same/different judgments about two faces presented sequentially. The two faces in each pair are identical except for small differences in either the *shape* of internal features in some blocks (Fig. 1, Panel A) – a measure of featural processing – or, in other blocks, differences in the *spacing* of the internal features (Fig. 1, Panel B)—a measure of sensitivity to second-order relations. The face stimuli were modified digitally so that the spacing (e.g., distance between eyes, and distance from eyes to mouth) covers most of the range that occurs naturally in adult Caucasian female faces (Farkas, 1981), and were titrated to avoid floor and ceiling effects on adults' accuracy. Because the faces are presented in blocks during which differences depend on detecting only featural or only spacing changes, participants are encouraged to emphasize different face processing strategies in different blocks. Several pieces of evidence from our previous behavioral research indicate that the two stimulus sets, when presented in separate blocks, elicit dif-

ferent types of face processing. First, accuracy in detecting a featural change decreases slightly (and linearly) with increasing rotation away from the canonical upright position, while accuracy in detecting a spacing change drops precipitously between 60° and 120° off upright, then asymptotes with further rotation from 120° to 180° (Le Grand & Maurer, 2003; Mondloch et al., 2002). Second, developmental studies show that 6-year-olds are almost as accurate as adults in discriminating faces in the featural set (Mondloch et al., 2002) but even 14-year-olds make more errors than adults in the spacing set (Mondloch, Le Grand, & Maurer, 2003). Third, LH, an adult with acquired prosopagnosia from a head injury (Levine, Calvanio, & Wolfe, 1980), is at chance on the spacing set even with simultaneous and unlimited exposure but performs well above chance on the featural set (Le Grand, Maurer, et al., 2003). Finally, children who suffered early visual deprivation from congenital cataracts that eliminated visual input to both hemispheres (or to mainly the right hemisphere) perform abnormally on the spacing but not the featural set (Le Grand et al., 2001; Le Grand, Mondloch, et al., 2003).

The second important difference between our study and that of Yovel and Kanwisher is that we did not restrict the analysis to the FFA but looked at cortical regions throughout the brain. To do this, we performed multivariate analyses to determine whole brain patterns of activity, that is, putative networks that were differentially recruited by discriminating faces on the basis of either spacing or features. These multivariate analyses allowed us to identify the brain regions, including the FFA, with differential activity to faces versus objects and houses during a localizer run, and then to ask whether a similar network, or different areas, characterized spacing and featural blocks. We also used this multivariate approach to evaluate the influence of any differences in task difficulty between the spacing and featural sets (Druzgal & D'Esposito, 2003; Grady et al., 1996, 1998; Haxby, Ungerleider, Horwitz, Rapoport, & Grady, 1995).

2. Materials and methods

2.1. Participants

Twelve healthy participants (between the ages of 18 and 30 years) were included in the experiment. One additional participant was unable to complete the scanning session because of discomfort. All participants (eight females, four males, mean age = 25.1 years, mean education = 18.2 years) were Caucasian and right-handed (score >45 on McMaster Handedness Questionnaire (Mondloch et al., 2002), a modified version of the Edinburgh Handedness Questionnaire). Each had normal or corrected-to-normal linear letter acuity tested with the Lighthouse Visual Acuity chart and normal stereo-acuity as measured by the Titmus test. None of the participants took medications that might affect brain function and none had overt brain abnormalities revealed by a structural MRI scan obtained during the same session. The Ethics Committees of Baycrest, Sunnybrook Health Science Centre and McMaster University approved this experiment and each participant gave informed consent.

2.2. Stimuli

2.2.1. Localizer task

For the localizer task, participants viewed 24-s blocks of gray-scale photographs from each of three categories: faces, houses, and common household objects.

2.2.2. Jane task

The stimuli were identical to those described previously in our behavioral studies (Mondloch et al., 2002). Briefly, gray scale digitized images of Caucasian female faces were taken under standard lighting conditions (Geldart, 2000). A photograph of a single face (called “Jane”) was modified with Adobe Photoshop to create eight new versions (“Jane’s sisters”). The four modified faces in the featural set (Fig. 1, Panel A) were created by replacing the model’s eyes and mouth with the features of the same length from different females. On every “different” trial, the two faces had different eyes and mouth. The four modified faces in the spacing set (Fig. 1, Panel B) were created by moving the eyes up or down from the original, the eyes closer together or farther apart, and the mouth up or down. We used all possible combinations of the five faces; because there were only two mouth positions, on 20% of the different trials the mouth was in the same location in the two faces and only the location of the eyes differed.³ According to anthropomorphic norms (Farkas, 1981), the movements correspond to shifts in Jane’s eyes of 1.3S.D.s up or down, of 2.4S.D.s closer together, or of 3.2S.D.s farther apart and shifts of Jane’s mouth by 0.79S.D.s up or down. Thus, the differences covered most of the variations in spacing among adult female faces in the population, without being so large that the faces appeared deformed or unnatural. Control stimuli consisted of scrambled Jane images created using custom MATLAB software. The original images were cut digitally into 20 × 20 pixel sections and reassigned randomly to positions in the display. Edges between the pieces were smoothed by convolving a Gaussian filter with the scrambled image (Fig. 1, Panel C).

2.3. Procedure

Prior to the experimental session, participants practiced the task outside the MRI scanner. They were shown Jane and her sisters and told that they would see one of the faces flash quickly on the screen followed by another face. They were instructed to press a key with the index finger if the second face matched the first face and to press with the middle finger if the two faces were different. Since the second face appeared for only 1.5 s, the speed of responding was emphasized in addition to accuracy. Participants also practiced making same/different judgments about the scrambled images.

After the practice session, participants lay supine on the MRI scanner bed with their head stabilized with snug foam cushions. They were fitted with MRI-compatible Silent Vision™ Goggles (Avotec Inc.) which were adjusted to correct vision (±6D) independently for each eye.

