



Neural correlates of temporal integration in face recognition: An fMRI study

Yunjo Lee ^{a,*}, David Anaki ^{b,1}, Cheryl L. Grady ^{a,c}, Morris Moscovitch ^{a,c}

^a Rotman Research Institute, Baycrest Centre, Toronto, Canada

^b Bar-Ilan University, Ramat-Gan, Israel

^c University of Toronto, Toronto, Canada

ARTICLE INFO

Article history:

Accepted 25 February 2012

Available online 5 March 2012

Keywords:

Analytic processing
Configural processing
Face identification
Face part
Part-based processing

ABSTRACT

Integration of temporally separated visual inputs is crucial for perception of a unified representation. Here, we show that regions involved in configural processing of faces contribute to temporal integration occurring within a limited time-window using a multivariate analysis (partial least squares, PLS) exploring the relation between brain activity and recognition performance. During fMRI, top and bottom parts of a famous face were presented sequentially with a varying interval (0, 200, or 800 ms) or were misaligned. The 800 ms condition activated several regions implicated in face processing, attention and working memory, relative to the other conditions, suggesting more active maintenance of individual face parts. Analysis of brain-behavior correlations showed that better identification in the 0 and 200 conditions was associated with increased activity in areas considered to be part of a configural face processing network, including right fusiform, middle occipital, bilateral superior temporal areas, anterior/middle cingulate and frontal cortices. In contrast, successful recognition in the 800 and misaligned conditions, which involve analytic and strategic processing, was negatively associated with activation in these regions. Thus, configural processing may involve rapid temporal integration of facial features and their relations. Our finding that regions concerned with configural and analytic processes in the service of face identification opposed each other may explain why it is difficult to apply the two processes concurrently.

© 2012 Elsevier Inc. All rights reserved.

Introduction

The visual world surrounding us is replete with complex stimuli that cannot be apprehended instantaneously. Perception of a unified representation, therefore, depends crucially on temporal integration of correlated information both across views and within a view. Despite growing interest in understanding the interaction between temporal structure (synchronized changes in visual information) and spatial vision (e.g., see reviews by Melcher and Colby, 2008 and Blake and Lee, 2005), the neural and anatomical correlates of temporal integration are largely unknown. Moreover, the temporal integration processes involved in perceiving complex stimuli are yet to be determined. In face processing, for example, most research has focused on how facial features are spatially combined to form a unified representation and only a small number of studies have examined temporal aspects of integration (e.g., Anaki and Moscovitch, 2007; Anaki et al., 2007; Singer and Sheinberg, 2006). While a few studies examined perceptual awareness of an occluded face (Hulme and Zeki, 2007; Yi et al., 2008) or flashed face (Keysers et al., 2005), the focus of those studies was to measure consciousness in the absence

of stimulus perception. Other studies examined the time course of whole-face recognition processes (Barbeau et al., 2008) or discrimination of face parts or spacing among them (Pitcher et al., 2007). Though related to some of the issues addressed in those studies, the present study differs from them in that we investigated neural correlates of temporal integration of static face parts when they are separated by varying time intervals that promote either configural or analytic processing of faces (Anaki and Moscovitch, 2007; Anaki et al., 2007). Although our study was concerned with temporal integration and faces, and in particular the distinction in this regard between configural (holistic) and non-configural processes, our findings and conclusions may not be specific to faces but may apply to other configural and non-configural processing in other domains.

Face perception is thought to entail particularly well-adapted perceptual processes, commonly referred to as *holistic* (Tanaka and Farah, 1993) or *configural*, which involve fine integration of facial features into a unitary representation. A typical marker of these processes is enhanced recognition of upright faces as compared to inverted faces (the face inversion effect, Maurer et al., 2002; Yin, 1969) or to misaligned faces whose top and bottom parts are spatially offset but shown simultaneously (Young et al., 1987). This impediment in processing misaligned or inverted faces is attributed to the difficulty in extracting holistic or configural information from them (Jacques and Rossion, 2010). Recently, we have shown that face parts, separated by blank intervals up to 400 ms, can be integrated and processed

* Corresponding author at: Rotman Research Institute, Baycrest Centre, University of Toronto, 3560 Bathurst Street, Toronto, ON, Canada M6A 2E1. Fax: +1 416 785 2862.

E-mail address: ylee@rotman-baycrest.on.ca (Y. Lee).

¹ These authors contributed equally to this research.

configurally, yielding inversion effects comparable in magnitude to those of faces presented as a whole (Anaki et al., 2007). Beyond that interval, *analytic* or *part-based* processing appears to prevail, indicated by a marked reduction in the behavioral face-inversion effect. Presentation of a random pattern mask during the interval between the two face parts disrupted integration in the 200 ms interval condition, resulting in decreased recognition; the mask had no effect either on integration or perception of the separate parts in the 800 ms condition (Anaki and Moscovitch, 2007). These findings, along with others (see Anaki and Moscovitch, 2007), indicate that integration is achieved through a short-lasting, limited capacity buffer which temporarily maintains the visual input while integration occurs, and allows configural processing. We speculated that facial temporal integration would likely occur within iconic memory during *information persistence* (Coltheart, 1980) which lasts 150–300 ms after stimulus offset (see discussion in Anaki et al., 2007). Although we tested only faces, it is likely that similar processes occur in other domains (Ruff et al., 2007; Saneyoshi et al., 2011), though the content on which these processes operate, and hence some of the regions that are implicated, may be specific to each domain.

To date, there are no studies on the neural and anatomical manifestations of temporal integration of separate facial parts leading to face identification. Are temporally integrated faces handled by the same regions that integrate spatial information into a configural representation of faces? Prime candidates include “core” face-sensitive areas, such as the fusiform gyrus. The fusiform face area (FFA), functionally defined by contrasting response to faces vs. response to other categories of objects (Kanwisher et al., 1997), is engaged in face detection (Nestor et al., 2008; Rossion, 2008; Tong et al., 2000), representation of generic faces (Loffler et al., 2005), and identification of individual faces (Grill-Spector et al., 2004; reviewed in Kanwisher and Yovel, 2006). Although the FFA is involved in holistic representation of faces (Andrews et al., 2010; Rossion et al., 2000; Schiltz and Rossion, 2006), it is equally activated to facial features, both internal and external (shape), and to their configuration (Liu et al., 2009; Rotshtein et al., 2007; Yovel and Kanwisher, 2004; also see Andrews et al., 2010; Axelrod and Yovel, 2010). Crucially, in Mukamel et al. (2004) where a stimulus was successively flashed, striate and extrastriate areas show persistent neural activity even after stimulus termination resulting in signal increases not proportional to a stimulus presentation rate. This nonlinearity was stronger in higher visual areas such as the FFA even for non-preferred stimuli (i.e., faces as well as houses), and it might provide the short-term visual memory buffer needed for the temporal integration to occur (Mukamel et al., 2004).

Other distinct areas within the fusiform gyrus, in the vicinity of the FFA but not encompassed by it, appear to be sensitive only to changes in face configuration (Maurer et al., 2007; Ng et al., 2006; Schiltz and Rossion, 2006; Schiltz et al., 2010). Furthermore, configural face processing may involve a number of regions outside the occipitotemporal cortex (Maurer et al., 2007; Ng et al., 2006; Rotshtein et al., 2007). For example, Rotshtein et al. correlated discrimination of configural change in the face (measured outside the scanner) with blood-oxygen-level dependence (BOLD) responses when the participant monitored such stimulus changes. They found a positive correlation in several areas, such as the left middle cingulate gyrus, right insula, putamen and prefrontal regions, as well as the right fusiform and bilateral inferior occipital gyri. Although the anterior/middle cingulate cortex is not traditionally considered part of the face network (Haxby et al., 2000a), significant activity in this region was observed during configural face processing (Ng et al., 2006) and face encoding and subsequent recognition (Haxby et al., 1996). Prefrontal areas were also observed in configural processing of faces as opposed to featural processing (Maurer et al., 2007). If a temporally integrated face is represented in a configural manner, we would expect to find a positive correlation between activity of

these regions and recognition performance in the short interval conditions. Taken together, we would expect the FFA proper to respond early in the short interval conditions providing a visual buffer facial parts to be used in temporal integration, but additional regions to contribute to configural representations of integrated faces.

Previous findings have shown that if face components were separated by a long enough interval such that the first one was not integrated with the second that arrived later in the visual buffer, configural representation would suffer and performance would depend on analytical processes based on individual face parts (Anaki and Moscovitch, 2007). In such cases, investigators have speculated that activity in configural processing regions may be detrimental to identification by component parts (de Gelder and Rouw, 2000; Macrae and Lewis, 2002; see Fig. 6 in Maurer et al., 2007), yet no one has provided neural evidence for the incompatibility of analytic and configural processing of faces. If such incompatibility exists, activation in configural regions should be positively correlated with performance on tests sensitive to configural processing but negatively correlated with tests sensitive to analytic processing. The reverse should hold for regions that support identification based on piecemeal information derived separately from each of the component parts. Such regions, however, are not as clearly delineated as those associated with configural processing; for example, Rotshtein et al. (2007) found no regions showing brain-behavior correlations for featural changes.

To investigate the neural correlates of facial temporal integration, we used an event-related fMRI design, in which we presented famous faces whose top and bottom halves were separated by either 0, 200 or 800 ms inter-stimulus intervals (ISI 0, ISI 200, ISI 800, respectively) and measured the participant's recognition of the faces (yes/no responses) as an index of temporal integration. Although whole faces were not shown in any condition, the 0 ms condition had no blank screen, so that the top and bottom halves were presented sequentially, creating a whole-face percept. In a comparison condition, we used a misaligned face (MIS) in which both parts were presented simultaneously. As noted, identification of such faces has been shown to be based on analytic, rather than configural, processes. We chose to use misaligned rather than inverted faces to maintain a common orientation across our stimuli.

We first assessed the magnitude of BOLD signals in the FFA using a univariate, region of interest (ROI) analysis. Then, we used a multivariate method, Partial Least Squares (PLS; McIntosh et al., 1996, 2004), to assess a functional network of distributed neural regions whose activity co-varies with the stimulus conditions (task PLS) and with recognition performance in each condition (behavior PLS). Behavior PLS was used to identify a set of regions that contributed directly, either positively or negatively, to recognition performance, i.e., areas where activity was correlated with recognition (see **Materials and methods** section for justification for using PLS).

In the univariate ROI analysis of task-related effects in the FFA, a couple of potential results are possible. If FFA activity is related to temporal integration then it should be more active in the 0 and 200 conditions (i.e., ISI 0, ISI 200 > ISI 800, MIS). On the other hand, it is possible that the FFA would show some increase of activity in the short interval conditions, but a larger increase in the long intervals, compared to no interval or MIS conditions (i.e., ISI 800 > ISI 200 > ISI 0, MIS), simply because in the former case there is a double pulse produced by the sequential presentation of the two face halves. Activity might also be larger in the FFA during the long interval condition (ISI 800) because this condition would involve the greatest demand from maintenance of individual facial parts that are clearly segregated.

