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The correlates of subjective perception of identity and expression in the face network: an fMRI adaptation study

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Abstract

The recognition of facial identity and expression are distinct tasks, with current models hypothesizing anatomic segregation of processing within a face-processing network. Using fMRI adaptation and a region-of-interest approach, we assessed how the perception of identity and expression changes in morphed stimuli affected the signal within this network, by contrasting (a) changes that crossed categorical boundaries of identity or expression with those that did not, and (b) changes that subjects perceived as causing identity or expression to change, versus changes that they perceived as not affecting the category of identity or expression. The occipital face area (OFA) was sensitive to any structural change in a face, whether it was identity or expression, but its signal did not correlate with whether subjects perceived a change or not. Both the fusiform face area (FFA) and the posterior superior temporal sulcus (pSTS) showed release from adaptation when subjects perceived a change in either identity or expression, although in the pSTS this effect only occurred when subjects were explicitly attending to expression. The middle superior temporal sulcus (mSTS) showed release from adaptation for expression only, and the precuneus for identity only. The data support models where the OFA is involved in the early perception of facial structure. However, evidence for a functional overlap in the FFA and pSTS, with both identity and expression signals in both areas, argues against a complete independence of identity and expression processing in these regions of the core face-processing network.

Keywords

face perception; OFA; FFA; STS; adaptation; identity; expression; fMRI

INTRODUCTION

Face perception involves multiple cortical regions (Gobbini and Haxby, 2007; Haxby et al., 2000; Ishai et al., 2005; Rossion et al., 2003). Current models divide these into a core system which is predominantly involved in the processing of facial stimuli, and an extended system which contributes to, but is not solely involved in, face perception (Haxby et al., 2000). The

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core system is comprised of three cortical regions which consistently show increased activity to faces over objects in functional magnetic resonance imaging (fMRI) studies: the occipital face area (OFA), located on the inferior occipital gyrus; the fusiform face area (FFA), located on the lateral fusiform gyrus; and a face-selective region in the posterior superior temporal sulcus (pSTS) (Haxby et al., 2000; Ishai et al., 2005; Kanwisher et al., 1997). Functionally, the OFA has been modeled as an 'entry point' region involved in the early perception of facial features or structure, with the FFA and pSTS as two subsequent independent and complementary modules, one (FFA) involved in the perception of temporally invariant aspects of faces (i.e.- facial identity), the other (pSTS) involved in the perception of dynamic aspects of the face (i.e.- facial expression) (Haxby et al., 2000). Regions of the extended system (i.e.- areas involved in the retrieval of semantic information, emotional connotations, etc.) are then activated by the output of this core system (Haxby et al., 2000).

However, a number of aspects of this model have been debated. First, the role of the OFA as an entry point for the core system of face perception has been challenged by the finding of an FFA in a prosopagnosic patient who lacks an ipsilateral OFA, suggesting that FFA activation is not dependent on input from the OFA (Rossion et al., 2003). On the other hand, a role for the OFA in the early perception of faces has received support from studies using fMRI adaptation (Rotshtein et al., 2005), which is thought to reflect reduced neural responses with repeated presentations of a stimulus (Grill-Spector et al., 2006). By varying certain aspects of a stimulus while holding others constant, one can use adaptation to determine which aspects of that stimulus a cortical region specifically encodes. In the OFA, adaptation was observed when the second face was identical to the first, but any structural change in the second face resulted in a release from adaptation (Rotshtein et al., 2005), regardless of whether this structural change crossed a categorical boundary between identities or not (Rotshtein et al., 2005). The authors conclude that the OFA is sensitive to any structural change in a face (i.e.- early perception of facial structure) but is not sensitive to facial identity (Rotshtein et al., 2005). This study did not examine the effects of expression changes, however, although current models suggest that the OFA also provides input to the pSTS. Thus the first aim of the present study was to determine whether the findings of Rotshtein et al (2005) regarding OFA adaptation can be replicated for facial identity and extended to facial expression.

Second, the proposal that the processing of facial identity and expression are independent of each other has been questioned (Calder and Young, 2005; Fox and Barton, 2007; Fox et al., 2008; Ganel et al., 2004; Ganel et al., 2005; Gorno-Tempini et al., 2001; Ishai et al., 2005; Kaufmann and Schweinberger, 2004; Palermo and Rhodes, 2007; Vuilleumier et al., 2001; Winston et al., 2004). Calder and Young (2005) suggest a relative rather than absolute segregation of identity and expression processing, with some regions involved in the perception of both. Behavioral studies of aftereffects (Fox and Barton, 2007; Fox et al., 2008), interference effects (Ganel et al., 2004) and recognition (Kaufmann and Schweinberger, 2004) all show functional interactions between facial identity and expression. Likewise, fMRI studies provide evidence for functional overlap: the pSTS shows significant fMRI adaptation not only to expression but also to identity (Winston et al., 2004). Despite its purported focus on identity, the FFA shows more activity for expressive than neutral faces (Ishai et al., 2005; Vuilleumier et al., 2001), and attending to facial expression increases activity not only in the pSTS as expected (Narumoto et al., 2001), but also in the FFA (Ganel et al., 2005; Gorno-Tempini et al., 2001).

As discussed for the OFA, the study of categorical effects can be of interest, in that this can establish sensitivity to specific representations beyond just the physical properties of the stimulus. The same study that showed a lack of categorical effects for identity in the OFA reported such effects in the FFA (Rotshtein et al., 2005), but since categorical effects for expression were not studied, it is unclear if this effect in the FFA is specific for facial identity.

The second aim of the present study is thus to examine categorical effects for both facial identity and expression within both the FFA and pSTS to determine if the pattern of effects suggests a complementary selectivity or functional overlap between these regions.

Our two experimental aims directly examine predictions made by the most widely accepted model of face perception (Haxby et al., 2000). First, we will examine whether the OFA shows functional sensitivity to changes in facial identity and/or facial expression. Evidence for either form of functional sensitivity would go against the modeled role of the OFA as an input module to the face network that does not participate in these perceptual discriminations. Second, we will examine the proposed independence of the FFA and pSTS in processing facial identity and facial expression respectively. Specifically, evidence for sensitivity to expression changes in the FFA and to identity changes in the pSTS would go against the current model of independent processing. As these experimental aims ask questions of specific regions of face-selective cortex (Haxby et al., 2000; Ishai et al., 2005; Kanwisher et al., 1997), we will perform region-of-interest based analyses on these regions as identified by a standard functional localizer (Ishai et al., 2005; Kanwisher et al., 1997; Rossion et al., 2003; Yovel and Kanwisher, 2005).

METHODS

Participants

Sixteen right-handed healthy participants (8 females; Mean age \pm SD: 24.2 \pm 3.4 years) with normal or corrected-to-normal vision and no history of neurological disorders participated. Informed consent was obtained and the protocol approved by the institutional review boards of the University of British Columbia and Vancouver General Hospital, in accordance with The Code of Ethics of the World Medical Association, Declaration of Helsinki (Rickham, 1964). One participant was excluded from all analyses due to excessive head motion ($>2^\circ$) during the fMRI scanning session.

Stimuli

Stimuli used within the experimental scans were selected from the Karolinska Database of Emotional Faces (Lundqvist and Litton, 1998). Images of eight different identities (4 female), displaying four different expressions (angry, afraid, disgusted, happy) were chosen, for a total of 32 images. We used Adobe Photoshop CS2 9.0.2 (www.adobe.com) to remove background, hair and neck, while preserving facial features and external jaw contour. Distinguishing marks, such as moles, were removed using the Spot Healing Brush Tool. Images were then cropped to ensure that all faces were centrally located in the image frame, and resized to a standard width of 400 pixels.