Following anatomical scans, two 5-min functional localizer scans were performed during which subjects were instructed to simply look at the screen. Each picture in the 24-s block was presented for 1900 ms, with an ISI of 100 ms. Blocks with only a fixation cross provided a low level baseline at the beginning, middle, and end of each run. Subjects then performed up to five runs of the “Jane task.” The instructions given during the practice session were repeated before the first run. Each trial consisted of the presentation of the first (model) face for 200 ms, an inter-stimulus interval of 300 ms, followed by the second face for 1500 ms. On half the trials, the correct response was “different.” Blocks of 22 trials with the same type (spacing, featural, or scrambled) were presented during 45-s intervals in a fixed order during each run (scrambled, spacing, feature, spacing, feature, scrambled, spacing, feature, spacing, feature, spacing, scrambled). Trial types were segregated to allow time for each style of processing to emerge, but the subjects were not explicitly informed about the distinctions. Each run lasted for 8 min and 15 s, and participants performed three to five runs, resulting in a total of 540–900 s of data from each face task across the runs. Responses

³ Our previous behavioral data indicate that accuracy is as good on trials where the location of only the eyes differ as on the majority of trials with differences in the location of both the eyes and mouth (Mondloch, Le Grand, & Maurer, unpublished data). This is not surprising since adults process faces holistically even in tasks where they are instructed not to and where it is disadvantageous to do so (e.g., Hole, 1994; Young, Hellawell, & Hay, 1987), making it unlikely that they relied only on eye position in the current study. Accuracy was also similar when different trials included pairings with the subtle makeup cues visible in Fig. 1 (89%) versus being restricted to pairings without those cues (92%) (Mondloch, Dobson, & Maurer, unpublished data).

were collected through a RURB (Rowland Universal Response Box, Rowland Institute for Science, Cambridge, MA). As our primary question here was the difference between the spacing and feature conditions, we included only these conditions in the analyses of the Jane task described below.

2.4. Scanning procedure

Imaging was performed with a 1.5 T whole-body GE Signa MRI scanner with a standard head coil (CV/i hardware, LX8.3 software; General Electric Medical Systems, Waukesha, WI). During the functional scans, the blood oxygenation level dependent (BOLD) MRI signal was measured in 26 5 mm slices (no gap). The imaging sequence was a single shot T2*-weighted pulse sequence with spiral readout, offline gridding, and reconstruction (TR = 2000 ms, TE = 40 ms, flip angle 80°). Structural scans were obtained prior to task performance by using a 3D T1-weighted pulse sequence (TR = 35.0 ms, TE = 6.0 ms, flip angle 35°, 22 × 16.5 field of view, 124 axial slices, 1.4-mm thick). For the functional scans, the in-plane resolution was 3 mm × 3 mm and the slice thickness was 5 mm.

2.5. Data analysis

Motion correction and linear de-trending of the images were performed using Analysis of Functional NeuroImages (AFNI, Cox & Hyde, 1997). Each volume in the time series was aligned to an early fiducial volume from the first imaging run in the scanning session, such that the amount of motion across all functional runs was at a minimum. Motion corrected images were spatially normalized to an fMRI spiral scan template in the brain space of the Montreal Neurological Institute (MNI) and smoothed with a Gaussian filter of 8 mm full-width-at-half-maximum (FWHM) in SPM99 (Wellcome Department of Imaging Neuroscience, <http://www.fil.ion.ucl.ac.uk/spm>).

Partial least squares, or PLS (McIntosh, 1999), was used to assess whole-brain patterns of activity during the localizer runs and during the spacing and featural conditions, as well as to examine how individual differences in behavior were related to brain activity (i.e., to assess the effects of task difficulty). This multivariate approach is similar to a principal component analysis (e.g., Fristen, Frith, Liddle, & Frackowiak, 1993) and assumes that brain function reflects the coordinated activity of groups of brain regions rather than the independent activity of any single brain region. As such, it is ideal for assessing patterns of activity across the whole brain. Specifically, we used PLS to determine how brain activity in all voxels covaried across the conditions, thus identifying a new set of variables (so-called latent variables or LVs, similar to principal components) that characterized this covariance and to determine how much covariance each LV explained. Each LV from such an analysis identifies a pattern of differences in brain activity across the experimental conditions and specifies which brain voxels show this effect. Each brain voxel has a weight on each LV, known as a salience, which indicates how strongly that voxel is related to the LV. A salience can be positive or negative, depending on whether the voxel shows a positive or negative relation with the pattern of task differences identified by the LV. We calculated a “brain score” for each condition in the LV for each subject by multiplying the salience of each voxel on that LV by its signal intensity in the subject’s brain, and then summing across all voxels. The brain score indicates the degree to which each subject expresses the pattern of brain activity seen on the LV. Examination of these scores indicates how brain activity varies across conditions, as greater activity in brain areas with positive (or negative) weights on an LV correspond to positive (or negative) mean brain scores for a given condition.

In the first analysis, we used PLS to examine the brain areas that differentiated the conditions in the localizer scan (i.e., faces, houses, objects, and fixation blocks). This analysis was carried out on the mean activity for each condition across the 12 participants. The second LV from this analysis identified regions with more activity for faces than the other conditions, and we report the results of this LV here. In the second analysis, we used PLS to identify brain areas whose activity differentiated the spacing and feature task conditions. In order to gain power and evaluate consistency across the runs, the data from each run were entered into the analysis separately, rather than averaging across the runs as we did for the localizer. Because 11 of the 12 participants had at least four runs of the tasks, we restricted the analyses to those 11 subjects and 4 runs (one female subject omitted). We calculated an average fMRI signal map for each of

the first four usable runs for spacing and featural tasks for each subject, resulting in a total of eight images for each subject. To examine task-related activity, an analysis was conducted on the images for all eight “conditions” (spacing in runs 1–4 and featural for runs 1–4).