We also considered it important to examine the activity in the rest of the brain to see how that activity was related specifically to recognition. To do so, we chose to use PLS analysis because we believed it to be the best tool for the purpose (see justification in

Materials and methods section). In the whole brain analysis of task effects, we would expect patterns of distributed activations in ISI 800 to differ from those of the other task conditions because of the relatively long time interval between presentation of the first and second face parts. Hence, if face parts are not temporally integrated, but are treated as discrete representations over a delay, we should see higher activation in a number of regions for the long interval condition relative to the misaligned and short-interval conditions, in which faces would be represented as a single percept (James et al., 2009). In addition to some ventral visual processing areas, we would expect regions associated with attention and WM maintenance (Courtney et al., 1997; Haxby et al., 2000b) to be more activated in the long, than the short, interval condition.

In terms of brain-behavior correlations, we hypothesized that activity in a distinct network of brain regions would be correlated with recognition success for short vs. long interval and misaligned conditions, reflecting the use of configural processing at the shorter intervals and analytic processing in the latter two conditions. Specifically, better face identification over a short interval (0 or 200 ms) would include areas implicated in configural face processing, such as regions in the right fusiform gyrus in the vicinity of FFA, and other areas which have been reported in tasks of configural processing, such as the middle cingulate gyrus, right insula and prefrontal regions (Maurer et al., 2007; Ng et al., 2006; Rotshtein et al., 2007). Conversely, recognition in the 800 ms interval and misaligned conditions would be negatively correlated with activity in these configural regions.

Materials and methods

Participants

Fourteen healthy participants were scanned using fMRI (mean age = 25.6 years, SD = 3.2, range = 21–33, 5 males). One participant did not come back for a post-scan behavioral test and another participant's response in the scanner was not recorded, resulting in 13 participants for task PLS analysis and 12 participants for behavior PLS analysis (mean age of 12 participants = 25.7, SD = 3.4, 5 males). All participants were right-handed and had normal or corrected-to-normal vision with no history of visual, psychiatric and neurological disorder. All participants provided written consents and procedures were approved by the Baycrest Centre Research Ethics Board.

Stimuli and tasks

The experimental stimuli consisted of 360 photographs of famous figures from various fields (e.g., movie, politics, sports) that were downloaded from the internet (see Anaki and Moscovitch, 2007). All pictures were converted into a 256 gray-level scale and equated for luminance. A full face (with top and bottom parts) subtended approximately $2.3^\circ \times 2.9^\circ$ in the scanner. Each face was divided into a top part (the upper half of the face containing the eyes) and a bottom part (the lower half of the face with the nose, mouth and the chin, Fig. 1a). In the misaligned condition, both the top and bottom parts were presented together but spatially misaligned (Fig. 1b). All stimuli were shown upright. For face localizer runs, photographs of non-famous faces, houses and watches were presented and each image subtended $5.7^\circ \times 6.8^\circ$.

Six runs of the experimental task and two runs of the face localizer task (to identify the FFA) were conducted in the scanner. During a trial of experimental runs, a fixation cross was displayed for 500 ms, followed by the top (or bottom) part of the face for 17 ms, a blank screen in black (lasting 0, 200, or 800 ms), and the bottom (or top) part for 17 ms (ISI 0, ISI 200, ISI 800, respectively), based on the experimental paradigm of our prior studies (Anaki and Moscovitch, 2007; Anaki et al., 2007). In the misaligned condition (MIS), following a 500 ms fixation cross, a misaligned face was presented for 17 ms (Anaki et al., 2007). Hence, the exposure duration to top and bottom face parts was constant at 17 ms in all conditions. After the presentation of the bottom part or a misaligned face, a black screen appeared for a period of time that varied from 2666 ms in ISI 800 to 3483 ms in MIS (i.e., a total duration of a trial was 4000 ms). During that time the participants pressed a button with their right hand to every trial whether or not they recognized the face (yes or no). We stressed that it is not necessary that they know the name of the person but only that they have some information about the person (e.g., profession) on which to base their decision. Trials were separated by fixation intervals that ranged from 0 to 4 s. Each run was preceded by an instruction screen for 20 s and ended with another 20 s fixation interval (a total duration was 400 s). In each run, there were 60 trials including 12 null events (with a fixation cross only) and 12 trials of each condition. The presentation of the four conditions was randomized within a run.

Localizer runs, which used a block design, were interleaved between the third and the fourth experimental runs: that is, three experimental runs, then two localizer runs, followed by three experimental runs. Each stimulus category (faces, houses, watches)

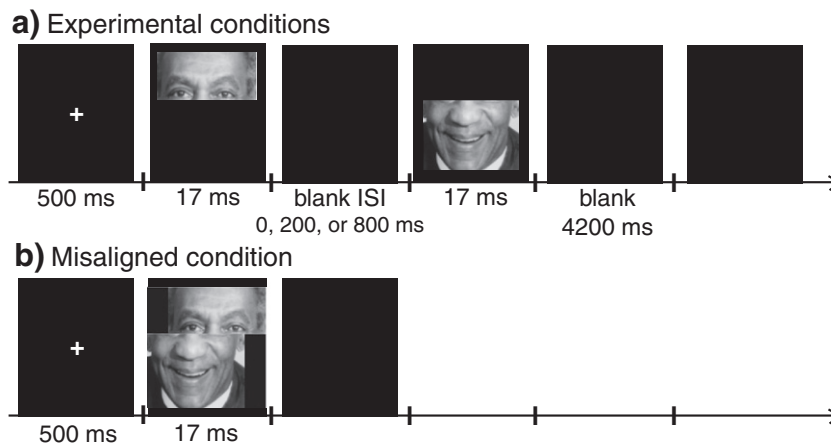


Fig. 1. Timeline of the events (one trial) shown for an experimental condition (ISI 0, ISI 200, ISI 800) and a misaligned comparison condition (MIS). (a) During an experimental trial, top and bottom parts of the face were presented with varying intervals (0, 200, or 800 ms) between the parts. Presentation order of the top and bottom parts was randomized across trials such that a top part appeared first in some trials while a bottom part was displayed first in other trials. (b) In a comparison condition, a misaligned face was displayed. Following the second part, participants had to decide whether or not they recognized the face.

was presented three times in each run (a total of 96 images per category) and each image block showed 15 images (4–5 repeated images per block). Participants performed a one-back task in which they had to press a button if an image was identical to the previous one. Fixation blocks (16 s) were alternated with stimulus blocks (30 s) and each localizer run lasted for 438 s.

A post-scan test was conducted approximately 24 h after the scan. Participants performed a recognition test of the famous faces that they viewed during fMRI. During the test, each face in its intact form was displayed for an unlimited time and the participant provided identifying information about the face (e.g., name, profession). Any trials with faces unknown to the participant were excluded from PLS analysis of the data. The final number of trials per run that was entered into PLS analysis was approximately equal across conditions: ISI0 [$M=9.8$, $SD=1.4$], ISI200 [$M=9.5$, $SD=1.7$], ISI800 [$M=9.8$, $SD=1.3$], and MIS [$M=9.7$, $SD=1.6$].

fMRI data acquisition

Data were acquired with a Siemens 3 T Tim Trio magnet with a 12-channel head coil at the Rotman Research Institute, Baycrest Centre, Toronto, Ontario. Functional images were collected in the axial oblique plane using a series of T2* weighted gradient echo (EPI) scans (TE = 30 ms; TR = 2 s; flip angle 70°; FOV = 200 mm; resolution = 3.125 × 3.125 × 5 mm; zero gap; 30 slices covering the entire cerebral cortex; interleaved acquisition). Anatomical images were obtained before the fMRI to co-register the functional images with brain anatomy (T1 weighted; TE = 2.63 ms; TR = 2 s; FOV = 256 mm; 1 mm isotropic voxels; 160 slices). Physiological respiratory and cardiac waveforms were recorded to remove these noise sources from fMRI time-series data.

Stimuli were presented using E-Prime software version 1.2 (Psychology Software Tools). Images were back-projected onto a screen (subtending 14.8° × 12.1° at a viewing distance of 132 cm) behind the scanner and shown to the participant using a mirror mounted on the head coil.

fMRI data analysis

Data preprocessing

Data preprocessing was carried out using AFNI (Analysis of Functional Neuroimages; Cox, 1996). The first 10 scans in each run, during which participants saw the experimental instructions on the screen and then maintained fixation, were excluded to allow for brain magnetization to reach a steady state. Further preprocessing of functional scans involved physiological noise correction, slice timing correction and 3D motion correction (using a 3D Fourier transform interpolation). Any individual run, in which the peak range of the participant's head motion exceeded 1.5 mm, was discarded. All functional scans were resampled to 2 mm isotropic voxel resolution, converted into MNI space (the Montreal Neurological Institute 152 template) and smoothed with a 6 mm Gaussian filter.

Region of interest (ROI) analysis

We used the general linear model (GLM) in AFNI to assess activity of functionally defined regions in each individual participant. The images were de-trended by means of 3dDeconvolve using a linear fitting. The shape of the hemodynamic response functions (HRFs) for block localizer scans was modeled as a gamma function convolved with a boxcar function of width equal to the duration of the block, and for event-related experimental scans, a tent function time locked on target onset for the duration of 7 TRs. The resultant β -coefficients represent activity from baseline (a constant mean level of signal). Statistical maps were converted into MNI space (the Montreal Neurological Institute 152 template) and smoothed with a Gaussian filter with a full-width half-maximum value of 4 mm. This relatively small

spatial filter was used to facilitate the localization of the FFA, which had a relatively small volume in each participant.

From localizer activation, face-preferring ROIs were functionally defined in each participant by identifying the voxels that showed greater responses to faces, compared to houses or objects, in the lateral/middle fusiform gyrus (Kanwisher et al., 1997), the inferior or middle occipital gyrus (Gauthier et al., 2000) and the superior temporal sulcus, with $p < 0.005$ (uncorrected). As only FFA was identifiable for the majority of participants (right: 13/14, left: 11/14), signals in bilateral FFA are reported in the results (also see Axelrod and Yovel, 2010 regarding reliability of FFA signal compared to other core face areas). The BOLD signal was extracted for each experimental condition from all trials (regardless of known or unknown faces in a post-scan test) and also from trials of known faces only (recognized on a post-scan test).

PLS analysis

In addition to assessing brain-behavior correlations by identifying ROIs using a univariate analysis and then individually correlating each ROI's activity with behavioral performance, we decided also to use PLS. We believe that PLS has an advantage over univariate methods because it examines activity across all regions of the brain and relates them to behavior scores simultaneously in a single step. Moreover, this focus on measuring brain-behavior correlations is adequate for the present study because brain-behavior correlations are less perturbed than activation measures by the effect of different stimulus presentation rates (e.g., Mukamel et al., 2004), or sustained and anticipatory activity during a delay between two face parts (e.g., Courtney et al., 1997; Haxby et al., 2000b; Olsen et al., 2009).