In order to test the perception of structural changes that do or do not cross categorical boundaries of facial identity and facial expression, morphed faces were used (Rotshtein et al., 2005). A morph matrix was created by selecting 4 images (2 different expressions for one identity and the same 2 different expressions for another identity), as the corners of the matrix. We then used Abrosoft Fantamorph 3.0 (www.fantamorph.com) to generate 1/3:2/3 morphs to fill in a two-dimensional 4X4 matrix of 16 images, with the two dimensions representing identity and expression (Figure 1). Sixteen unique matrices were created for each gender, for a total of 32 morph matrices.

Images were then paired to create the five experimental conditions (Figure 1). One trial for each condition was selected from each morph matrix for a total of 32 trials per condition, and 160 unique trials in total. All five trials selected from the same morph matrix shared the same first image ($2/3_{ID1}:1/3_{ID2}$ and $2/3_{EX1}:1/3_{EX2}$, where ID = identity and EX = expression). In

the *identical* condition the second image was identical to the first. In the *similar-identity category* condition the second image was a 33% morph difference that did not cross the category boundary for identity ($3/3_{ID1}:0/3_{ID2}$ and $2/3_{EX1}:1/3_{EX2}$). (This identity boundary should be approximately located around a morph that contains equal amounts of the two identities.) In the *different-identity category* condition the second image was a 33% morph step across an identity boundary ($1/3_{ID1}:2/3_{ID2}$ and $2/3_{EX1}:1/3_{EX2}$), so that the image now contained more of identity 2 than identity 1. In the *similar-expression category* condition the second image was a 33% morph step within an expression boundary ($2/3_{ID1}:1/3_{ID2}$ and $3/3_{EX1}:0/3_{EX2}$). In the *different-expression category* condition the second image was a 33% morph step across an expression boundary ($2/3_{ID1}:1/3_{ID2}$ and $1/3_{EX1}:2/3_{EX2}$), so that it now contained more of expression 2 than 1. With this strategy, any change in the second stimulus occurs along either the expression or identity axis, but not both simultaneously, and second, both *similar* and *different* conditions have the same size of morph step, or structural change, so that the only difference between *similar* and *different* conditions is whether the change crossed a categorical boundary.

To establish familiarity with the chosen identities, and the development of identity categories, participants were given one uncropped neutral image for each of the 8 identities and a name for each one, and were asked to learn to recognize each person during the few days before testing. Immediately prior to the fMRI scan, participants performed a familiarity test on a 17" widescreen Compaq nx9600 notebook. Fourteen uncropped images (2 versions of angry, afraid, happy, disgusted, surprised, sad, and neutral images) of each of the 8 identities (112 images total) were presented in a random order using SuperLab Pro 2.0.4 (www.cedrus.com). Participants were given unlimited time to select the appropriate name with a key press. Immediate feedback was given in the form of the correct name presented on the screen for 500ms, after which the next image was presented. If >95% accuracy was achieved, participants began the fMRI session, otherwise the familiarity test was repeated until >95% accuracy was achieved.

FMRI Data Acquisition

All scans were acquired in a 3.0 Tesla Philips scanner. Stimuli were presented using Presentation 9.81 software and rear-projected onto a mirror mounted on the head coil. Whole brain anatomical scans were acquired using a T1-weighted echoplanar imaging (EPI) sequence, consisting of 170 axial slices of 1mm thickness (1mm gap) with an in-plane resolution of 1mm X 1mm (FOV=256). T2-weighted functional scans (TR=2s; TE=30ms) were acquired using an interleaved ascending EPI sequence, consisting of 36 axial slices of 3mm thickness (1mm gap) with an in-plane resolution of 1.875mm X 1.875mm (FOV = 240). The functional scans consisted of 224 functional volumes, with the first volume of each functional scan discarded to allow for scanner equilibration.

The first functional scan, a functional localizer, was used to identify face-selective regions-of-interest. During the localizer, participants viewed static photographs of non-living objects (e.g. - television, basketball) and faces (neutral and expressive) presented in separate blocks (Kanwisher et al., 1997; Saxe et al., 2006). Participants performed an irrelevant 'one-back task', pressing a button if an image was identical to the previous one. The localizer began and ended with a fixation block showing a cross in the centre of an otherwise blank screen. Additional fixation blocks were alternated with image blocks, with all blocks lasting 12 seconds. Six blocks of each image category (object, neutral face, expressive face) were presented in a counterbalanced order. Each image block consisted of 15 images (12 novel and 3 repeated), all sized to a standard width of 400 pixels and presented at screen center for 500ms, with an inter-stimulus-interval of 300ms.

Following the localizer scan, participants underwent two experimental scans. Experimental scans began with 6 fixation trials, followed by 160 experimental trials (32 for each of 5 conditions) and 50 fixation trials in one of five random orders, and ended with 6 fixation trials. During each trial the first image was presented 150 pixels to the left of center for 500ms followed by a 300ms inter-stimulus-interval. The second image was then presented 150 pixels to the right of center for 500ms followed by a 700ms inter-trial-interval. Left/right image presentation was used to ensure participants made perceptual decisions on the correct image pairs (i.e. always responding after the right-sided image). Face images were replaced with a fixation cross during fixation trials. Jittering was achieved through the randomized presentation of fixation trials throughout the scan (Dale, 1999; Serences, 2004).

We had subjects perform two experimental runs because of the potential for the effects to be modulated by task. Most fMRI adaptation studies have required participants to perform irrelevant tasks during functional scans, while maintaining attention on the face (Rotshtein et al., 2005; Winston et al., 2004). Attention is critical since others have shown that when a face is not attended (because of a distracter face, for example) adaptation is no longer observed (Ishai et al., 2004). Other studies have shown task-modulation of the BOLD signal in several face areas: OFA- greater activity during expression than gender identification tasks (Gorno-Tempini et al., 2001); FFA – greater activity when attending facial identity than facial contour in a delayed match to sample task (Narumoto et al., 2001), or when explicitly judging expression as compared to identity changes (Ganel et al., 2005); pSTS - greater activity when attending facial expression than facial identity in a delayed match to sample task (Narumoto et al., 2001). In our experiment we decided to ask subjects to engage directly in tasks relevant to the dimensions we were exploring. Thus, in one experimental run participants made same/different judgments about the facial identity of image pairs, while in the other they made same/different judgments about the facial expression of image pairs. The order of the two experimental runs was determined randomly for each subject. The same stimuli were used during both runs but in a different random order, so that task effects were not confounded by stimulus differences.

Functional Localization

All MRI data were analyzed using BrainVoyager QX Version 1.8 (www.brainvoyager.com). Anatomical scans were not preprocessed. Preprocessing of functional scans consisted of corrections for slice scan time acquisition, head motion (trilinear interpolation), and temporal filtering with a high pass filter in order to remove frequencies less than 3 cycles/time course. For each participant, functional scans were individually co-registered to their respective anatomical scan, using the first retained functional volume to generate the co-registration matrix.