To assess whether the differential activity between featural and spacing runs could be attributed to task difficulty, we did a similar analysis based on performance accuracy. Specifically, we used PLS to calculate the correlation between the fMRI signal in each brain voxel and accuracy within each of the eight task conditions (four runs of the featural task and four runs of the spacing task), and then contrasted these correlations across tasks (McIntosh, 1999). The logic of this analysis is that if activity were increased in any brain region because of greater difficulty in performing the tasks, the increase would be greatest in those participants who experienced the greatest difficulty with the task as indicated by the poorest performance. One male participant was omitted from this analysis because a technical problem caused a loss of behavioral data.

Two independent statistical measures were obtained for each PLS analysis. The reliability of each voxel’s contribution to each LV was determined through bootstrap resampling (Efron & Tibshirani, 1986; Sampson, Streissguth, Barr, & Bookstein, 1989). A reliable contribution for a given voxel was defined as a ratio of its salience to the standard error of the salience greater than or equal to 3.0, which approximates $p < 0.005$ (Sampson et al., 1989). The bootstrap also gives confidence intervals for each correlation between performance accuracy and the brain scores for each LV, which provide a measure of how strongly the pattern of activity seen on the LV is correlated with performance. The 95% confidence interval was used as the threshold for reliability for these correlations. In addition to these bootstrap measures, we assessed the statistical significance of each LV by means of a permutation test (Edgington, 1980; McIntosh, Bookstein, Haxby, & Grady, 1996). In both the permutation and bootstrap procedures all saliences are calculated in a single analytical step; hence there is no need for correction for multiple comparisons (McIntosh et al., 1996). The clusters reported here contained at least five voxels (i.e., 320 μ l).

3. Results

3.1. Behavioral results

Participants performed well on both the spacing and featural tasks. Although the “Jane” stimulus set was constructed originally with the goal of equating difficulty on the featural and spacing tasks as much as possible without going outside the bounds of normal variation of face configurations, participants performed somewhat better on the featural set during the scanning session, consistent with previous behavioral studies (Mondloch et al., 2002). Accuracy was significantly higher for featural (91% correct) than for spacing (80% correct) blocks ($t = 6.79$, $p < 0.0001$). The difference in reaction times between the two face sets was also significant (featural = 723 ms; spacing = 752 ms; $t = 2.68$, $p < 0.05$).

3.1.1. fMRI results: localizer scans

The analysis of the localizer data revealed a widely distributed set of regions ($p = 0.02$) with more activity for faces than for houses, objects, and baseline (Fig. 2; Table 1). These included the right fusiform gyrus, in a region consistent with the FFA identified in other studies using more traditional univariate analyses (Downing et al., 2006; Grill-Spector et al., 2006; Haxby et al., 1994; Kanwisher et al., 1997). More activity for faces also was seen in the left middle frontal gyrus, bilateral middle occipital gyri, and left parahippocampal gyrus. Interestingly, more activity for faces also was found in the right amygdala, consistent with the proposed role of the amygdala in identifying emotional expressions in faces (e.g., Adolphs, 2002; Anderson, Christoff,

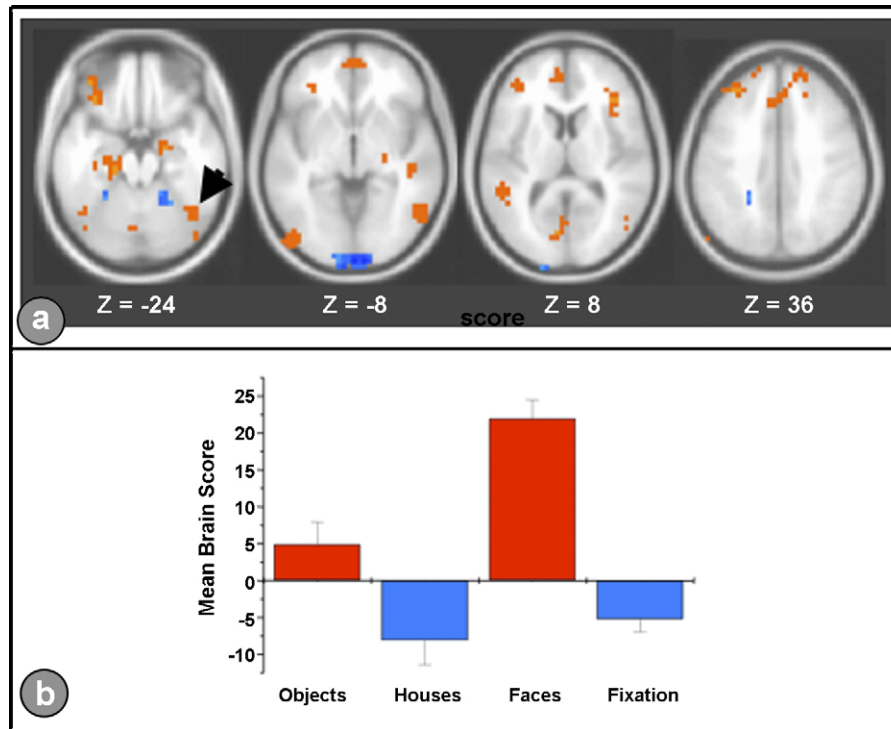


Fig. 2. The results of the PLS analysis of the localizer scans is shown on an average MRI (Panel a). The axial levels relative to the AC-PC line are provided under each image. The graph (Panel b) indicates how the pattern of activity seen in the images differentiated the three stimulus conditions and fixation. Brain scores are a summary measure of activity across all voxels. Positive brain scores for faces, and to a lesser extent for objects (red bars), indicate that activity was increased in regions shown in red, including the right fusiform gyrus (indicated by arrow). Negative brain scores (blue bars) indicate that activity increased for houses and fixation in the brain areas shown in blue. Error bars represent the standard error. In this figure, and all subsequent figures, the right hemisphere is shown on the right side of the images.