Thus, the analysis of experimental runs was performed using PLS (for a detailed tutorial and review of PLS, see Krishnan et al., 2011). PLS examines the coordinated activity of brain regions showing similar activity patterns rather than the independent activity of a single brain region. Briefly, PLS identifies a set of latent variables (LVs) that account for maximum covariance between brain activity (X matrix) and the experimental conditions or behavioral measurements (Y matrix). The major difference between task and behavior PLS resides in the Y matrix: in task PLS, Y is a matrix coding for experimental task conditions (category membership), and in behavior PLS, Y stores behavioral measures (in our case, proportion of recognized responses). PLS performs a singular value decomposition (SVD) on the cross-product of X and Y (i.e., on a single matrix containing all participants' data) and decomposes the data into orthogonal dimensions. Resembling principal component analysis, PLS thus enables one to differentiate the contribution of different regions associated with task or performance differences.

In task PLS, the X and Y matrices are centered by subtracting the grand mean of the matrix (either X or Y) from each value in that matrix. The X and Y matrices are then normalized so that the sum of the squared values for each column is equal to one (i.e., transformed into Z-scores). Normalization ensures that the variable scales are comparable. The cross-product of the centered, normalized X and Y matrices is then computed. This results in a correlation matrix, denoted M. The SVD is then run on the M matrix. Note that for task PLS, the Y matrix is a matrix of dummy codes indicating task/group membership. This effectively gives the correlation between task/group membership and brain activity. For behavior PLS, X and Y are again mean-centered and normalized. Behavior PLS then proceeds in a similar way as task PLS: given the relationship between behavior and brain activity, correlations are first computed between activity and behavior across subjects, for each condition on a voxel-wise basis, and the condition-wise matrices are stacked on top of the other to build the combined matrix of correlations; then this correlation matrix is subjected to SVD. The SVD results in a set of LVs each of which has (a) a singular value that indicates the amount of covariance accounted for by the LV, (b) a vector showing condition-dependent differences in the brain-behavior

correlation and (c) a brain image that shows the voxels that express the pattern of brain-behavior correlations seen across conditions (Bookstein, 1994). For each condition in each LV, we calculate summary measures of how strongly each participant expresses the particular pattern of activity seen on the LV. These measures, called brain scores, are calculated by multiplying brain activity in each voxel by the voxel's weight (salience) on the LV's pattern and summing across all voxels. Brain scores can be positive or negative depending on the voxels' relation with the pattern of task differences identified by the LV.

SVD identifies independent (uncorrelated) LVs that account for covariance among brain activity and behavior measures. The first LV always accounts for the largest amount of covariance (i.e., has the largest singular value), with subsequent LVs accounting for progressively smaller amounts. Permutation tests assess the significance of each LV by determining the probability that a singular value from permuted data (resampled 700 times) is larger than the obtained value (McIntosh et al., 1996). Bootstrap resampling (100 bootstraps) is used to estimate standard errors of the salience for each voxel to assess the robustness of each voxel's contribution to a given pattern of activity. Because extraction of the LVs and corresponding brain images is done in a single analytic step, no correction for multiple comparisons is required.

PLS was carried out on activity across 7 TRs from the onset of the first face part. Activity at each time point was normalized to activity at 0 time point. Voxels with a bootstrap ratio or BSR (salience/standard error) > 3.0 were considered to be reliable, approximating $p < 0.005$ (Sampson et al., 1989). Clusters of active voxels were based on local maxima of BSR > 3.0, contiguous clusters of ≥ 100 voxels, a minimum distance between peaks of 1 cm, and were taken from the peak BSR between TR1 to TR4 (BOLD signal tended to decline following TR 4). Anatomical labels in tables were assigned according to the Eickhoff Anatomy Toolbox (Eickhoff et al., 2005). The bootstrap also calculated confidence intervals (CIs) for mean brain scores from the task-PLS and for each correlation between recognition and brain scores from the behavior-PLS. The 95% CI was used in the current study. Differences in brain score or correlations between conditions were determined by a lack of overlap in these CIs.

Results

Behavioral performance

In the post-scan test, participants recognized 80.8% of the famous faces used as stimuli (s.d. = 10.8). Fig. 2 shows participants' recognition performance in the scanner for these known faces, i.e., the proportion of the total number of faces per condition recognized in the post-scan test that received a "yes" response during scanning. Behavioral performance was assessed using repeated-measures ANOVA comparing the proportion of recognition responses across the four

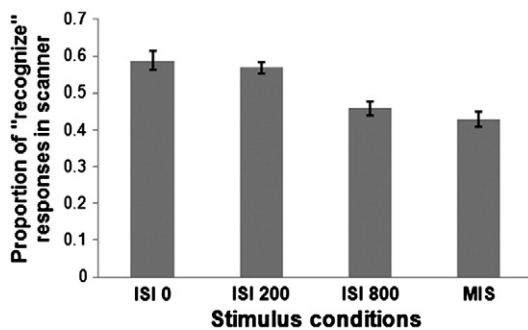


Fig. 2. Proportion of "recognize" responses in the scanner for the faces that were known to each participants. Performance in ISI 0 and ISI 200 was significantly better than that of ISI 800 or MIS. Error bars indicate ± 1 standard error corrected for repeated measures.

conditions. The effect of condition was significant [$F(3,33) = 10.86$, $p < 0.001$, $\eta_p = 0.50$, two-tailed]. Pairwise comparisons with Bonferroni corrections found a marginal difference between ISI 0 and ISI 800 [mean difference or MD = 0.13, $p = 0.074$] and a significant difference between ISI 0 vs. MIS [MD = 0.16, $p = 0.009$], ISI 200 vs. ISI 800 [MD = 0.11, $p < 0.001$] and ISI 200 vs. MIS [MD = 0.14, $p = 0.006$] (all tests were two-tailed). Replicating the results of previous studies (Anaki and Moscovitch, 2007; Anaki et al., 2007), the behavioral data from the scanner indicate that recognition of faces whose parts were separated by a 200 ms interval was as good as that of facial parts shown with no interval [MD = 0.02, $p = 1.0$]. As expected, recognition accuracy was lower in ISI 800 compared to performance in ISI 0 and ISI 200, but similar to that of misaligned faces.

fMRI

We begin with results from the region of interest (ROI) GLM analysis followed by the PLS analyses.

GLM results: regional activity

Average MNI coordinates of FFA across participants were as follows (peak voxel location, average $\pm 1SD$): right FFA [41 ± 4 , -54 ± 10 , -20 ± 3] and left FFA [-39 ± 4 , -52 ± 8 , -19 ± 4]. Fig. 3 provides time course plots of right and left FFA for trials of known faces

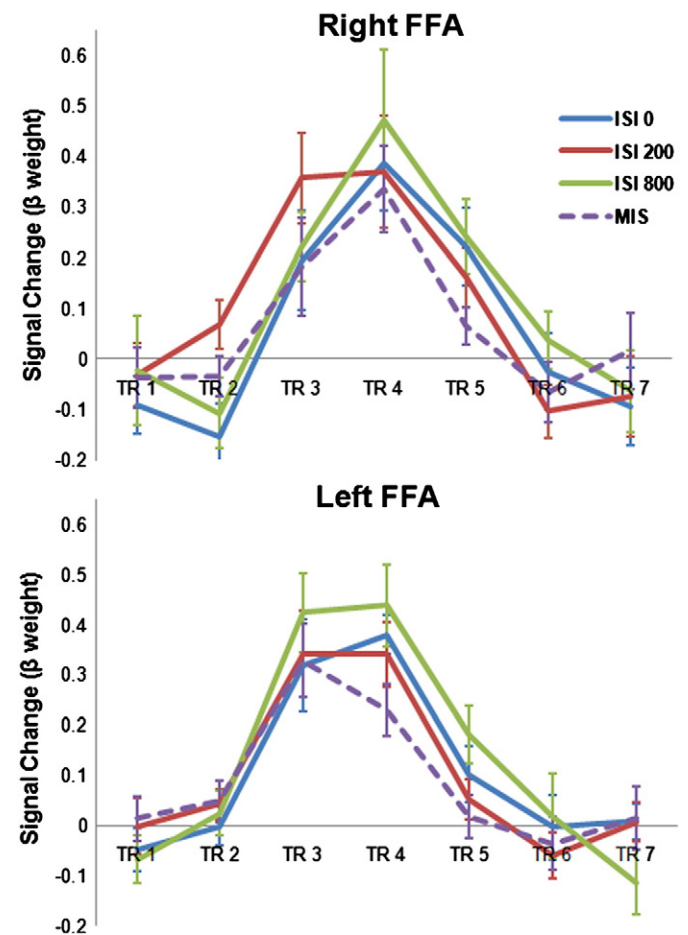


Fig. 3. Time courses of the BOLD signal change for the bilateral FFA (known face trials only based on a post-scan test). Displayed are average time courses for each of the four experimental conditions. The FFA was individually localized in each participant from localizer scans. In right FFA, signals rose earlier in ISI 200 than the other conditions (TR 2) but the peak activity (TR 3 and 4) did not differ across task conditions. The left FFA showed a marginal effect of task (higher peak response in ISI 800; also see supplementary material). Error bars ± 1 s.e. (corrected for repeated measures).

as determined by a post-scan test. The Supplementary figure depicts bilateral FFA responses of *all* trials (regardless of post-scan test results). For the ANOVAs, BOLD signals were taken from TR 2, 3 and 4 and a one-way repeated-measures ANOVA compared the experimental task conditions (ISI 0, ISI 200, ISI 800, MIS) in each of these TRs. In case of violation of homogeneity of variance, the Greenhouse–Geisser estimates were used. Given a significant effect of task conditions, correlation between BOLD signals and recognition performance (proportion of recognized faces) was additionally examined.

In right FFA (with known trials), a one-way repeated-measures ANOVA found a significant task effect in TR 2, [$F(3,33)=3.66$, $p=0.02$, $\eta_p^2=0.25$]. Pairwise comparisons with Bonferroni corrections revealed higher signal levels in ISI 200 compared to ISI 800 [$p<0.05$]. However, the correlation between the BOLD response at ISI 200 and recognition of known faces was negative [$r=-0.66$, $p=0.03$]. No significant difference was found in TR 3 and 4 (with known trials and with all trials). Intriguingly, the increased signal of ISI 200 in TR 2 was no longer observed when all known and unknown faces were included [$F(3,36)=1.47$, $p=0.24$, $\eta_p^2=0.11$] (also see Supplementary figure).

The left FFA showed a different pattern of results. A one-way repeated-measures ANOVA (with known trials) found a marginal task effect in TR 3, [$F(3,27)=2.47$, $p=0.08$, $\eta_p^2=0.22$] reflecting greater responses in ISI 800. However, correlation between ISI 800 activity and recognition performance was not significant [$r=0.28$, $p=0.47$]. No significant difference was found in TR 2 and 4. The marginal effect in ISI 800 reached significance in both TR 3 and 4 when all trials were included (see Supplementary figure), TR 3 [$F(3,30)=3.08$, $p=0.04$, $\eta_p^2=0.24$] and TR 4 [$F(3,30)=6.03$, $p=0.002$, $\eta_p^2=0.38$]. Pairwise comparisons with Bonferroni corrections also showed a significant increase in ISI 800 compared to ISI 200 [$p=0.02$] and to MIS [$p=0.01$] in TR 4. Even with all trials, correlations between ISI 800 signals and recognition of known faces were not significant, TR 3 [$r=0.31$, $p=0.42$] and TR 4 [$r=0.28$, $p=0.47$].