The localizer time course was analyzed using a single subject GLM, with object (O), neutral (NF) and expressive (EF) faces as predictors. Analysis of $NF+EF > 2*O$ was overlaid on the whole brain and significance was set at a False Discovery Rate of $q < 0.05$, corrected for multiple comparisons. Within each participant, we attempted to define five regions-of-interest. Contiguous clusters of >10 voxels located on: i) the lateral surface of the inferior occipital gyrus were designated as the OFA; ii) the lateral temporal portion of the fusiform gyrus were designated as the FFA; iii) the posterior segment of the superior temporal sulcus were designated as the pSTS. In addition, we assessed responses in two other areas beyond the classic core system: iv) the middle segment of the superior temporal sulcus were designated as the mSTS; v) the hemispheric midline, anterior to the occipitotemporal fissure, were designated as the precuneus. Extensive evidence from neuroimaging studies (Kanwisher et al., 1997) and brain-damaged patients with deficits in the perception of identity (Barton, 2003) or expression (Adolphs et al., 1996) points to right hemisphere dominance in face processing. Additionally,

the model of face perception which we are directly examining herein is primarily based on data collected from right-hemisphere components of the face network (Haxby et al., 2000). As a result we focus our analyses on the right-hemisphere dominant version of the OFA, FFA, pSTS and mSTS only. As the precuneus was located at the hemispheric midline, right and left hemisphere regions were indistinguishable.

Adaptation effects

We first verified that our stimuli generated behavioral responses consistent with the proposal that the two stimuli in the *different* conditions were located across the appropriate category boundary while the two stimuli in the *similar* conditions were located on the same side of the appropriate category boundary. If so, subjects should respond significantly more frequently that the two faces differ in terms of identity in the *different-identity category* condition than in the *different-expression category*, *similar-expression category*, or *similar-identity category* conditions. Likewise, they should respond more often that the two faces differ in terms of expression in the *different-expression category* condition than in the other three conditions. For each subject we calculated the proportion of different responses for each experimental condition and performed a general linear model (GLM) with condition (*identical*, *similar-identity category*, *different-identity category*, *similar-expression category*, *different-expression category*) and task (identity run, expression run) as fixed factors, subject as a random factor, and proportion of different responses as the dependent measure. Linear contrasts were used to examine any significant main or interaction effects. An interaction, with significantly more different responses for the *different-identity* condition during the identity run and for the *different-expression* condition during the expression run would indicate categorical perception of this stimulus set.

Experimental MRI scans were analyzed using a deconvolution analysis that accounts for non-linear summation of the blood oxygen level dependent (BOLD) response in rapid event-related designs. The deconvolution analysis samples BOLD activity at trial onset (time = 0sec) and again 9 more times in 2sec intervals, resulting in an unbiased model of the hemodynamic response (HDR). HDRs were estimated independently for each experimental condition.

From the estimated HDRs we can compare adaptation across different experimental conditions. In discussing adaptation of the BOLD signal, Grill-Spector et al. (2006) suggest three possible means through which reduced activity could be achieved; a general neural fatigue, neural sharpening of the response to include only highly selective neurons, or a facilitation of the response resulting in faster activation and deactivation (Grill-Spector et al., 2006). Translating these postulated changes in the BOLD signal to changes in the shape of the HDR one could expect adaptation to result in either a reduction in the HDR peak (fatigue) or a narrowing of the HDR (facilitation). In order to account for both options we chose to examine the area-under-the-curve (AUC) of the HDR. The hemodynamic response normally begins its ascent after 2sec post-stimulus and has returned to baseline by 12sec post-stimulus (Serences, 2004). With a 2sec TR, this leaves 4 consecutive time points (4sec, 6sec, 8sec, 10sec) representing the full positive component of the HDR, although there is some variability in this timing (Yovel and Kanwisher, 2005). We determined the AUC of each HDR by finding the 4 consecutive time points with the maximal summed percent signal change (%SC), resulting in an AUC value in units of % signal change/ 6 sec.

To analyze the effect of condition in the adaptation data we performed two types of analysis, a stimulus-based analysis and a perception-based analysis. Since fMRI results during a face/object detection task showed that the participant's perception drive the measured effects more than the stimulus categories (Grill-Spector et al., 2004), it is possible that 'categorical' effects may be driven less by the morph characteristics of the image pairs and more by whether the subject perceives the image pairs as same or different. For both types of analysis, the responses

during all trials in the *identical* condition were averaged to give the baseline estimate of full adaptation. The *identical* condition consists of two face images which are identical and the fMRI signal elicited by this face-pair represents maximal adaptation. In all other conditions, the second image in the face-pair differs from the first image, and regions sensitive to this difference will exhibit a larger signal to the changed face-pair than to the *identical* face-pair. The way in which the second image differs from the first creates our various experimental conditions. First, the stimulus-based analysis used our *a priori* stimulus categories (*similar-identity category*, *different-identity category*, *similar-expression category*, and *different-expression category*), reflecting whether image pairs lay on the same side or different sides of the 50:50 morph boundary. Our second analysis reclassified trials from these four experimental conditions based on whether they were perceived as same or different identities during the experimental run requiring identity judgments, and again as to whether they were perceived as same or different expressions during the run requiring expression judgments. Importantly, the new perception-based classification determined by behavioral response during the identity run was used to analyze hemodynamic activity during both the identity run and during the expression run (and similarly, the perception-based classification determined by behavioral response during the expression run was used to assess hemodynamic activity in both runs). Thus, these perception-based classifications are not confounded by any potential cognitive difference between ‘same’ and ‘different’ responses, since the responses made during the expression run do not correspond to the perceptual classifications derived from the identity run, and vice versa. In the first ‘stimulus-based’ analysis, the other experimental conditions were labeled as *similar-identity category*, *different-identity category*, *similar-expression category*, and *different-expression category* as above. In the second ‘perception-based’ analysis, the experimental conditions were labeled as *similar-identity perception*, *different-identity perception*, *similar-expression perception*, and *different-expression perception*. A GLM was then performed, with condition (*identical*, *similar-identity*, *different-identity*, *similar-expression*, *different-expression*), task (identity run, expression run) and analysis (stimulus-based, perception-based) as fixed factors, subject as a random factor and AUC as the dependent measure. Linear contrasts were used to examine any significant main or interaction effects. Significance on all statistical tests was set at $\alpha < 0.05$.

For graphical purposes, and to account for between-subject variability in baseline hemodynamic activity, the AUC of the *identical* condition (representing maximal adaptation) was subtracted from the AUC of other experimental conditions. Thus positive values seen in Figures 3–7 indicate a larger signal in the experimental condition than in the *identical* condition, a “release from adaptation”. Cortical regions which show a release from adaptation are, by definition, sensitive to the facial change made in that particular experimental condition. Further comparisons can be made between experimental conditions that differ in the magnitude of release from adaptation. Experimental conditions which elicit greater release from adaptation indicate stronger regional sensitivity to the facial change associated with that experimental condition. All release from adaptation values are presented in units of % signal change/ 6 sec (Figures 3–7).

RESULTS

Behavioral Data

The GLM of responses recorded during the scanning session revealed a main effect of condition [$F(1,14)=36.36$; $p<0.001$], which was modified by an interaction between condition and task [$F(1,14)=30.31$; $p<0.001$]. This was due to a significantly higher frequency of different responses for the *different-identity category* condition (Mean frequency of different responses \pm SEM = 0.37 ± 0.05) than for any other condition ($p<0.01$, all tests) during the identity run, and a significantly higher frequency of different responses for the *different-expression*

category condition (mean frequency of different responses \pm SEM = 0.50 ± 0.03) than for any other condition ($p < 0.001$, all tests) during the expression run (Figure 2). The increased proportion of different responses for face pairs that crossed a categorical boundary than those within a category satisfies the chief criterion of categorical perception, namely increased discriminative power across a categorical boundary (Angeli et al., 2007; Beale and Keil, 1995; Etcoff and Magee, 1992; Rotshtein et al., 2005). Thus the behavioral data are consistent with the classification of our stimuli regarding category boundaries for both identity and expression. In addition, the proportion of different responses for the *identical* condition was lower than any other condition during both runs (identity run – 0.02 ± 0.01 ; $p < 0.05$, all tests. expression run – 0.03 ± 0.01 ; $p < 0.01$, all tests), making the *identical* condition an appropriate baseline measure of maximal adaptation for the subsequent fMRI analyses.