Table 1
Brain areas with activity differentiating faces from houses

Region	Hem	BA	X	Y	Z	Ratio
(a) More activity for faces						
Inferior Frontal gyrus	R	45	36	32	4	5.7
Middle Frontal gyrus	L	46	-40	40	32	5.1
Middle Frontal gyrus	L	11	-36	44	-20	6.8
Medial Frontal gyrus	L	10	-8	56	4	4.7
Middle Temporal gyrus	L	21	-48	-52	0	5.1
Middle Occipital gyrus	R	19	60	-72	4	7.0
Middle Occipital gyrus	L	19	-52	-80	-12	5.4
Cuneus	L	18	-8	-76	8	6.0
Fusiform gyrus	R	37	44	-60	-24	4.6
Fusiform gyrus	L	37	-48	-60	-28	3.7
Parahippocampal gyrus	L	35	-20	-24	-24	5.9
Amygdala	R		20	-8	-24	5.3
(b) More activity for houses						
Calcarine sulcus	R	17	8	-100	-8	-7.9
Fusiform gyrus	R	19	20	-52	-20	-6.0
Fusiform gyrus	L	19	-28	-48	-20	-5.2

All regions are reliable at $p < 0.005$. Coordinates are in MNI space. Positive ratios correspond to regions with positive salience on the LV (seen in red in Fig. 2). Negative ratios correspond to regions with negative salience on the LVs (seen in blue in Fig. 2). X (right/left): Negative values are in the left hemisphere; Y (anterior/posterior): negative values are posterior to the zero point (located at the anterior commissure); Z (superior/inferior): negative values are inferior to the plane defined by the anterior and posterior commissures. Abbreviations: Hem, hemisphere; R, right; L, left; BA, Brodmann's area; ratio, salience/S.E. ratio from the bootstrap analysis, which is a measure of each voxel's reliability.

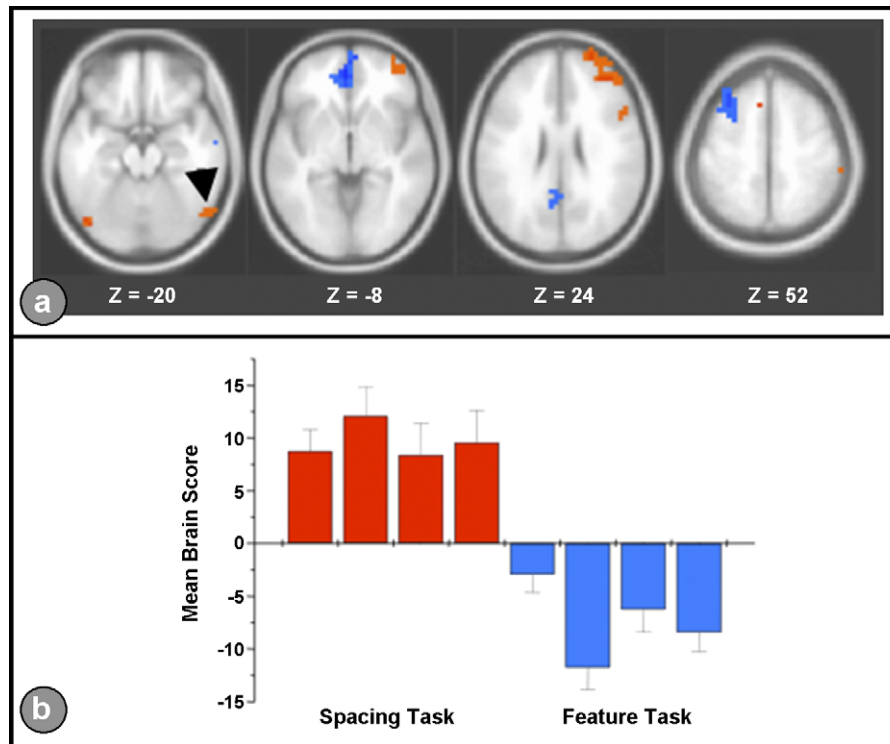


Fig. 3. Brain areas with task-related modulation of activity across the spacing and feature runs are shown on an average MRI (Panel a). The axial levels relative to the AC-PC line are provided under each image. The graph (Panel b) indicates how the pattern of activity seen in the images differentiated the spacing and feature tasks across the four runs of each task. Positive brain scores in the spacing task (red bars) indicate that activity was increased in regions shown in red, including the right fusiform region indicated by the arrow. Negative brain scores in the feature task (blue bars) indicate that activity increased during this task in the brain areas shown in blue. Error bars represent the standard error.

Panitz, De Rosa, & Gabrieli, 2003; Glascher & Adolphs, 2003; Morris et al., 1998). Less activity for faces compared to houses was seen in bilateral medial fusiform gyrus, consistent with other studies reporting medial occipital or parahippocampal activity for houses (Aguirre, Zarahn, & D'Esposito, 1998; Epstein & Kanwisher, 1998; Haxby et al., 1999).

3.1.2. fMRI results: spacing versus feature blocks

A significant pattern of activity ($p < 0.02$) differentiated the spacing and featural tasks across all four runs, although there was some variability in the strength of this dissociation across the feature runs (Fig. 3). There were several regions of right prefrontal cortex, where activity was greater during the spacing task compared to the feature task (Table 2a). The area that maximally differentiated the two tasks was in the right middle frontal gyrus. In addition to frontal regions, the right fusiform gyrus showed greater activation during the spacing task in a region adjacent to, but not overlapping, the FFA defined from the localizer runs (Fig. 4; see Fig. 5 for a conventional univariate analysis that shows a similar result: a region in the right fusiform that is sensitive to faces, when compared to scrambled faces, but no difference between spacing and feature in this region). Inspection of the time course indicates that this region in the right fusiform gyrus shows increased activation over the course of a block for spacing blocks but decreased activation (and perhaps adaptation) for feature blocks (Fig. 6). There also was greater activation during the spacing task in two additional

posterior regions, in the left posterior fusiform gyrus and right inferior parietal cortex. In contrast, the areas with more activity in the feature task were almost exclusively in the left hemisphere, including the middle temporal gyrus, middle frontal gyrus, and the posterior cingulate gyrus (Table 2b).