Additionally, the correlation between recognition performance and FFA signal was examined with peak BOLD signals averaged between TR 3 and 4. No significant results were found: right FFA, ISI 0 [$r=-0.41$, $p=0.21$], ISI 200 [$r=-0.13$, $p=0.71$], ISI 800 [$r=0.12$, $p=0.72$], MIS [$r=0.29$, $p=0.39$]; left FFA, ISI 0 [$r=0.39$, $p=0.30$], ISI 200 [$r=0.28$, $p=0.47$], ISI 800 [$r=0.35$, $p=0.36$], MIS [$r=0.21$, $p=0.58$].

These ROI results indicate that right FFA may be involved in temporal integration of known faces over a brief interval although it does not support recognition. By contrast, left FFA showed greater responses to ISI 800 irrespective of knowledge of the face. The peak activity of the FFA alone was not significantly associated with recognition of known faces in either the short or long interval conditions.

Task PLS results: whole brain activity co-varying with task conditions

The task PLS analysis examined whole brain activity changes across the experimental task conditions. A single LV was significant with $p<0.001$, accounting for 63.4% of the covariance. This LV identified a contrast between ISI 800 and ISI 0, ISI 200 and MIS (see Fig. 4) that included a number of regions showing greater activation for ISI 800, but only left insula for the other conditions (see Table 1). The clusters showing greater activity in ISI 800 were found in the occipital cortex (left inferior, left superior occipital, bilateral middle occipital), inferior temporal cortex (bilateral lingual, bilateral fusiform, right parahippocampal, right inferior temporal), temporal cortex (right middle temporal, left superior temporal), parietal cortex (left superior parietal, right supramarginal), bilateral insula, anterior cingulate and prefrontal cortex.

Increased activity for ISI 800 included diffuse areas in occipitotemporal cortex, overlapping with the functionally defined FFA in both hemispheres (see Fig. 4). However, the maxima of these clusters of activation were either medial (right hemisphere) or lateral (left hemisphere) to the

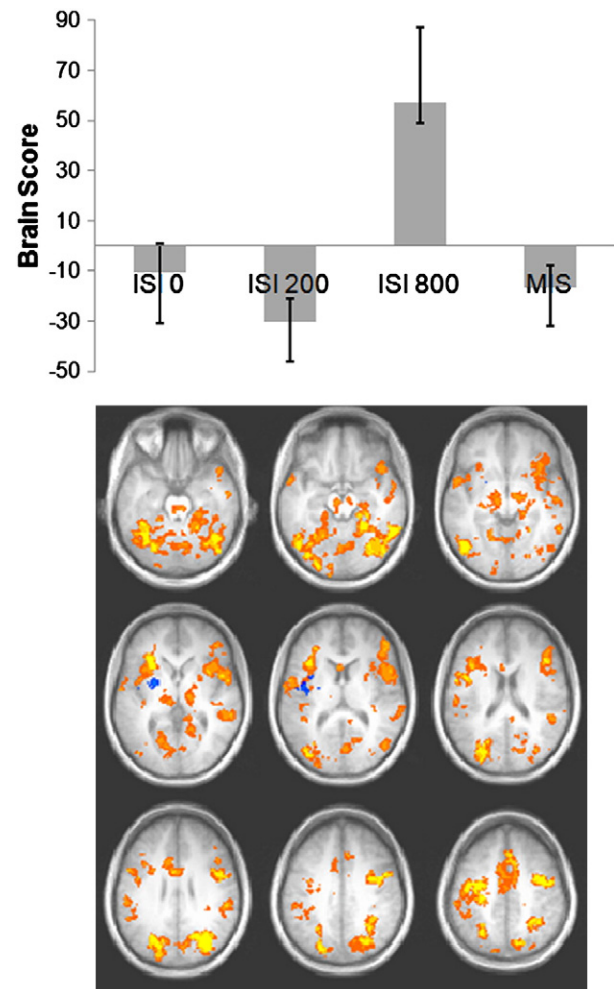


Fig. 4. Results of the task PLS analysis contrasting four experimental conditions. The pattern identified by LV 1 separated ISI 800 from the rest of conditions. The graph shows the mean-centered brain scores (error bar=95% CIs from bootstrapping). Regions colored in red and yellow showed higher activity to ISI 800, whereas the blue area showed higher activity to ISI 200 and MIS. Regions were averaged from TR 2 to TR 4 (no reliable cluster was found in TR 1). All maxima have BSR ≥ 3.0 and cluster size ≥ 100 voxels (800 mm³). Top left corner slice $z=-20$, slice space = 8 mm.

average FFA coordinates, and outside the range of values for FFA as reported in previous studies.² The superior temporal sulcus (STS) was found on the left only. The involvement of the parietal cortex points to a role of attention (Caramelli et al., 2008). The inferior frontal areas were found in pars opercularis as well as insula bilaterally (Table 1). The right inferior frontal area and left insula approximate the posterior mid-frontal/inferior frontal gyrus and left anterior insula, respectively, which are implicated in face working memory (Courtney et al., 1997). Medial regions such as the superior medial frontal gyrus and the caudal part of the anterior cingulate have been shown in various types of

² We have reviewed 19 studies to obtain an average and range of FFA coordinates across the studies. Average of right FFA [43 ± 4 , -54 ± 6 , -18 ± 6], range $x=32$ to 49 , $y=-64$ to -43 , $z=-28$ to -6 . Average of left FFA [-41 ± 5 , -58 ± 8 , -16 ± 7], range $x=-53$ to -34 , $y=-73$ to -45 , $z=-27$ to -5 . In our study, fusiform clusters in both Table 1 (task PLS) and 2 (behavior PLS) are medial to any of the FFAs previously reported. All coordinates are converted to MNI. The studies include Andrews et al. (2010), Andrews and Ewbank (2004), Epstein et al. (2003), Fairhall and Ishai (2007), Gauthier et al. (2000), Grill-Spector et al. (2004), Haist et al. (2010), Hoffman and Haxby (2000), Horner and Andrews (2009), Kanwisher et al. (1997), Large et al. (2008), Li et al. (2010), Liu et al. (2009), Nestor et al. (2011), Rhodes et al. (2009), Rotshtein et al. (2005), Schiltz et al. (2010), Spiridon et al. (2006), and Yi et al. (2006).

Table 1
Brain areas where activity is modulated with experimental conditions (task PLS).

Region	Hemi-sphere	MNI coordinates			BSR
		x	y	z	
<i>Regions showing higher activity to ISI 800</i>					
Fusiform	R	22	−46	−12	8.05
	L	−32	−46	−16	7.47
Inferior occipital	L	−44	−66	−4	7.05
Middle occipital	R	32	−68	30	4.43
	L	−28	−86	24	6.33
	L	−34	−82	4	5.66
	L	−18	−74	32	6.52
Parahippocampal	R	28	−32	−14	7.98
Lingual	R	18	−82	−2	7.06
	R	16	−52	2	5.27
	L	−12	−88	−10	5.21
	R	54	−54	−12	7.07
Middle temporal	R	48	−70	14	5.66
Superior temporal (sulcus)	L	−48	−28	18	6.03
Superior parietal	L	−28	−60	44	6.12
Supramarginal	R	56	−28	28	6.84
Anterior cingulate	L	−4	8	28	8.75
Insula	R	48	6	2	9.80
	L	−34	24	8	9.41
Inferior frontal (p. Opercularis)	R	32	4	34	6.37
	L	−50	8	26	5.60
Superior medial frontal	R	4	28	42	4.42
Precentral	R	40	−4	44	6.59
	L	−34	−12	48	8.88
Thalamus	L	−14	−20	0	8.75
Cuneus	R	20	−64	30	7.37
	L	−18	−64	22	5.84
Cerebellum	R	18	−46	−44	7.80
<i>Regions showing higher activity to ISI 200, MIS:</i>					
Insula	L	−42	−2	10	7.02

R = right; L = left; BSR = bootstrap ratio; voxels = number of voxels (one voxel volume = 8 mm³). All reported activations are from LV 1, ≥ 100 voxels (800 mm³) and peak BSR between TR 2 and TR 4 (no reliable cluster was found in TR 1).

working memory tasks (Petit et al., 1998). Thus, ISI 800 activated a number of areas to a greater extent than the other conditions, such as the occipitotemporal cortex for visual face processing, the parietal lobes for attention control and the frontal cortices for the maintenance of individual facial parts that were not integrated.

Behavior PLS results: whole brain correlations with recognition performance

Task PLS delineated a network of regions showing differences in activity across the conditions, mainly greater activity for the long interval condition. Behavior PLS examined a different question, i.e., how whole-brain activation patterns correlated with recognition success. The behavior PLS analysis identified a single significant LV ($p = 0.023$) that accounted for 34.2% of the covariance in the data (Fig. 5). This LV identified a pattern of correlations that differentiated ISI 0 and ISI 200 from ISI 800 and MIS. A set of regions was identified where activity and recognition performance were positively correlated in ISI 0 and ISI 200, but negatively correlated in the ISI 800 and MIS conditions. There were no regions with the opposite pattern (i.e., positively correlated only with identification at ISI 800 and MIS) that survived the cluster thresholding. All of the correlations were reliably different from zero (based on the 95% confidence intervals seen in the top part of Fig. 5). In addition, the correlations for ISI 0 and ISI 200 reliably differed from those seen in ISI 800 and MIS.

As predicted, better recognition in ISI 0 and ISI 200 was associated with increased activity in a number of areas (Table 2). By contrast, increased activity in these areas resulted in poorer performance in ISI 800 and MIS. Areas supporting recognition in ISI 0 and ISI 200 were found in the occipital cortex (right middle occipital, bilateral superior occipital gyri), inferior temporal cortex (right medial fusiform and lingual gyri) and bilateral superior temporal regions (Fig. 6). In addition,

other areas implicated were the cingulate cortex (bilateral middle, left anterior), the right insula and the frontal cortex (see Table 2). Some of these regions include proposed core and extended configural face processing networks. In addition, the areas identified by the behavioral PLS were largely non-overlapping with those found by the task PLS. For example, the right fusiform cluster was medial to the right FFA and posterior to the cluster found for ISI 800 in the task PLS. Also, the cluster in left anterior cingulate gyrus in the behavioral analysis was anterior to the one found to be more active for ISI 800 in the task PLS results. Finally, the frontal areas where activity was related to recognition performance were distinct from the task PLS results, and included clusters in the right orbital (BA 10) and left middle frontal gyri (BA 9), both of which have been implicated in face processing (Gobbini and Haxby, 2007; Haxby et al., 1996). We will discuss each of the areas in detail in the discussion section.