Adaptation – Core system

We identified the OFA in 13 of 15 participants (Table 1; Figure 3A). The GLM revealed a significant main effect of condition [$F(4,48) = 3.32$; $p < 0.05$], due to a significantly smaller AUC in the *identical* condition (Mean AUC \pm SEM; 1.69 ± 0.11) than in any other condition ($p < 0.05$, all tests). The remaining four experimental conditions did not differ from each other ($p > 0.20$, all tests). Thus, a significant release from adaptation occurs in the OFA with any structural change in the face, whether along an identity or expression axis, and regardless of whether the structural change crosses a categorical boundary for identity or expression (Figure 3B and C). No other main effects or interactions were significant, indicating that this effect in the OFA is independent of task demands and independent of whether the trials are classified by stimulus characteristics or by the perceptual experience of the individual subject.

We identified the FFA in all 15 participants (Table 1; Figure 4A). The GLM revealed a significant main effect of condition [$F(4,56) = 10.67$; $p < 0.001$] modified by a significant interaction between condition and analysis [$F(4,56) = 3.41$; $p < 0.05$]. Examining the stimulus-based analysis alone showed a significantly smaller AUC in the *identical* condition (1.32 ± 0.10) than in any other condition ($p < 0.05$, all tests), but the remaining four experimental conditions did not differ from each other ($p > 0.40$, all tests; Figure 4B). In the perception-based analysis there was again a significantly smaller AUC in the *identical* condition (1.28 ± 0.09) than in any other condition ($p < 0.001$, all tests). However, categorical effects were also apparent in the perception-based analysis, with a significantly larger AUC in the *different-expression perception* condition (1.75 ± 0.11) than in the *similar-expression perception* condition (1.55 ± 0.11 ; $p < 0.01$) and a trend to a larger AUC in the *different-identity perception* condition (1.69 ± 0.12) than the *similar-identity perception* condition (1.56 ± 0.11 ; $p = 0.06$). Thus, the perception-based analysis suggests that when subjects perceive a change in identity or expression there is release from adaptation in the FFA (Figure 4C). No other main effects or interactions were significant, indicating that this effect in the FFA is independent of task demands.

We identified the pSTS in all 15 participants (Table 1; Figure 5A). The GLM revealed a significant main effect of condition [$F(4,56) = 4.59$; $p < 0.01$], modified by an interaction between condition and analysis [$F(4,56) = 2.97$; $p < 0.05$] and a three-way interaction between condition, task and analysis [$F(4,56) = 2.76$; $p < 0.05$]. Examining data from the identity experimental run showed that the *identical* condition did not differ from any other condition ($p > 0.20$, all tests), within either the stimulus-based analysis (Figure 5B) or the perception-based analysis (Figure 5C). No categorical effects were observed ($p > 0.10$, all tests). Thus, when attention is focused on facial identity there is no measurable adaptation within the pSTS. However, examining the expression experimental run revealed a pattern similar to that seen in the FFA. The stimulus-based analysis showed a significantly smaller AUC in the *identical* condition (0.42 ± 0.08) than in the *similar-identity perception*, *similar-expression perception*,

or *different-expression perception* conditions ($p < 0.05$, all tests) with a trend in the same direction for the *different-identity perception* condition ($p = 0.07$). The remaining four experimental conditions did not differ from each other ($p > 0.15$, all tests; Figure 5D). The perception-based analysis showed a significantly smaller AUC in the *identical* condition (0.44 ± 0.08) than in any other condition ($p < 0.05$, all tests). In addition, categorical effects were apparent with a significantly larger AUC in the *different-identity perception* condition (0.83 ± 0.10) than the *similar-identity perception* condition (0.60 ± 0.06 ; $p < 0.01$) and a trend to a larger AUC in the *different-expression perception* condition (0.77 ± 0.09) than the *similar-expression perception* condition (0.58 ± 0.08 ; $p = 0.052$). Thus, the perception-based analysis of the pSTS data showed a release from adaptation when subjects perceived a change in either identity or expression, but only when task demands direct attention toward facial expression (Figure 5E).

Adaptation – Beyond the core system

The face that both the FFA and pSTS showed a similar release from adaptation for perceived changes in either identity or expression led us to ask if there were other cortical regions that might show more selective effects for identity alone or expression alone. Prior work has suggested that the mSTS is more selective than the pSTS for expression (Winston et al., 2004), and the precuneus has shown some form of identity discrimination with greater responses for familiar than novel faces (Gobbini and Haxby, 2006, 2007; Kosaka et al., 2003); therefore, these two regions seemed appropriate candidates for further region-of-interest analyses.

We identified the mSTS in 13 of 15 participants (Table 1; Figure 6A). The GLM revealed a significant interaction between condition and analysis [$F(4,48) = 2.57$; $p = 0.05$]. Examining the stimulus-based analysis alone revealed no significant differences between any of the five experimental conditions ($p > 0.20$; Figure 6B). Examining the perception-based analysis alone showed that the *identical* condition (0.59 ± 0.11) again did not differ significantly from any of the other experimental conditions ($p > 0.05$, all tests). However, a categorical effect of expression was observed, with a significantly larger AUC in the *different-expression perception* condition (0.69 ± 0.09) than the *similar-expression perception* condition (0.42 ± 0.05 ; $p < 0.01$). No such effect was observed between *identity* conditions ($p > 0.15$). Thus, the perception-based analysis suggests a release from adaptation in the mSTS when subjects perceive a change in expression, but not when they perceive a change in identity (Figure 6C). As no other main or interaction effects were significant, this effect in the mSTS is not modulated by task demands.

We localized the precuneus in 10 of 15 subjects (Table 1; Figure 7A). The GLM revealed a significant main effect of condition [$F(4,36) = 4.90$; $p < 0.01$], which was modified by a significant interaction between condition and analysis [$F(4,36) = 3.98$; $p < 0.01$]. Examining the stimulus-based analysis alone showed that the *identical* condition (0.52 ± 0.05) did not differ significantly from any of the other experimental conditions ($p > 0.05$, all tests), nor was there evidence for any categorical effects ($p > 0.05$, all tests; Figure 7B). However, when examining the perception-based analysis alone a significantly smaller AUC in the *identical* condition (0.48 ± 0.04) than in the *different-identity perception* condition (0.80 ± 0.06) was observed ($p < 0.001$). The AUC in the *different-identity perception* condition was also significantly larger than that in the *similar-identity perception* condition (0.48 ± 0.04 ; $p < 0.001$). No other conditions differed from the *identical* condition ($p > 0.30$), nor was there evidence for the categorical perception of expression ($p > 0.60$). Thus, the perception-based analysis suggests a release from adaptation in the precuneus when subjects perceive a change in identity, but not when they perceive a change in expression (Figure 7C). As no other main or interaction effects were significant, this effect in the precuneus is not modulated by task demands.

DISCUSSION

The current experiment had two principle aims, each examining specific hypotheses made by the most widely accepted model of face perception (Haxby et al., 2000). First, we examined the modeled role of the OFA as an input module to the core face network (i.e.- the FFA and pSTS) involved in the early perception of facial structure (Haxby et al., 2000). This role predicts OFA sensitivity to changes in facial structure, but does not predict discriminative power for changes in facial identity or facial expression. Second, we examined the independent model of facial identity and facial expression processing within the FFA and pSTS respectively (Haxby et al., 2000). This model predicts sensitivity to identity changes in the FFA and to expression changes in the pSTS, but importantly, also predicts insensitivity to expression changes in the FFA and insensitivity to identity changes in the pSTS.