The analysis correlating task performance with brain activity identified a set of brain regions ($p < 0.002$) where activity was positively correlated with accuracy during both feature and spacing conditions during the early runs (Fig. 7). Better performance

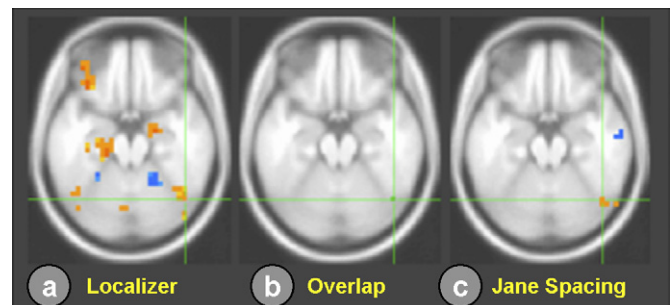


Fig. 4. Images at $Z = -24$ mm illustrating the overlap (b) of activity in the right fusiform gyrus during the localizer scan (a) and the Jane tasks (c). The orange areas from the localizer scan are those where there was more activity for faces than for houses and objects. The orange regions from the Jane task are those where there was more activity for the spacing condition than the feature condition. The green area in the middle image (location indicated by green cross hairs in all images) indicates the overlap between the localizer and Jane clusters. The overlap in the right fusiform is limited to a single voxel.

Table 2
Brain areas with activity differentiating spacing from feature conditions

Region	Hem	BA	X	Y	Z	Ratio
(a) Spacing > featural						
Middle Frontal gyrus	R	10/46	40	48	-4	4.2
Middle Frontal gyrus	R	10	32	44	24	5.2
Inferior Frontal gyrus	R	44	48	24	16	3.7
Inferior Frontal gyrus	R	44	48	8	36	4.4
Inferior Frontal gyrus	R	11	36	28	-16	3.9
Medial Frontal gyrus	L	8	-8	20	56	5.2
Fusiform gyrus	R	37	56	-64	-20	3.7
Fusiform gyrus	L	18	-44	-76	-16	5.6
Inferior Parietal	R	40	51	-32	48	3.9
(b) Featural > spacing						
Middle Frontal gyrus	L	8	-28	12	56	-5.5
Medial Frontal gyrus	L	10	0	60	-4	-6.1
Middle Temporal gyrus	L	39	-52	-80	20	-5.3
Posterior Cingulate	L	29	-8	-60	28	-3.7
Lingual gyrus	R	19	4	-60	-4	-4.6

All regions are reliable at $p < 0.005$. Coordinates are in MNI space. Positive ratios correspond to regions with positive salience on the LV (seen in red in Fig. 3). Negative ratios correspond to regions with negative salience on the LVs (seen in blue in Fig. 3). X (right/left): Negative values are in the left hemisphere; Y (anterior/posterior): negative values are posterior to the zero point (located at the anterior commissure); Z (superior/inferior): negative values are inferior to the plane defined by the anterior and posterior commissures. Abbreviations: Hem, hemisphere; R, right; L, left; BA, Brodmann's area; ratio, salience/S.E. ratio from the bootstrap analysis, which is a measure of each voxel's reliability.

on the spacing task across the first three runs, and for the first two runs of the feature task, was associated with increased activity in bilateral temporal regions and the right thalamus (Table 3a). Conversely, worse performance on the spacing and feature tasks

was associated with activity in the right middle frontal gyrus, left parietal cortex, cerebellum, and caudate nuclei (Table 3b). This pattern of correlations was reversed for the last run, so that the activity correlated with worse performance in the early runs, such as in the right middle frontal gyrus, was correlated with better performance as the participants had more experience with the tasks (see Fig. 7).

It is important to note that the regions identified by the analysis of spacing versus feature blocks and the analysis of correlates of task performance are largely independent: that is, there is almost no overlap in the regions that showed modulations of activity dependent on task type (featural versus spacing) and regions where activity indexed task difficulty. There was one exception, in right frontal cortex. The region of right prefrontal cortex that maximally differentiated the spacing from

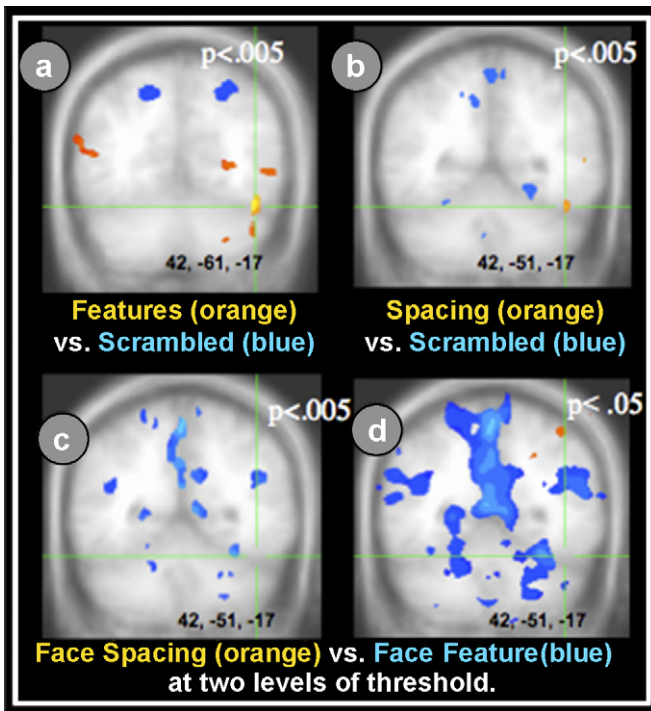


Fig. 5. Results of a typical univariate analysis (t -tests carried out using AFNI) are shown on coronal slices (averaged MRI from the study participants). An area of right fusiform was activated for both the featural (a) and spacing (b) conditions, relative to scrambled faces. The bottom images show that there is no differential activation within the right fusiform (c), even at a very lenient threshold (d).