Discussion

Summary of results

To delineate the neural correlates involved in facial temporal integration, we used a ROI (GLM) analysis to examine activity in the functionally-defined FFA from each participant, and also applied multivariate PLS analyses to assess whole brain activity. The ROI analysis revealed that in the right FFA, signals rose earlier in ISI 200 than the other conditions, but the peak activity did not significantly differ across task conditions. In left FFA, the peak activity was higher in ISI 800 than any other task conditions, probably to maintain representations of individual facial parts that were separated by a long interval. However, the neural responses in the functionally-defined right and left FFA were not related to better recognition performance (and, in fact, right FFA activity at TR2 was related to worse performance in the ISI 200 condition) and did not reflect the distinction between configural and part-based processing associated with the behavioral results for the different conditions. PLS analyses proved more sensitive in that regard. In task PLS, neural activity patterns for ISI 800 were distinct from those in the other conditions (ISI 0, 200, MIS), in which top and bottom parts were treated as a single percept. Importantly, behavior PLS, unlike ROI analysis, differentiated the short interval conditions, 0 and ISI 200, from ISI 800 and MIS, reflecting the relation between temporal integration, configural processing and recognition. Activations across regions that are part of a face network were positively related to recognition performance in ISI 0 and ISI 200 conditions which are associated with configural processing, but negatively related in ISI 800 and MIS, which are associated with part-based processing. With respect to FFA, areas active for ISI 800 in the task PLS overlapped with the FFA, but the maxima of activation for these areas were elsewhere in the occipitotemporal cortex. In behavior PLS, the activated regions associated with temporal integration at short ISIs were not in FFA proper, but adjacent to it. These findings help identify the neurocognitive mechanisms needed for temporal integration of face parts into a configural representation that can support face recognition (Anaki and Moscovitch, 2007). We now discuss these results in more detail.

Face representations in the FFA

The latency of the activity increase in right FFA for the face stimuli as revealed by ROI analysis was significantly shorter in ISI 200, possibly indicative of summation of neural activity in that region (Mukamel et al., 2004). As the activation associated with this early component was negatively correlated with recognition performance, i.e., hinders recognition, it suggests that this activity was not conducive to temporal integration underlying configural processing. As all other latencies (TRs), the peak activity in right FFA did not significantly differentiate task conditions, while that of left FFA was greater in ISI

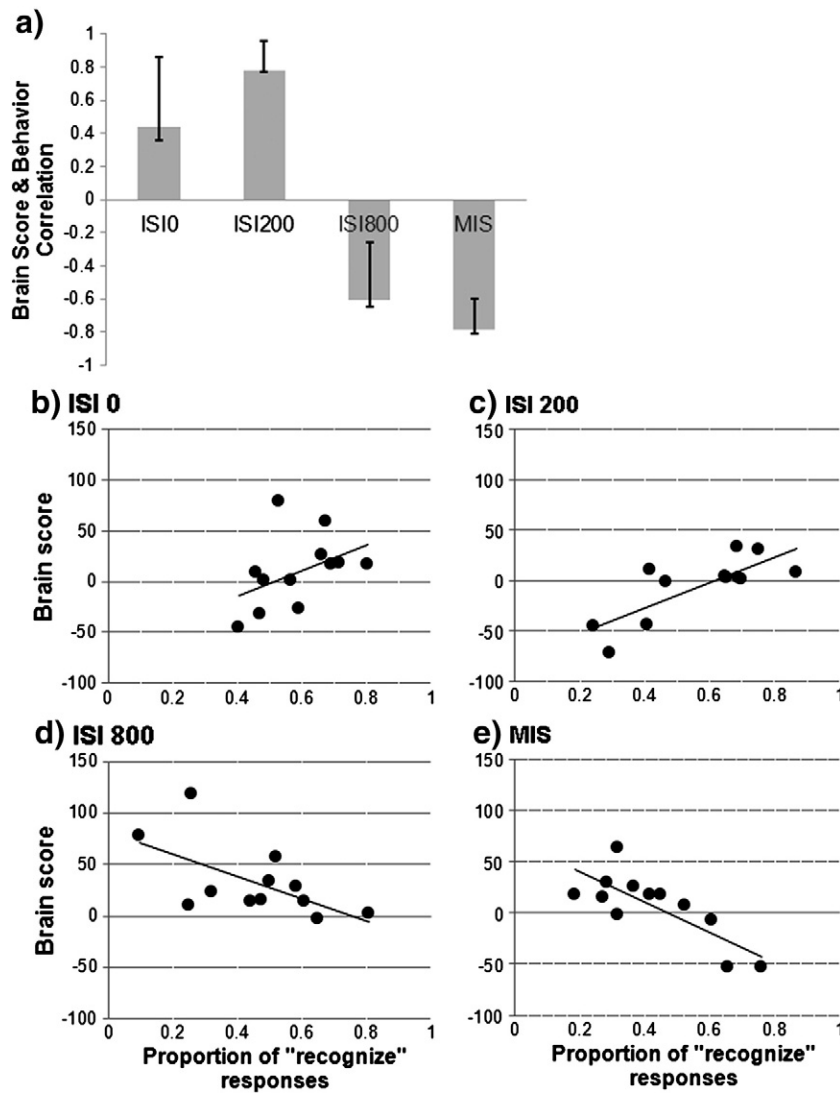


Fig. 5. Results of the behavior PLS analysis. Opposite brain-behavior correlations revealed in ISI 0 and ISI 200 vs. ISI 800 and MIS. (a) The LV profile plot summarizes brain score and behavior correlations across conditions (error bar = 95% CIs from bootstrapping). (b–e) The scatter plots show correlations of brain score and recognition response in each condition.

800. The increased response in ISI 800 might be due to the double pulse associated with presentation of two stimuli separated by a long interval (Ogawa et al., 2000). This increase also may be related to increased feedback from downstream regions implicated in attention (e.g., anticipation of the second face part; O'Craven et al., 1999), visual imagery (Ishai et al., 2002) and/or working memory (to maintain the representations of individual facial parts; Vuilleumier et al., 2001). The involvement of left FFA in ISI 800 hints at the functional dissociation of right and left FFA, such that left FFA may be more sensitive to part-based processing than the right. Overall, however, peak activation in the FFA proper, which was within the range of coordinates reported for other studies (see footnote 2), was not correlated with recognition performance with the exception, which we noted, of a negative correlation at ISI 200 in right FFA at TR2.

Behavior PLS identified a region in the right fusiform area that was positively correlated with performance in the short-interval conditions. This region, however, was not in the FFA as traditionally defined by face localizers (see footnote 2), but in its vicinity, consistent with previous fMRI findings comparing configural to analytic face processing (Harris and Aguirre, 2008; Liu et al., 2009; Maurer et al., 2007; Ng et al., 2006). It has been argued that traditional localizers based on stimulation from a collection of randomly

chosen faces would activate areas comprising broadly tuned face-responsive neurons (Ng et al., 2006; Tong et al., 2000), such that the FFA would be a face detector pertaining to information about *both* face parts and face configuration. This interpretation is consistent with recent reports that these regions do not respond as a function of stimulus change as much as to task demands, which can draw on both types of representations (Cohen Kadosh et al., 2009; Ganel et al., 2005). Signals from the FFA would then be sent to the appropriate network for specific aspects of face processing (Cohen Kadosh et al., 2009; Kriegeskorte et al., 2007; Maurer et al., 2007; Rossion, 2008; Steeves et al., 2006; Tong et al., 2000). Thus, temporal integration of face parts draws on this initial information from FFA proper, but depends on a further network of cortical areas, comprised of regions adjacent to the FFA proper and of an extensive set of regions in the temporal and frontal cortices.

Different processes underlying the short vs. long interval conditions

Task PLS results distinguished ISI 800 from the other conditions presumably because the large temporal separation effectively resulted in the presentation of two separable face-part events containing information which had to be retained over the interval,

Table 2
Brain areas where activity is correlated with recognition performance (behavior PLS).

Region	Hemi-sphere	MNI coordinates			BSR
		x	y	z	
<i>Regions associated with better performance in ISI0 and ISI200 and worse performance in ISI800 and MIS</i>					
Fusiform	R	28	-66	-6	6.61
Middle occipital	R	40	-80	10	7.57
Superior occipital	R	28	-70	26	6.98
	L	-14	-82	26	6.62
Parahippocampal	R	28	-40	-4	5.95
Lingual	R	14	-40	-2	5.99
Middle temporal	L	-58	-56	2	7.24
Superior temporal (sulcus)	R	66	-12	8	5.82
	L	-40	-32	4	7.36
Anterior cingulate	L	-2	24	16	4.51
Middle cingulate	R	8	-4	38	6.35
	R	6	4	34	6.85
	L	-12	-34	42	6.47
Insula	R	34	20	-14	6.53
Middle orbital frontal	R	8	56	-8	4.81
Middle frontal	L	-26	48	4	5.43
Precentral	R	20	-24	64	6.62
Postcentral	L	-26	-30	64	7.15
Supplementary motor area	R	12	-20	60	7.49
	R	10	-10	72	6.23
	L	-2	-6	58	5.88
Heschls	L	-32	-26	8	6.18
Cerebellum	R	38	-82	-22	5.22
	L	-24	-32	-32	7.79

R = right; L = left; BSR = bootstrap ratio; voxels = number of voxels (one voxel volume = 8 mm³). All reported activations are from LV1, ≥100 voxels (800 mm³) and peak BSR between TR 2 and TR 4 (no reliable cluster was found in TR 1).

whereas in the other conditions, there is only one percept (ISI 0, and MIS) or a temporally-integrated event across a brief interval (ISI 200) (e.g., Saneyoshi et al., 2011). This segregation of two separated percepts was associated with increased activity in a number of brain regions during the ISI 800 condition, relative to the other conditions. The involvement of the parietal regions for ISI 800 suggests that this double-pulse may have been accompanied by a heightened state of attention or anticipation of the second part (Corbetta and Shulman, 2002; Cabeza et al., 2008) or greater working memory load (Vilberg and Rugg, 2008), which may also have led to increased activity in other regions. In line with our fMRI results, viewing faces in piecemeal fashion through an aperture activated a number of areas to a greater extent than viewing a whole face for the same duration

(James et al., 2009), indicating that an active maintenance of information would produce higher BOLD responses (also see Saneyoshi et al., 2011). Similarly, during the delay period of a match-to-sample face task, sustained activity was found in a number of brain areas (reviewed in Haxby et al., 2000b) which corresponded to some of the regions found for ISI 800 by task PLS: left insula, inferior frontal and superior medial frontal gyri. Also, consistent with our interpretation, activity in posterior parietal regions, including the supramarginal gyrus, has been reported during maintenance in working memory of verbal and nonverbal information (Cohen et al., 1997; Danckert and Ferber, 2006), including faces (Rämä et al., 2001). Converging evidence, therefore, suggests that the ISI 800 condition, when face parts were likely perceived as two sequential events (Anaki and Moscovitch, 2007), produced sustained neural responses in the brain, whereas the other conditions, in which the face parts were perceived as a single event, elicited transient responses.