We chose to address these two experimental aims using fMRI adaptation to examine the categorical perception of facial identity and expression. Categorical perception suggests sensitivity to physical changes which cross a categorical boundary, but not to physical changes of an equal magnitude which do not cross a categorical boundary, and is evidenced by increased discrimination accuracy for those pairs which do cross the categorical boundary (Angeli et al., 2007; Beale and Keil, 1995; Etcoff and Magee, 1992; Rotshtein et al., 2005). The use of morphed faces allows one to create stimuli with approximately equivalent physical differences between face pairs that do or do not cross categorical boundaries (Figure 1). An analysis of behavioral responses gathered from participants during the fMRI scanning session suggested that our classification of stimulus pairs as crossing or not crossing category boundaries for expression or identity was correct (Figure 2), validating the use of this stimulus-based classification in the fMRI analysis. However, it is also clear from Figure 2 that a substantial proportion of stimulus pairs that cross categorical boundaries were perceived as 'same' by participants, while a smaller proportion of stimulus pairs that did not cross the categorical boundary were perceived as 'different'. This result does not negate our finding of a categorical perception, as it is not the absolute level of discrimination accuracy that determines a categorical boundary, but rather the difference in discrimination accuracies between pairs which either do or do not cross a categorical boundary (Angeli et al., 2007; Beale and Keil, 1995; Etcoff and Magee, 1992; Rotshtein et al., 2005). Furthermore a previous fMRI study of categorical perception reported a similar ~50% proportion of different responses to face pairs which cross a categorical identity boundary (Rotshtein et al., 2005). However, this pattern of behavioral data led us to construct a second 'perception-based' analysis with stimulus pairs classified according to the perceptual experience of each subject. Our results clearly show that adaptation effects emerged more distinctly in the perception-based analysis, consistent with prior reports which show that functional effects follow subjective experience more than stimulus properties (Grill-Spector et al., 2004; Tong et al., 1998).

1. OFA involved in the early perception of facial structure

The first aim of this study was to examine the modeled role of the OFA as an input module to the core face network and whether the OFA demonstrated sensitivity to structural changes, irrespective of whether that change crossed a categorical boundary of identity or expression. As expected, maximal adaptation in the OFA was observed for the *identical* condition. A release from adaptation was apparent for all other conditions (*similar-identity*, *different-identity*, *similar-expression*, *different-expression*), and there was no difference in the magnitude of this release across the four conditions (Figure 3). Thus, the OFA appears to show sensitivity to any structural change in a face, along both identity and expression dimensions, regardless of the categorical effects of these changes, and independent of task demands. These findings replicate the findings of Rotshtein et al (2005) for identity, show that the same pattern is observed even if the analysis is based upon the subjective perception of an identity change,

and more importantly extend these findings to show that they also apply to physical changes related to facial expression. These results provide strong support for the predicted role of the OFA in the early perception of facial structural properties related to the perception of both facial identity and expression (Haxby et al., 2000).

2. Independent processing of identity and expression is not observed in the FFA or pSTS

The second aim of the present study was to examine the independent processing of identity and expression within the FFA and pSTS. The FFA, like the OFA, showed maximal adaptation for the *identical* condition and release from adaptation was observed in all other conditions (*similar-identity*, *different-identity*, *similar-expression*, *different-expression*). The stimulus-based analysis of FFA activity showed no difference between any of these four experimental conditions, suggesting that, like the OFA, the FFA may be sensitive to any structural change in the face. However, the perception-based analysis showed greater release from adaptation in the FFA when subjects perceived a difference in facial identity. This result supports the predicted sensitivity to identity changes in the FFA (Haxby et al., 2000), replicates the findings of others (Rotshtein et al., 2005), and suggests that identity sensitivity in the FFA is driven by the subjective perception of differences in facial identity.

Importantly, the perception-based analysis also showed greater release from adaptation in the FFA to perceived changes in facial expression, a finding which does not satisfy the prediction of insensitivity to facial expression inherent in the independent model of face perception (Haxby et al., 2000). However, this finding may be consistent with other evidence of expression-based modulation of FFA activity (Ganel et al., 2005; Ishai et al., 2005; Palermo and Rhodes, 2007; Vuilleumier et al., 2001). Some of these studies demonstrate increased activity in the FFA when viewing expressive faces as compared to neutral ones (Ishai et al., 2005; Vuilleumier et al., 2001), while others show increased activity in the FFA for expression changes, even while attending to facial identity (Ganel et al., 2005). Thus, in contrast to the current model (Haxby et al., 2000), our results suggests that FFA activity is modulated not only with the subjective perception of facial identity, but also with the subjective perception of facial expression (Figure 4).

The pattern of adaptation seen in the pSTS closely resembles that of the FFA, in that there is general non-specific release from adaptation compared to the *identical* condition in the stimulus-based analysis, but greater release from adaptation for perceived changes in either identity or expression in the perception-based analysis. While prior adaptation studies have shown evidence that the pSTS is sensitive to changes in facial expression in the image (Winston et al., 2004), our data shows more specifically that release from adaptation is enhanced not just when there is a change in the image, but when the viewer *perceives a change* in the image's expression. Furthermore, our finding of a similar effect for facial identity again replicates previously reported sensitivity to changes in facial identity in the pSTS (Winston et al., 2004), and again shows that this release from adaptation is driven by the *perceived change* in the image's identity. Unlike the FFA in our study, the pSTS only shows this adaptation pattern during the expression experimental run, when attention is directed specifically toward facial expression (Figure 5). This task-modulation may parallel other reports of increased activity in the pSTS when the subject explicitly attends to facial expression (Narumoto et al., 2001). Again, as in the FFA, our pSTS data satisfy the predicted sensitivity to changes in facial expression but do not satisfy the predicted insensitivity to changes in facial identity of the current independent model (Haxby et al., 2000).

Functional dissociation in the extended system of face processing

The lack of specificity for identity versus expression in our analysis of the FFA and pSTS led us to ask if whether a functional dissociation in identity and expression perception could be

observed within the extended system of face processing. Based on prior work, which suggested involvement in expression and identity perception, we focused this secondary analysis on two additional regions, the mSTS and the precuneus. Winston et al. (2004) used fMRI adaptation to show that the mSTS is sensitive to changes in facial expression but not to changes in facial identity. In support, we find that the mSTS showed release from adaptation when the subject perceived a change in expression, but not when they perceived a change in identity (Figure 6). Winston et al (2004) suggest that, “contrary to current models, the independent processing of expression may occur in a portion of the superior temporal sulcus more anterior to the pSTS,” and our findings are consistent with this conclusion.