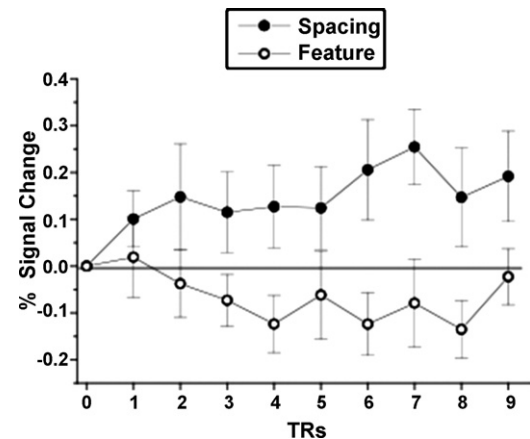


Fig. 6. Time courses (averaged over all spacing and feature blocks) of activity in the right fusiform region with more activity for spacing than for feature (indicated by arrow in Fig. 3a). The signal is normalized to the first time point (0) in each block.

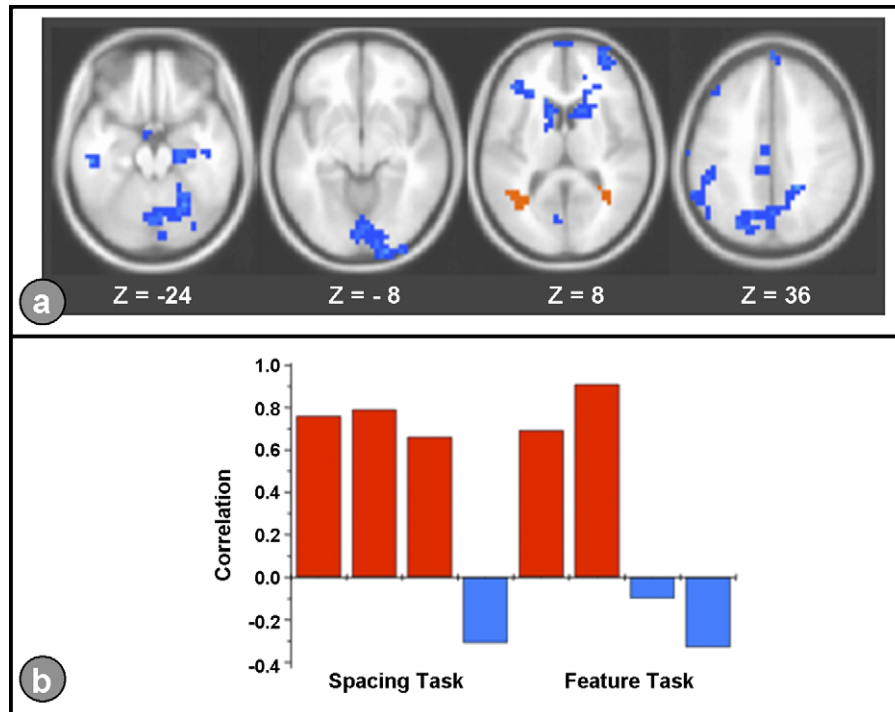


Fig. 7. Brain areas where activity was correlated with task performance (proportion correct) are shown on an average MRI (Panel a). The axial levels relative to the AC-PC line are provided under each image. The graph (Panel b) shows the values of the correlations between brain scores and performance accuracy for the four runs of the spacing and feature tasks. All correlations are reliable at the 95% confidence interval except for run 3 of the feature task. A positive correlation in the earlier runs indicates that as activity increases in red areas (and the brain scores become more positive), accuracy of performance improves. Conversely, as activity in the blue areas increases (and the brain scores become more negative), accuracy decreases. In both tasks, the pattern changes for the fourth run, in which more activity in the areas shown in blue is associated with better performance.

the featural task (see Fig. 8c) was a relatively large cluster of voxels whose anterior extent overlapped slightly with the region where activity was associated with poorer performance on the tasks (see Fig. 8a). However, the maxima of these two regions differed by more than 12 mm. In addition, there was no overlap

with any of the other right frontal regions with more activity for spacing than feature blocks. Overall, the behavioral PLS supports the idea that the brain activity distinguishing the processing of second-order relations from that of facial features is largely due to differences in the type of processing necessary to

Table 3
Brain areas with activity related to task performance in early runs of the spacing and feature tasks

Region	Hem	BA	X	Y	Z	Ratio
(a) Correlations with better task performance						
Middle temporal gyrus	R	21	32	-48	4	5.5
Middle temporal gyrus	L	37	-32	-56	4	4.6
Thalamus (Pulvinar)	R		12	-36	0	4.8
(b) Correlations with worse task performance						
Middle frontal gyrus	R	10	36	56	12	-6.3
Inferior frontal gyrus	L	45	-44	36	4	-10.8
Inferior parietal	L	40	-60	-56	44	-6.4
Parahippocampal gyrus	R	36	20	-20	-24	-6.1
Lingual gyrus	R	18	20	-100	-12	-7.0
Cingulate gyrus	R	31	20	-44	36	-6.7
Cingulate gyrus	L	23	-8	-24	28	-5.1
Caudate nucleus	R		16	16	8	-6.0
Caudate nucleus	L		-12	12	8	-5.7
Cerebellum	R		24	-60	-24	-7.6

All regions are reliable at $p < 0.005$. Coordinates are in MNI space. Positive ratios correspond to regions with positive salience on the LV (seen in red in Fig. 7). Negative ratios correspond to regions with negative salience on the LV (seen in blue in Fig. 7). X (right/left): Negative values are in the left hemisphere; Y (anterior/posterior): negative values are posterior to the zero point (located at the anterior commissure); Z (superior/inferior): negative values are inferior to the plane defined by the anterior and posterior commissures. Abbreviations: Hem, hemisphere; R, right; L, left; BA, Brodmann's area; ratio, salience/S.E. ratio from the bootstrap analysis, which is a measure of each voxel's reliability.