Areas showing greater activity in the long interval condition included core face areas for visual face recognition, such as bilateral fusiform, left inferior occipital, bilateral middle occipital gyrus and left STS, and extended areas including left anterior cingulate, right insula, and right lateral inferior frontal and bilateral precentral gyri (Barbeau et al., 2008; Gobbi and Haxby, 2007; Haxby et al., 1996; Leveroni et al., 2000; Ramon et al., 2010). The clusters found in the fusiform and inferior temporal gyrus overlapped with the FFA proper and were consistent with the ROI results of more activity in the ISI 800 condition in the left FFA. Finding a right fusiform cluster for the long interval condition is not surprising. In Orlov et al. (2010) which delineated regions responding to human body parts in the occipitotemporal cortex, the top and bottom parts of the face were represented in adjacent but distinct clusters in the inferior occipital and fusiform gyri bilaterally, overlapping with the occipital face area (OFA) and the FFA. This indicates that neural representations in the fusiform gyrus, including the FFA, are heterogeneous (Betts and Wilson, 2009) in that different populations of neurons represent different types of information.

While core and extended face regions were found for ISI 800, greater activation of such areas in the long interval condition did not lead to better face recognition. Instead, behavior PLS provided evidence that a different set of regions distinguished the long (800) interval and misaligned conditions from the 0 and short (200) interval conditions. Significantly, we found opposite patterns of correlations between the two different types of processes, such that activity was positively correlated with recognition performance in regions associated with ISI 0 and 200, but negatively correlated in ISI 800 and MIS. The results show that temporal integration of face parts over a brief

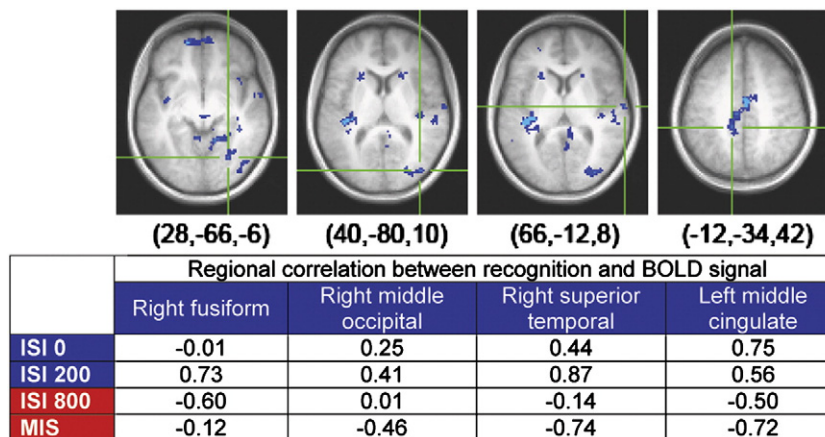


Fig. 6. Brain regions showing the pattern of correlated activity with recognition performance. As activity in regions colored in blue increased, recognition improved in ISI 0 and ISI 200 and decreased in ISI 800 and MIS. Regions were averaged from TR 2 to TR 4 (no reliable cluster was found in TR 1). All maxima (in blue) have BSR ≥ 3.0 and cluster size ≥ 100 voxels (800 mm³). The coordinates indicate a location of the peak voxel (in MNI space). Pearson correlations between recognition score and BOLD signal were shown to illustrate the patterns of correlations in each region identified by whole-brain PLS analysis.

interval (from ISI 0 to 200), leading to successful recognition, is dependent on coordinated activity of a distributed network, including visual areas (such as right fusiform, right middle occipital, bilateral superior temporal regions) and domain-general cognitive frontal areas (such as left anterior cingulate, bilateral middle cingulate, right orbital frontal, left middle frontal and right precentral gyrus). Some of this coordinated activity may result from re-entrant inputs from the higher areas to the primary visual cortex which in turn would enhance the integration performance for shorter ISIs. Specifically, for short intervals (ISI 200) the more active the areas of the network were, the better the recognition, similar to the pattern of activation found for face parts that were presented with no temporal interval (ISI 0). This time course of temporal integration is commensurate with our behavioral findings, namely, that temporal integration leading to configural face representations can occur for complex visual stimuli, such as faces, over intervals lasting in the range of 200–400 ms (Anaki and Moscovitch, 2007; Anaki et al., 2007).

For longer temporal intervals (ISI 800) and for misaligned faces, the opposite pattern of results was found, such that the more active the configural face processing areas were, the worse the performance. To our knowledge, this is the first demonstration that engaging face processing areas implicated in configural processing is *detrimental* when the input is conducive to analytic or part-based processing. Consistent with this interpretation is that the results observed in ISI 800 were comparable to those found with misaligned faces which have been shown to disrupt configural processing, and allow analytic processes to dominate.

The long interval condition also uniquely involved the parietal cortex, as identified by task PLS, which was not part of the configural processing network in behavior PLS. The superior parietal lobule is implicated in the voluntary allocation of attention to strategic memory retrieval, and the supramarginal gyrus, part of the inferior parietal lobule, mediates the automatic capture of attention to salient stimuli (Cabeza et al., 2008; Ciaramelli et al., 2008). Consistently, the superior parietal lobule is also implicated in visual imagery of faces and objects (Ishai et al., 2000), as imagery requires prior knowledge of the stimulus, and the supramarginal gyrus is involved in visual and verbal working memory. Activation of the superior parietal lobule is associated with top-down strategic access to memory (Cabeza et al., 2008; Ciaramelli et al., 2008), and of the supramarginal gyrus, with maintenance of information in working memory (Cohen et al., 1997; Danckert and Ferber, 2006), consistent with the strategic and part-based (analytic) nature of face processing in the long interval condition. Thus, although part-based face recognition is possible when parts are misaligned or temporally separated by a long interval, it is not optimal. Significantly, within the configural processing network, the analytic and configural processing are in mutual opposition. We return to this point at the end of the discussion.

Regions contributing to temporal integration vs. strategic analysis of facial parts

Behavior and task PLS results identified several common regions of activation in the short interval (ISI 0, ISI 200) and long interval (ISI 800) conditions, respectively. One might think that such common areas likely reflect processes, or information, that also are common to these conditions. However, despite these regional similarities, the overall correlation pattern associated with ISI 0 and ISI 200 in behavioral PLS does not overlap substantially with the set of regions activated during ISI 800 in task PLS, suggesting types of face processing differ (e.g., configural for ISI 0 and ISI 200 vs. part-based for ISI 800). For example, the regions associated with better recognition in the short-interval conditions are in agreement with previous evidence for areas implicated in configural face processing. First, activity in *right* occipitotemporal regions (fusiform, middle occipital, lingual,

parahippocampal gyri) was predominantly observed in conjunction with successful recognition of face parts over a short interval, while the activity increase for ISI 800 was more bilateral (and included left inferior occipital, left STS). The ROI analysis also showed that ISI 800 yielded greater responses in left FFA but not in right FFA. This laterality effect fits with an important role of the right occipitotemporal cortex demonstrated in *spatial* integration of individual face parts into a global face representation (e.g., Harris and Aguirre, 2008; Maurer et al., 2007; Schiltz and Rossion, 2006; Schiltz et al., 2010). Also, the time course is in the range observed by Cohen Kadosh et al. (2011) in which transcranial magnetic stimulation (TMS) over right occipitotemporal cortex can disrupt integration. Secondly, other areas such as the middle cingulate cortex and right anterior insula associated with performance in the short interval conditions, coincide with areas previously reported to contribute to configural face recognition (Rotshtein et al., 2007).

Additional areas associated with ISI 0 and ISI 200 were part of the proposed extended face processing network implicated in perception of dynamic facial movements (STS), assessment of facial beauty (orbitofrontal cortex) (Gobbini and Haxby, 2007; Haxby et al., 2000a, 2000b), categorical perception of familiar faces (precentral gyrus, Ramon et al., 2010) and of emotionally expressive faces (precentral gyrus, Cohen Kadosh et al., 2009). The cluster found in right superior temporal gyrus by the behavioral PLS was anterior to the pSTS region conventionally thought to be involved in gaze perception and changeable aspects of faces (Haxby et al., 2000a, 2000b). Although future studies are needed, it is speculated that the anterior parts of the superior temporal gyrus might receive signals from its posterior part and play a role in holding features in a temporary buffer to help process the facial configuration (e.g., Keysers et al., 2005). The role of left middle frontal gyrus in face processing is not clear but increased activity in the right middle frontal gyrus, as well as the cerebellum, is found during face recognition (Haxby et al., 1996). Likewise, clusters in the supplementary motor area were found not only on the left, where they would be expected in participants responding with the right hand, but also on the right. Recent evidence indicates that a subset of neurons in the supplementary motor area is involved in perception but not motor execution (Mukamel et al., 2010).

As the aforementioned areas are known for general cognitive functions while being activated during face processing, we do not argue that the configural processing network associated with the short interval conditions is specific to faces. We note that our study did not contrast the face integration task with a non-face integration task but delineated temporal integration areas in the context of configural face processing. Thus far, only one fMRI study investigated temporal integration of objects (Saneyoshi et al., 2011). They presented arrays of circles with a short (10, 130 ms) or long ISI (2530 ms), so temporally integrated representations would not require configural processing as in faces. The results showed that the frontoparietal attention network was activated in all conditions (and to a greater extent in the long ISI condition). Similarly, we found frontal and parietal areas greatly activated in ISI 800, largely different from those for ISI 0 and ISI 200. Hence, we are inclined to conjecture that the network associated with the short interval conditions likely reflect configural processes, crucial for faces, although whether it is specific to faces is yet to be determined.

While recognition performance was associated with a number of regions in the short interval conditions, no unique region was reliably correlated with performance in ISI 800 and MIS. These results cannot be explained by lack of power because the number of trials after excluding unknown faces (based on the post-scan test) was equal across conditions. Interestingly, Rotshtein et al. also did not find any region showing a correlation between discrimination of featural change (measured outside the scanner), a part-based process, and BOLD responses during such stimulus changes. One reason for such a lack of correlation is that part-based processes might lend

themselves more easily to a variety of cognitive strategies to support face recognition in ISI 800 and MIS, unlike the presumably more consistent configural strategy that would be used for the shorter intervals. We also note that visual stimulus processing (without taking account of behavior) may differ in the two conditions (i.e., temporal processing in ISI 800 vs. spatial processing in MIS).

Our results indicate that the neural substrates utilized in part-based face recognition in ISI 800 and MIS (i.e., analytic approach) were distinct from configural processes used in the short interval conditions (also see Maurer et al., 2007). It is possible, however, that these distinct networks draw on information represented in a common set of structures, with the respective involvement depending on the cognitive strategy used. This interpretation is plausible in that the FFA and OFA respond flexibly to different aspects of the face (e.g., identity, expression, gaze) depending on task demands (Cohen Kadosh et al., 2009; Ganel et al., 2005). While this may be true for the FFA proper, which is involved in both configural and part-based processing (Harris and Aguirre, 2008; Liu et al., 2009), our results demonstrate that distributed regions associated with the short interval condition did not encompass the FFA (as discussed in Section 4.2 and footnote 2) but showed negative correlation with recognition for the long interval or misaligned conditions. Thus, the use to which information from a common network is put may depend on processes mediated by different regions. Moreover, TMS of right OFA disrupted discrimination of part changes within a face but not that of spacing between parts (Pitcher et al., 2007), indicating relative independence of part-based and relational (and possibly configural) processing.