The precuneus showed the opposite pattern of adaptation to the mSTS, with release from adaptation when subjects perceived a change in facial identity but not when they perceived a change in facial expression (Figure 7). Prior studies have shown that the precuneus holds some discriminative power for facial identity, with familiar faces eliciting stronger activity than novel ones (Gobbini and Haxby, 2006; Kosaka et al., 2003). However, two alternate interpretations of these findings exist. First, the precuneus shows increased activity during the visual imagery of faces, a task which requires access to facial memory stores (Ishai et al., 2002). To divorce the perceptual role of the precuneus from its role in facial memory storage our stimulus set used faces previously unknown to the subjects. However, it is possible that the learning of names and the few days of training was sufficient for participants to create semantic associations for these faces. In that case, a perception of changed facial identity would also be accompanied by a change in semantic associations. Therefore our data cannot definitively state whether the release of adaptation seen in the precuneus is related to the specific perception of facial identity, or to the processing of semantic associations linked to facial identity, even though these were relatively weak given our use of novel faces. Second, other studies of the posterior parietal cortex, including the precuneus, have pointed to old/new recognition effects for faces, in which newly-learned faces elicit a stronger signal than novel faces (Leveroni et al., 2000; Wagner et al., 2005). However, these studies contrast newly learned faces with novel faces, whereas all faces used in our paradigm are morphs of newly learned faces. While arguments can be made that the same/different task employed by us may tap into this old/new recognition effect in the precuneus, it is unclear whether such effects occur at the time scale we use (<2s). Furthermore we observe an asymmetric sensitivity to identity changes but not expression changes, suggesting that simple recognition effects cannot explain our results. Additionally, a recent case study suggests that recognition memory is unaffected following damage to the posterior parietal cortex, including the precuneus (Haramati et al., 2008). Further studies of patients with selective damage of the mSTS and precuneus, accompanied by comprehensive evaluations of their face processing abilities, will help clarify the role of these regions in the perception of facial identity and expression.

By limiting our secondary analysis to the middle STS and precuneus we do not imply that other regions of the extended system are not involved in identity and/or expression processing. As stated, we chose these two regions based on prior evidence pointing to their independent involvement in the processing of facial identity and expression. Future studies of identity and expression perception within additional regions of the extended system for face processing may well add to the findings we report (see Supplementary Table 1 and Supplementary Figures 1–3).

Implications for current and future models of face perception

In a recent review challenging the independence of facial identity and expression processing in current models (Haxby et al., 2000), Calder and Young (2005) argued for a relative rather than absolute segregation of identity and expression perception. They based this argument on findings from principle component analyses showing that certain components are necessary

for discriminating facial identity, others for discriminating facial expression, and yet others for discriminating either. They suggest that the network underlying face perception may follow this pattern, with both modules that are selective for identity and expression and modules that participate in both identity and expression discriminations (Calder and Young, 2005).

Our data suggest that, as currently modeled (Haxby et al., 2000), the OFA is involved in the early perception of facial structural properties related to either facial identity or expression; however, activity in the OFA does not vary with whether the subject perceives a change in the face or not. As long as there is a structural change in the face the OFA shows release from adaptation, whether or not this change causes a change in the percept of expression or identity. In contrast, change in percept does lead to release from adaptation in the FFA and pSTS; however, against complete independence of processing at this level, we find that both the FFA and the pSTS show this release from adaptation for both expression and identity.

Several interpretations of this finding are possible. It may be that both the pSTS and the FFA make complementary contributions to expression and identity recognition: this would not necessarily deny a dominant role for the FFA in identity processing and the pSTS in expression processing, but it would imply relative rather than absolute independence. If so, this hypothesis predicts (1) more severe deficits in expression or identity processing from lesions of both the pSTS and FFA than from lesions of either alone, and (2) partial defects in expression processing along with more severe deficits in identity processing from an FFA lesion, and the reverse with a pSTS lesion. Both of these predictions could be tested in a lesion model. A second interpretation is that the expression signal in the FFA and the identity signal in the pSTS are modulatory. Thus, for example, the identity signals in the pSTS might not indicate that it is involved in recognizing identity, but that these identity signals may be modulating expression processing in the pSTS. There is some work showing that correct interpretations of facial expressions requires modulation by identity (Ganel et al., 2004; Martinez and Neth, 2007), and therefore some interaction is required for optimal recognition performance. In this scenario, lesions of the FFA or pSTS alone would still be selective for identity or expression processing respectively.

Our data also raise the possibility that selective processing may involve the precuneus for identity and the mSTS for expression. Prior fMRI studies support a role for the mSTS in selective expression processing (Winston et al., 2004), though there is as yet no lesion data on the impact of selective lesions of the mSTS on expression processing. The greater response of the precuneus to familiar than novel faces has been interpreted as due to retrieval of semantic associations, but it is also likely that familiar faces have stronger identity representations. The precuneus has been included in the lesions of at least some patients with prosopagnosia (Suzuki et al., 1996), but these lesions have been large and involved multiple areas, limiting the conclusions possible about the role of the precuneus in identity recognition.

In summary, the findings of the present experiment do not suggest complete segregation of expression and identity processing (Haxby et al., 2000). We find strong support for the OFA as currently modeled; a region involved in the early perception of facial structure and not in the perception of facial identity or expression. However, we do not find evidence to support the independent processing of identity and expression within the FFA and pSTS. Rather the fMRI signal from both regions seems to discriminate between different identities and different expressions. Further studies will provide more insight into the role of the FFA in expression perception and the pSTS in identity perception. Revisions of the current model of face processing may be required if further evidence against independent processing accumulates (Calder and Young, 2005). More detailed analyses of regions comprising the extended system of face processing are also needed and the results incorporated into such revisions of the model. Last, the present results also raise the possibility that the middle STS and precuneus may play

more significant roles in identity and expression perception than currently suggested and further investigations are required to clarify their specific contributions.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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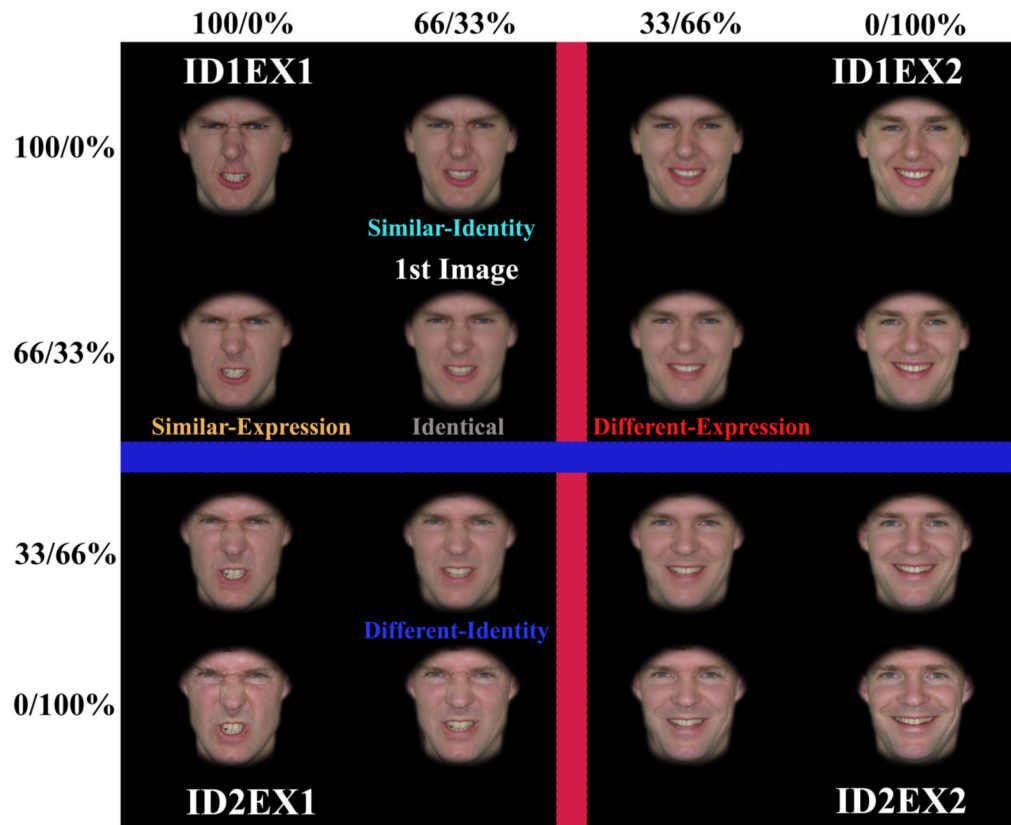


Figure 1.