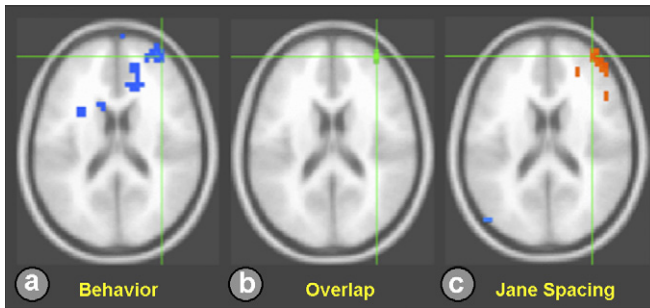


Fig. 8. A single slice is shown ($Z=16$ mm) to illustrate the overlap of activity in the right frontal cortex between the behavior and task PLS analyses. The blue areas from the behavioral analysis are those where increased activity was correlated with worse performance on the spacing and feature tasks. The orange regions from the Jane task are those where there was more activity during the spacing condition than the feature condition. The green area in the middle image (location indicated by green cross hairs in all images) indicates the overlap. Although there were several voxels where these two clusters overlapped, the maxima for these two regions were different (behavior: $X=36$, $Y=56$, $Z=12$; spacing > feature: $X=32$, $Y=44$, $Z=24$).

carry out these two tasks and not the result of differences in task difficulty.

4. Discussion

The results reveal three novel findings: (1) increased activity in the right fusiform gyrus adjacent to, but not overlapping the classic FFA, is involved in the processing of facial identity based on second-order relations; (2) the right fusiform activity for second-order relations is part of a distributed set of regions extending into the right frontal cortex; and (3) frontal cortex activity correlated with task difficulty is largely distinct from frontal activity involved in the processing of facial identity.

4.1. Specialization of the fusiform face area

Using a localizer scan, we were able to identify a region of the right fusiform gyrus that was more active for faces than other stimulus types, as others have shown before (e.g., Downing et al., 2006; Grill-Spector et al., 2006; Haxby et al., 1994; Kanwisher et al., 1997; Tong et al., 2000). In addition, our results showed that there were differences between the spacing and feature conditions in right fusiform activity, but not in the FFA per se. The fusiform area with more activity for spacing than features was adjacent to the FFA defined by the localizer runs, but slightly superior and posterior to it. Our findings are consistent with the findings of Yovel and Kanwisher (2004) for the FFA, as both indicate that FFA activity does not distinguish between face processing strategies. Our results further suggest that there are multiple regions in the right fusiform gyrus that respond to faces, one (the FFA) responding selectively to faces—and perhaps other objects of expertise, and another specialized for a specific type of face processing, namely the processing of second-order relations. Note that these conclusions are based on clusters containing at least five voxels, as is typical in the literature. With a smaller unit of analysis, we might have found islands of activation within the FFA that differentiate the processing of

features versus spacing that are equal in overall signal strength and hence disappear at larger cluster sizes. That possibility is suggested by a recent report by Grill-Spector et al. (2006) that identified different small clusters in the FFA highly selective for faces, for cars, for animals, and for sculptures, with the difference between face and non-face objects residing only in a greater number of clusters favoring faces. In any event, our results indicate that with the unit of analysis typically used to study the selectivity of responding in the FFA, like Yovel and Kanwisher (2004) we found no differential activation for the processing of facial identity based on features versus second-order relations.

4.2. Involvement of right frontal cortex

In addition to the difference in the right fusiform gyrus, there was increased activity in several areas of right frontal cortex when the discrimination was based on spacing rather than on features. This finding echoes a previous report of right frontal activity for comparing whole faces versus comparing just noses within faces (Paller, Gonsalves, Grabowewy, Bozic, & Yamada, 2000) and recent evidence for a role of right frontal cortex in recognizing one's own face (Platek et al., 2006; Uddin, Kaplan, Molnar-Szakacs, Zaidel, & Iacoboni, 2005). Our results indicate that there is a lateralized network of activity in the right hemisphere for the processing of second-order relations in faces.

One concern is that the increased right frontal activation might reflect increased difficulty or effort during the spacing task: behavioral results from the Jane task indicate that the featural task is somewhat easier than the spacing task, as measured by accuracy and reaction time. Since increased difficulty is known to produce increased activity in frontal cortex (Braver et al., 1997; Grady et al., 1996), it is important to evaluate this alternative interpretation. To probe this possible confound, we assessed whether any of the areas that formed part of the network active during the spacing task also showed a correlation between this activity and difficulty in performing the task, as measured by accuracy. The set of regions where activity was correlated with greater task difficulty, as indexed by worse accuracy, differed from the regions where activity differentiated the two face processing conditions. In particular, there were several areas of right frontal cortex with activity related to the spacing blocks. Only one of these regions, in BA 10, showed any overlap with the region that was related to worse performance on the spacing and feature tasks (see Fig. 8; Table 3). This region of BA 10 is similar in location to a region that has been shown to be more active during difficult face discrimination tasks (Grady et al., 1996), so activity in this region during the spacing task may be partly related to the greater difficulty of the task. On the other hand, the distance between the maximum of this region, and that of the frontal area correlated with worse performance in the early runs of the tasks, suggests that these may be two distinct regions of frontal cortex.

The other right frontal regions that responded differently during spacing compared to feature blocks did not show any correlation with performance. One of these regions, BA 44 in the inferior frontal gyrus (see Table 3), has been reported to differentiate faces from non-face stimuli (Henson et al., 2003;

Kelley et al., 1998). Another, in the ventral and anterior portion of the right frontal lobe (see Table 3), is active when individuals identify their own face (Uddin et al., 2005), and when they discriminate famous faces from one another (Rotshtein, Henson, Treves, Driver, & Dolan, 2005) or from non-famous faces (Leveroni et al., 2000). This region also responds to a specific target face among other equally familiar faces (Jiang, Haxby, Martin, Ungerleider, & Parasuraman, 2000). Collectively, these results suggest that this region in the ventral frontal cortex is involved specifically in identifying particular individuals and/or retrieving person-specific semantic information. All of these processes could depend to some extent on perceiving the second-order relations in a face, that is, the spacing of features; indeed, it may be that these right frontal areas work together, along with activity in the right fusiform gyrus, to mediate this aspect of face processing. The activity in the right inferior parietal lobe for spacing is consistent with the role of this area in spatial attention, since the spacing task requires more attention to the relations among spatial locations than the feature task (Corbetta, Miezin, Shulman, & Petersen, 1993; Losier & Klein, 2001; Nobre et al., 1997).