Incompatibility of configural and strategic processing

Our observation that the regions supporting configural face processing operate in mutual opposition with analytic processing may help explain the interference between perception of concurrently presented faces and objects (Moscovitch and Klein, 1980; see Experiments 16 and 18 in Moscovitch et al., 1997) especially if the latter are associated with expertise (Behrmann et al., 2005; Gauthier et al., 2004; Rossion et al., 2007). A number of interpretations have been proposed to account for this interference effect, the main one being that both objects and faces compete for the same perceptual mechanisms. Our results suggest an alternate, though not mutually exclusive, interpretation: Insofar as perception of objects is primarily part-based (Biederman, 1987; Hayworth and Biederman, 2006), processing objects is likely to involve analytic processing which may inhibit the configural processing regions necessary for good face identification. It is interesting to note in this regard that Rossion et al. (2007) found that the interfering effects of processing objects on the N170, a neural marker of face processing, occurred only if the two types of stimuli were presented within about 200 ms of each other, the time during which temporal integration of face-parts occurs in the service of forming a configural representation. It is the same time course in which TMS over occipitotemporal cortex can disrupt integration (Cohen Kadosh et al., 2011). The greater interference associated with objects of expertise may arise because such objects are the best activators of part-based processing regions, which inhibit or suppress regions associated with configural processing. Additionally, and in line with the observation that a common set of regions represents information used for part-based and configural processing (Cohen Kadosh et al., 2009; Ganel et al., 2005), it may be the case that different populations of neurons within the same regions code for the different types of information, such that activating one set in the service of one task, mutually inhibits the activation of another set used for the other task. Future studies using voxel-based pattern analysis may help test this hypothesis.

Conclusion

We provide the first demonstration of a cortical network that is associated with recognition of temporally separated face parts over brief intervals. We found that neural substrates involved were similar for recognition of faces perceived as wholes (ISI 0) and as integrated parts (ISI 200) and these regions did not contribute to recognition of the face whose parts were separated over longer temporal intervals (ISI 800) or misaligned. It is possible that configural processing of faces to achieve identification is accomplished by not only concurrently processing all facial features that are presented simultaneously but also by integrating these features across time. In addition to this type of integration, our study indicates that analytic processes focused on face parts, though not as effective, can support identification via other (as yet unidentified) regions that are concerned more with strategic processing that may vary across individuals. We also show that activity in the regions supporting configural face processing is negatively correlated with recognition carried out by strategic and analytic processing, which may account for behavioral evidence that configural and analytic face processes interfere with one another (de Gelder and Rouw, 2000). Thus, the present study has important implications for models of face and object processing that have focused mainly on spatial, but not temporal, integration of features to construct holistic or analytic representations (e.g., Maurer et al., 2002; Moscovitch and Moscovitch, 2000; Moscovitch et al., 1997).

Supplementary materials related to this article can be found online at doi:10.1016/j.neuroimage.2012.02.073.

Acknowledgments

This work was supported by a Canadian Institutes of Health Research grant to M.M. and C.L.G. (MOP106301), the Canadian Research Chair program, the Ontario Research Fund, the Canadian Foundation for Innovation, and the Heart and Stroke Foundation Centre for Stroke Recovery.

References

- Anaki, D., Moscovitch, M., 2007. When a face is (or is not) more than the sum of its features: configural and analytic processes in facial temporal integration. *Vis. Cogn.* 15, 741–763.
- Anaki, D., Boyd, J., Moscovitch, M., 2007. Temporal integration in face perception: evidence of configural processing of temporally separated face parts. *J. Exp. Psychol. Hum. Percept. Perform.* 33, 1–19.
- Andrews, T.J., Ewbank, M.P., 2004. Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe. *Neuroimage* 23, 905–913.
- Andrews, T.J., Davies-Thompson, J., Kingstone, A., Young, A.W., 2010. Internal and external features of the face are represented holistically in face-selective regions of visual cortex. *J. Neurosci.* 30, 3544–3552.
- Axelrod, V., Yovel, G., 2010. External facial features modify the representation of internal facial features in the fusiform face area. *Neuroimage* 52, 720–725.
- Barbeau, E.J., Taylor, M.J., Regis, J., Marquis, P., Chauvel, P., Liegeois-Chauvel, C., 2008. Spatio temporal dynamics of face recognition. *Cereb. Cortex* 18, 997–1009.
- Behrmann, M., Marotta, J., Gauthier, I., Tarr, M.J., McKeef, T.J., 2005. Behavioral change and its neural correlates in visual agnosia after expertise training. *J. Cogn. Neurosci.* 17, 554–568.
- Betts, L.R., Wilson, H.R., 2009. Heterogenous structure in face-selective human occipito-temporal cortex. *J. Cogn. Neurosci.* 22, 2276–2288.
- Biederman, I., 1987. Recognition-by-components: a theory of human image understanding. *Psychol. Rev.* 94, 115–147.
- Blake, R., Lee, S.-H., 2005. The role of temporal structure in human vision. *Behav. Cogn. Neurosci. Rev.* 4, 21–42.
- Bookstein, F.L., 1994. Partial least squares: a dose-response model for measurement in the behavioral and brain sciences. *Psychology* 5.
- Cabeza, R., Ciaramelli, E., Olson, I.R., Moscovitch, M., 2008. The parietal cortex and episodic memory: an attentional account. *Nat. Rev. Neurosci.* 9, 613–625.
- Ciaramelli, E., Grady, C.L., Moscovitch, M., 2008. Top-down and bottom-up attention to memory: a hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia* 46, 1828–1851.
- Cohen Kadosh, K., Henson, R.N., Cohen Kadosh, R., Johnson, M.H., Dick, F., 2009. Task-dependent activation of face-sensitive cortex: an fMRI adaptation study. *J. Cogn. Neurosci.* 22, 903–917.
- Cohen Kadosh, K., Walsh, V., Cohen Kadosh, R., 2011. Investigating face-property specific processing in the right OFA. *Soc. Cogn. Affect. Neurosci.* 6, 58–65.