An example of a 4X4 morph matrix used to create the five experimental conditions. Thirty-two unique matrices were created. Experimental conditions consisted of a pair of face images. The first image in each experimental condition, and the second image in the *identical* condition, was always the same. The second images in each of the other four conditions are labeled. Pairs in the *different-identity* condition cross a categorical boundary of identity (blue line), while pairs in the *different-expression* condition cross a categorical boundary of expression (red line). Subsequent figures use the same coloring to represent the five experimental conditions; gray = *identical*, pale blue = *similar-identity*, dark blue = *different-identity*, pale red = *similar-expression*, dark red = *different-expression*.

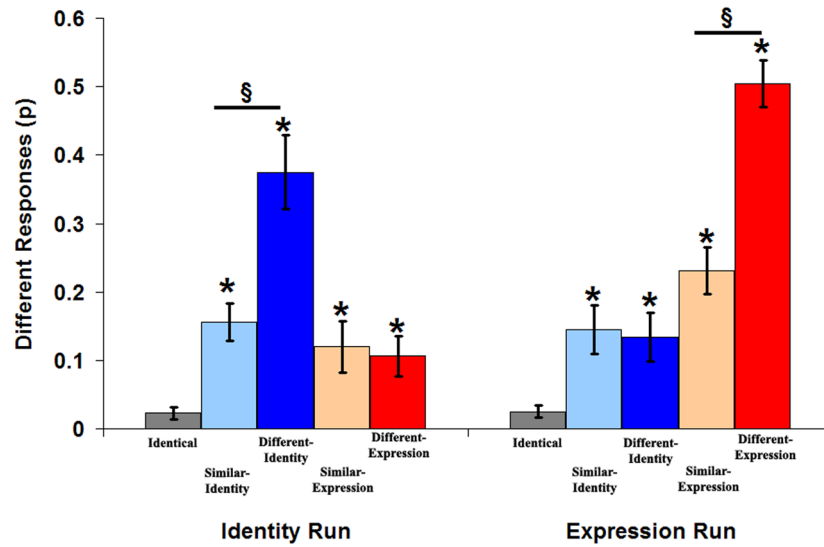


Figure 2. Results of behavioral responses recorded during the fMRI session (Mean p of different response \pm SEM; gray = *identical*, pale blue = *similar-identity*, dark blue = *different-identity*, pale red = *similar-expression*, dark red = *different-expression*). Categorical effects can be seen during both the identity and expression runs (indicated with a $\$$), with significantly more different responses for stimulus pairs that cross the task-specific category boundary than those that do not. Significantly more different responses were observed in all conditions (indicated with an *) as compared to the *identical* condition, validating this condition as a baseline measure of maximal adaptation.

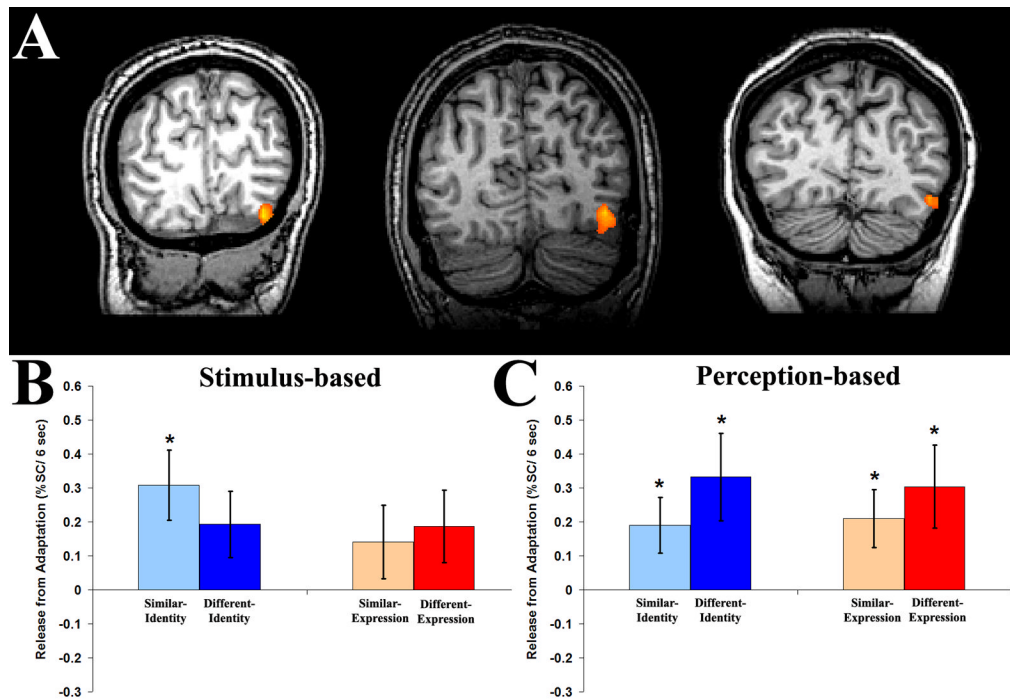


Figure 3.

(A) Examples of the right occipital face area in three subjects (coronal slices). (B) Results of the stimulus-based (B) and perception-based analyses (C) in the right OFA, demonstrating sensitivity to structural changes (indicated with an *), as compared to the *identical* condition. No categorical effects of identity or expression are observed, suggesting the OFA does not participate in the perception of these facial characteristics. Bars in this and subsequent figures represent mean release from adaptation values (AUC of the experimental condition > AUC of the *identical* condition) \pm SEM.