Because second-order relations are by definition distributed across the face, our findings of greater activation in the right fusiform, and other right hemisphere regions, during spacing than during featural blocks is consistent with the well known finding that global processing of visual information relies more on the right hemisphere (e.g., Fink et al., 1997; Martinez et al., 1997; Robertson & Delis, 1986). It is also consistent with the finding that children for whom a unilateral left cataract reduced visual input during infancy mainly to the right hemisphere later have deficits in the processing of the Jane spacing set but not the Jane feature set (Le Grand, Mondloch, et al., 2003).

4.3. Featural processing

The featural condition activated some posterior regions of the visual cortex and a number of other areas in the left hemisphere. The activation of posterior areas of visual cortex is not surprising given that the featural differences contained greater low-level stimulus changes to which early visual cortex would be selective. In addition, the activity in left frontal and temporal regions that was greater during the feature task was not correlated with task performance, a pattern suggesting that these regions mediate the discrimination of facial features independently of the difficulty of the discrimination. The left lateralization of areas more active during the featural than during spacing blocks fits well with evidence for left lateralization of local as opposed to global processing (e.g., Fink et al., 1997; Hellige, 1996; Ivry & Robertson, 1998; Martinez et al., 1997). It is also interesting in light of a recent demonstration of the importance of high spatial frequencies for featural processing: subjects were much more accurate in discriminating featural differences in a Jane-like task when the faces contained all spatial frequencies or only high spatial frequencies than when the faces contained only low spatial frequencies (Goffaux et al., 2005). The same manipulations had little impact on subjects' accuracy in discriminating spacing differences, although there was a small but significant

difference favoring low spatial frequencies. The importance of high spatial frequencies for featural processing fits with decades of evidence of the importance of the left hemisphere for processing high spatial frequencies (e.g., Kitterle, Hellige, & Christman, 1992).

4.4. Are these networks face-specific?

The networks identified here for the processing of facial features versus second-order relations may play similar roles for the processing of non-face objects. That likelihood is suggested by the fact that most of the areas identified as preferring faces in the localizer runs (Table 1) were not identified in the contrast between spacing and feature blocks (Table 2). The networks identified for processing features versus second-order relations could be involved in the processing of stimuli, including non-face objects, at different scales involving high versus low spatial frequencies or emphasizing more local versus more global processing. The processing of features requires the decoding of information at high spatial frequencies in a small region of a face. The processing of second-order relations, in contrast, involves the processing of low spatial frequency information about the space between two features and, hence, by definition, processing a larger region of the face than that occupied by any single feature (Goffaux et al., 2005). Thus, the networks we identified may represent general object processing networks that are recruited, as needed, for different aspects of face processing.

We note, however, that behavioral evidence is difficult to reconcile with this view. Adults are unable to attend to just the features in one part of a face, ignoring incongruent information in the other parts of the face, and this mandatory holistic processing does not occur for inverted faces or for non-face objects with which they do not have expertise (Gauthier & Tarr, 2002; Hole, 1994; Robbins & McKone, 2003, Robbins & McKone, 2006; Tanaka & Farah, 1993; Young et al., 1987). Moreover, adults' reliance on second-order relations appears to be restricted to upright human faces: they are unable to use it effectively to identify monkey faces or inverted human faces and the absence of an inversion effect suggests they do not rely on it for recognizing objects (e.g., Mondloch, Maurer, & Ahola, 2006; Yin, 1969). Thus, it is unlikely that the networks identified here are identical to those used for object processing.

4.5. Implications for understanding the nature of face processing

Because they found no difference in FFA activity for trials in which subjects made same/different judgments about faces differing only in features or differing only in the spacing of features, Yovel and Kanwisher (2004) argued "against a differential role to configuration and parts in face perception" (see Riesenhuber et al., 2004, for a similar argument based on similar inversion cost for their faces with spacing and featural differences). Our results are consistent with the idea that there is no differential FFA activity during the processing of features versus their spacing. However, our whole brain analysis, like the behavioral evidence summarized in Section 1, suggests that adults do use

differentiable types of face processing involving second-order relations versus features when decoding facial identity that are mediated by non-overlapping neural networks distributed across the brain.

5. Conclusions

We found evidence of a cortical network that is active during the processing of facial identity based on second-order relations but not on features. The network includes a region in the fusiform gyrus close to, but not overlapping, the classic right FFA that responds more to faces than most other categories. The absence of differential activity in the right FFA for featural and spacing blocks confirms the findings of Yovel and Kanwisher (2004) with a different stimulus set and is consistent with evidence that the FFA responds fairly indiscriminately on the initial presentation of faces, whether they are upright or inverted, and whether they are intact or have features missing (Aguirre et al., 1999; Epstein et al., 2006; Haxby et al., 1999; Kanwisher et al., 1998; Mazard et al., 2006; Schiltz & Rossion, 2006; Tong et al., 2000; but see Yovel & Kanwisher, 2004, 2005 for a different fMRI pattern for inversion). The FFA may act as a rapid “face detector” that forms an overall representation of the whole face (Schiltz & Rossion, 2006) and then sends information to the appropriate network for further processing. When the further processing involves determining the second-order relations in order to decode the identity of the face, our results indicate that the network includes nearby regions in the fusiform gyrus and an extensive set of regions in the right frontal cortex. Feedback from that network may minimize the adaptation of neurons in the FFA if the identity of the face changes during a block, but only if it is presented under conditions that allow adults to use second-order relations to decode identity, i.e., upright and with the top and bottom halves aligned (Loffler, Yourganov, Wilinson, & Wilson, 2005; Mazard et al., 2006; Schiltz & Rossion, 2006).

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