- Cohen, J.D., Perlstein, W.M., Braver, T.S., Nystrom, L.E., Noll, D.C., Jonides, J., Smith, E.E., 1997. Temporal dynamics of brain activation during a working memory task. *Nature* 386, 604–608.
- Coltheart, M., 1980. Iconic memory and visible persistence. *Percept. Psychophys.* 27, 183–228.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3, 201–215.
- Courtney, S.M., Ungerleider, L.G., Keil, K., Haxby, J.V., 1997. Transient and sustained activity in a distributed neural system for human working memory. *Nature* 386, 608–611.
- Cox, R.W., 1996. AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Comput. Biomed. Res.* 29, 162–173.
- Danckert, J., Ferber, S., 2006. Revisiting unilateral neglect. *Neuropsychologia* 44, 987–1006.
- de Gelder, B., Rouw, R., 2000. Structural encoding precludes recognition of face parts in prosopagnosia. *Cogn. Neuropsychol.* 17, 89–102.
- Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., Zilles, K., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *NeuroImage* 25, 1325–1335.
- Epstein, R., Graham, K.S., Downing, P.E., 2003. Viewpoint-specific scene representations in human parahippocampal cortex. *Neuron* 37, 865–876.
- Fairhall, S.L., Ishai, A., 2007. Effective connectivity within the distributed cortical network for face perception. *Cereb. Cortex* 17, 2400–2406.
- Ganel, T., Valyear, K.F., Goshen-Gottstein, Y., Goodale, M.A., 2005. The involvement of the “fusiform face area” in processing facial expression. *Neuropsychologia* 43, 1645–1654.
- Gauthier, I., Skudlarski, P., Gore, J.C., Anderson, A.W., 2000. Expertise for cars and birds recruits brain areas involved in face recognition. *Nat. Neurosci.* 3, 191–197.
- Gauthier, I., Behrmann, M., Tarr, M.J., 2004. Are Greebles like faces? Using the neuropsychological exception to test the rule. *Neuropsychologia* 42, 1961–1970.
- Gobbini, M.I., Haxby, J.V., 2007. Neural systems for recognition of familiar faces. *Neuropsychologia* 45, 32–41.
- Grill-Spector, K., Knouf, N., Kanwisher, N., 2004. The fusiform face area subserves face perception, not generic within-category identification. *Nat. Neurosci.* 7, 555–562.
- Haist, F., Lee, K., Stiles, J., 2010. Individuating faces and common objects produces equal responses in putative face-processing areas in the ventral occipitotemporal cortex. *Front. Hum. Neurosci.* 4, 181. doi:10.3389/fnhum.2010.00181.
- Harris, A., Aguirre, G.K., 2008. The representation of parts and wholes in face-selective cortex. *J. Cogn. Neurosci.* 20, 863–878.
- Haxby, J.V., Ungerleider, L.G., Horowitz, B., Maisog, J.M., Rapoport, S.L., Grady, C.L., 1996. Face encoding and recognition in the human brain. *Proc. Natl. Acad. Sci. U. S. A.* 93, 922–927.
- Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000a. The distributed human neural system for face perception. *Trends Cogn. Sci.* 4, 223–233.
- Haxby, J.V., Petit, L., Ungerleider, L.G., Courtney, S.M., 2000b. Distinguishing the functional roles of multiple regions in distributed neural systems for visual working memory. *NeuroImage* 11, 145–156.
- Hayworth, K.J., Biederman, I., 2006. Neural evidence for intermediate representations in object recognition. *Vision Res.* 46(23), 4024–4031.
- Hoffman, E.A., Haxby, J.V., 2000. Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nat. Neurosci.* 3, 80–84.
- Horner, A.J., Andrews, T.J., 2009. Linearity of the fMRI response in category-selective regions of the human visual cortex. *Hum. Brain Mapp.* 30, 2628–2640.
- Hulme, O.J., Zeki, S., 2007. The sightless view: neural correlates of occluded objects. *Cereb. Cortex* 17, 1197–1205.
- Ishai, A., Ungerleider, L.G., Haxby, J.V., 2000. Distributed neural systems for the generation of visual images. *Neuron* 28, 979–990.
- Ishai, A., Haxby, J.V., Ungerleider, L.G., 2002. Visual imagery of famous faces: effects of memory and attention revealed by fMRI. *NeuroImage* 17, 1729–1741.
- Jacques, C., Rossion, B., 2010. Misaligned face halves increases and delays the N170 specifically for upright faces: implications for the nature of early face representations. *Brain Res.* 1318, 96–109.
- James, T., Huh, E., Jim, S., 2009. The fusiform face area is recruited more for sequential than holistic processing: an aperture viewing study. *J. Vis.* 9 (8), 556. doi:10.1167/9.8.559 [abstract].
- Kanwisher, N., Yovel, G., 2006. The fusiform face area: a cortical region specialized for the perception of faces. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 361, 2109–2128.
- Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17, 4302–4311.
- Keysers, C., Xiao, D.-K., Földiák, P., Perrett, D.I., 2005. Out of sight but not out of mind: the neurophysiology of iconic memory in the superior temporal sulcus. *Cogn. Neuropsychol.* 22, 316–332.
- Kriegeskorte, N., Formisano, E., Sorger, B., Goebel, R., 2007. Individual faces elicit distinct response patterns in human anterior temporal cortex. *Proc. Natl. Acad. Sci. U. S. A.* 104, 20600–20605.
- Krishnan, A., Williams, L.J., McIntosh, A.R., Abdi, H., 2011. Partial least squares (PLS) methods for neuroimaging: a tutorial and review. *NeuroImage* 56, 455–475.
- Large, M.-E., Cavina-Pratesi, C., Vilis, T., Culham, J.C., 2008. The neural correlates of change detection in the face perception network. *Neuropsychologia* 46, 2169–2176.
- Leveroni, C.L., Seidenberg, M., Mayer, A.R., Mead, L.A., Binder, J.R., Rao, S.M., 2000. Neural systems underlying the recognition of familiar and newly learned faces. *J. Neurosci.* 20, 878–886.
- Li, J., Liu, J., Liang, J., Zhang, H., Zhao, J., Rieth, C.A., Huber, D.E., Li, W., Shi, G., Ai, L., Tian, J., Lee, K., 2010. Effective connectivities of cortical regions for top-down face processing: a dynamic causal modeling study. *Brain Res.* 1340, 40–51.
- Liu, J., Harris, A., Kanwisher, N., 2009. Perception of face parts and face configurations: an fMRI study. *J. Cogn. Neurosci.* 22, 203–211.
- Loffler, G., Yourganov, G., Wilkinson, F., Wilson, H.R., 2005. fMRI evidence for the neural representation of faces. *Nat. Neurosci.* 8, 1386–1390.
- Macrae, C.N., Lewis, H.L., 2002. Do I know you? Processing orientation and face recognition. *Psychol. Sci.* 13, 194–196.
- Maurer, D., Le Grand, R., Mondloch, C.J., 2002. The many faces of configural processing. *Trends Cogn. Sci.* 6, 255–260.
- Maurer, D., O’Craven, K.M., Le Grand, R., Mondloch, C.J., Springer, M.V., Lewis, T.L., Grady, C.L., 2007. Neural correlates of processing facial identity based on features versus their spacing. *Neuropsychologia* 45, 1438–1451.
- McIntosh, A.R., Bookstein, F.L., Haxby, J.V., Grady, C.L., 1996. Spatial pattern analysis of functional brain images using partial least squares. *NeuroImage* 3, 143–157.
- McIntosh, A.R., Chau, W.K., Protzner, A.B., 2004. Spatiotemporal analysis of event-related fMRI data using partial least squares. *NeuroImage* 23, 764–775.
- Melcher, D., Colby, C.L., 2008. Trans-saccadic perception. *Trends Cogn. Sci.* 12, 466–473.
- Moscovitch, M., Klein, D., 1980. Material-specific perceptual interference for visual words and faces: implications for models of capacity limitations, attention, and laterality. *J. Exp. Psychol. Hum. Percept. Perform.* 6, 590–604.
- Moscovitch, M., Moscovitch, D.A., 2000. Super face-inversion effects for isolated internal or external features, and for fractured faces. *Cogn. Neuropsychol.* 17, 201–219.
- Moscovitch, M., Winocur, G., Behrmann, M., 1997. What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *J. Cogn. Neurosci.* 9, 555–604.
- Mukamel, R., Harel, M., Hendler, T., Malach, R., 2004. Enhanced temporal non-linearities in human object-related occipito-temporal cortex. *Cereb. Cortex* 14, 575–585.
- Mukamel, R., Ekstrom, A.D., Kaplan, J., Jacoboni, M., Fried, I., 2010. Single-neuron responses in humans during execution and observation of actions. *Curr. Biol.* 20, 750–756.
- Nestor, A., Vettel, J.M., Tarr, M.J., 2008. Task-specific codes for face recognition: how they shape the neural representation of features for detection and individuation. *PLoS One* 3, e3978.
- Nestor, A., Plaut, D.C., Behrmann, M., 2011. Unraveling the distributed neural code of facial identity through spatiotemporal pattern analysis. *Proc. Natl. Acad. Sci. U. S. A.* 108, 9998–10003.
- Ng, M., Ciaramitaro, V.M., Anstis, S., Boynton, G.M., Fine, I., 2006. Selectivity for the configural cues that identify the gender, ethnicity, and identity of faces in human cortex. *Proc. Natl. Acad. Sci. U. S. A.* 103, 19552–19557.
- O’Craven, K.M., Downing, P.E., Kanwisher, N., 1999. fMRI evidence for objects as the units of attentional selection. *Nature* 401, 584–587.
- Ogawa, S., Lee, T.-M., Stepnoski, R., Chen, W., Zhu, X.-H., Ugurbil, K., 2000. An approach to probe some neural systems interaction by functional MRI at neural time scale down to milliseconds. *Proc. Natl. Acad. Sci.* 97, 11026–11031.
- Olsen, R.K., Nichols, E.A., Chen, J., Hunt, J.F., Glover, G.H., Gabrieli, J.D.E., Wager, A.D., 2009. Performance-related sustained and anticipatory activity in human medial temporal lobe during delayed match-to-sample. *J. Neurosci.* 29, 11880–11890.
- Orlov, T., Makin, T.R., Zohary, E., 2010. Topographic representation of the human body in the occipitotemporal cortex. *Neuron* 68, 586–600.
- Petit, L., Courtney, S.M., Ungerleider, L.G., Haxby, J.V., 1998. Sustained activity in the medial wall during working memory delays. *J. Neurosci.* 18, 9429–9437.
- Pitcher, D., Walsh, V., Yovel, G., Duchaine, B., 2007. TMS evidence for the involvement of the right occipital face area in early face processing. *Curr. Biol.* 17, 1568–1573.
- Rämä, P., Sala, J.B., Gillen, J.S., Pekar, J.J., Courtney, S.M., 2001. Dissociation of the neural systems for working memory maintenance of verbal and nonspatial visual information. *Cogn. Affect. Behav. Neurosci.* 1, 161–171.
- Ramon, M., Dricot, L., Rossion, B., 2010. Personally familiar faces are perceived categorically in face-selective regions other than the fusiform face area. *Eur. J. Neurosci.* 32, 1587–1598.
- Rhodes, G., Michie, P.T., Hughes, M.E., Byatt, G., 2009. The fusiform face area and occipital face area show sensitivity to spatial relations in faces. *Eur. J. Neurosci.* 30, 721–733.
- Rossion, B., 2008. Constraining the cortical face network by neuroimaging studies of acquired prosopagnosia. *NeuroImage* 40, 423–426.
- Rossion, B., Dricot, L., Devolder, A., Bodart, J.M., Crommelinck, M., de Gelder, B., Zoontjes, R., 2000. Hemispheric asymmetries for whole-based and part-based face processing in the human fusiform gyrus. *J. Cogn. Neurosci.* 12, 793–802.
- Rossion, B., Collins, D., Goffaux, V., Curran, T., 2007. Long-term expertise with artificial objects increases visual competition with early face categorization processes. *J. Cogn. Neurosci.* 19, 543–555.
- Rotshtein, P., Henson, R.N.A., Treves, A., Driver, J., Dolan, R.J., 2005. Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nat. Neurosci.* 8, 107–113.
- Rotshtein, P., Geng, J.J., Driver, J., Dolan, R.J., 2007. Role of features and second-order spatial relations in face discrimination, face recognition, and individual face skills: behavioral and functional magnetic resonance imaging data. *J. Cogn. Neurosci.* 19, 1435–1452.
- Ruff, C.C., Kristjánsson, Á., Driver, J., 2007. Readout from iconic memory and selective spatial attention involve similar neural processes. *Psychol. Sci.* 18, 901–909.
- Sampson, P.D., Streissguth, A.P., Barr, H.M., Bookstein, F.L., 1989. Neurobehavioral effects of prenatal alcohol: part II. Partial least squares analysis. *Neurotoxicol. Teratol.* 11, 477–491.
- Saneyoshi, A., Niimi, R., Suetsugu, T., Kaminaga, T., Yokosawa, K., 2011. Iconic memory and parietofrontal network: fMRI study using temporal integration. *Neuroreport* 22, 515–519.
- Schiltz, C., Rossion, B., 2006. Faces are represented holistically in the human occipito-temporal cortex. *NeuroImage* 32, 1385–1394.

- Schiltz, C., Dricot, L., Goebel, R., Rossion, B., 2010. Holistic perception of individual faces in the right middle fusiform gyrus as evidenced by the composite face illusion. *J. Vis.* 10 (2) (25: 1–16).
- Singer, J.M., Sheinberg, D.L., 2006. Holistic processing unites face parts across time. *Vision Res.* 46, 1838–1847.
- Spiridon, M., Fischl, B., Kanwisher, N., 2006. Location and spatial profile of category-specific regions in human extrastriate cortex. *Hum. Brain Mapp.* 27, 77–89.
- Steeves, J.K.E., Culham, J.C., Duchaine, B.C., Pratesi, C.C., Valyear, K.F., Schindler, I., Humphrey, G.K., Milner, A.D., Goodale, M.A., 2006. The fusiform face area is not sufficient for face recognition: evidence from a patient with dense prosopagnosia and no occipital face area. *Neuropsychologia* 44, 594–609.
- Tanaka, J.W., Farah, M.J., 1993. Parts and wholes in face recognition. *Q. J. Exp. Psychol. A* 46, 225–245.
- Tong, F., Nakayama, K., Moscovitch, M., Weinrib, O., Kanwisher, N., 2000. Response properties of the human fusiform face area. *Cogn. Neuropsychol.* 17, 257–279.
- Vilberg, K.L., Rugg, M.D., 2008. Memory retrieval and the parietal cortex: a review of evidence from a dual-process perspective. *Neuropsychologia* 46, 1787–1799.
- Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2001. Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron* 30, 829–841.
- Yi, D.-J., Kelley, T.A., Marois, R., Chun, M.M., 2006. Attentional modulation of repetition attenuation is anatomically dissociable for scenes and faces. *Brain Res.* 1080, 53–62.
- Yi, D.-J., Turk-Browne, N.B., Flombaum, J.I., Kim, M.-S., Scholl, B.J., Chun, M.M., 2008. Spatiotemporal object continuity in human ventral visual cortex. *Proc. Natl. Acad. Sci. U. S. A.* 105, 8840–8845.
- Yin, R.K., 1969. Looking at upside-down faces. *J. Exp. Psychol.* 81, 141–145.
- Young, A.W., Hellawell, D., Hay, D.C., 1987. Configurational information in face perception. *Perception* 16, 747–759.
- Yovel, G., Kanwisher, N., 2004. Face perception: domain specific, not process specific. *Neuron* 44, 889–898.