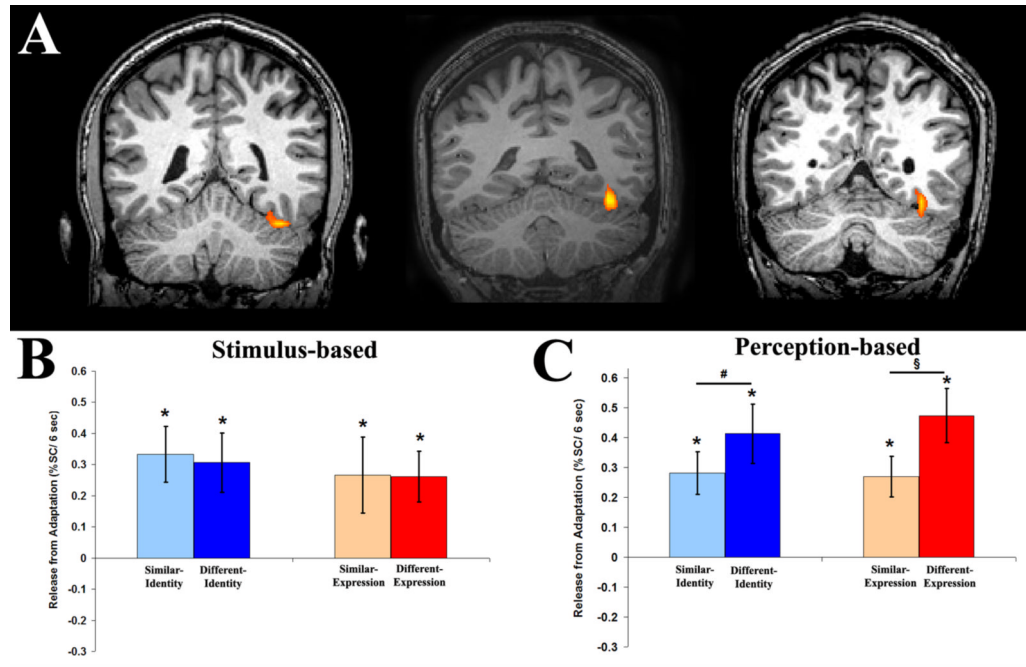
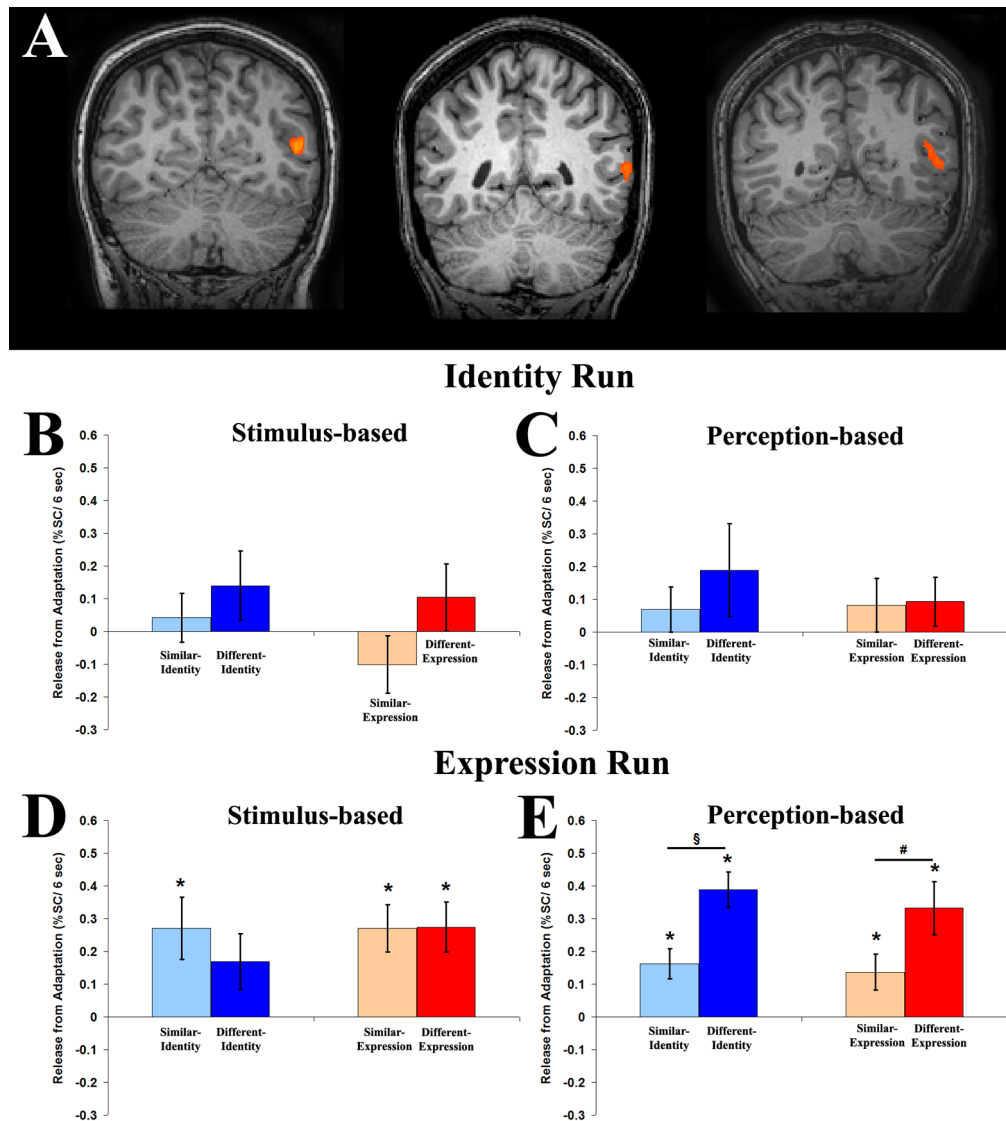


Figure 4.

(A) Examples of the right fusiform face area in three subjects (coronal slices). (B) The stimulus based analysis reveals a significant release from adaptation with any structural change (indicated with an *), as compared to the *identical* condition. (C) The perception-based analysis reveals a significant release from adaptation for perceived expression changes (indicated with an §) with a trend to the same effect for perceived identity changes (indicated with an #), evidence for a functional overlap of identity and expression processing within the FFA.

**Figure 5.**

(A) Examples of the right posterior superior temporal sulcus in three subjects (coronal slices). No release from adaptation is apparent during the identity run, in either the stimulus-based (B) or perception-based (C) analyses. (D) During the stimulus based analysis of the expression run a significant release from adaptation (indicated with an *), as compared to the *identical* condition is observed in all but one condition (stimulus analysis, *different-identity* condition). (E) The perception-based analysis of the expression run reveals a significant release from adaptation for perceived identity changes (indicated with an §) with a trend to the same effect for perceived expression changes (indicated with an #), evidence for a functional overlap of identity and expression processing within the pSTS.

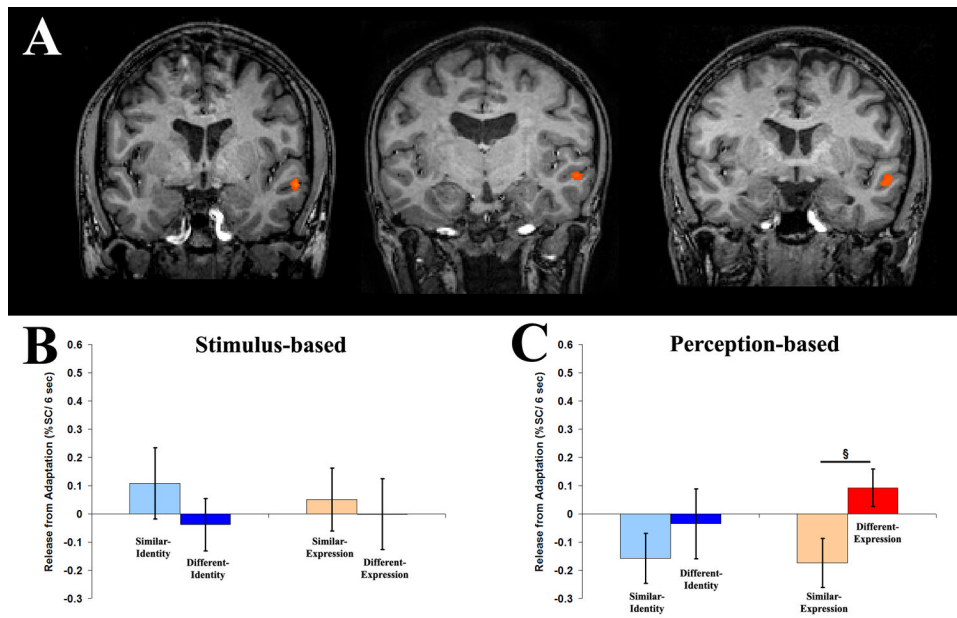


Figure 6. (A) Examples of the right middle superior temporal sulcus in three subjects (coronal slices). (B) The stimulus-based analysis does not reveal a significant release from adaptation in any experimental condition. (C) However, the perception-based analysis demonstrates a significant release from adaptation for perceived changes in expression (indicated with a §), evidence for the mSTS involvement in the perception of facial expression only.

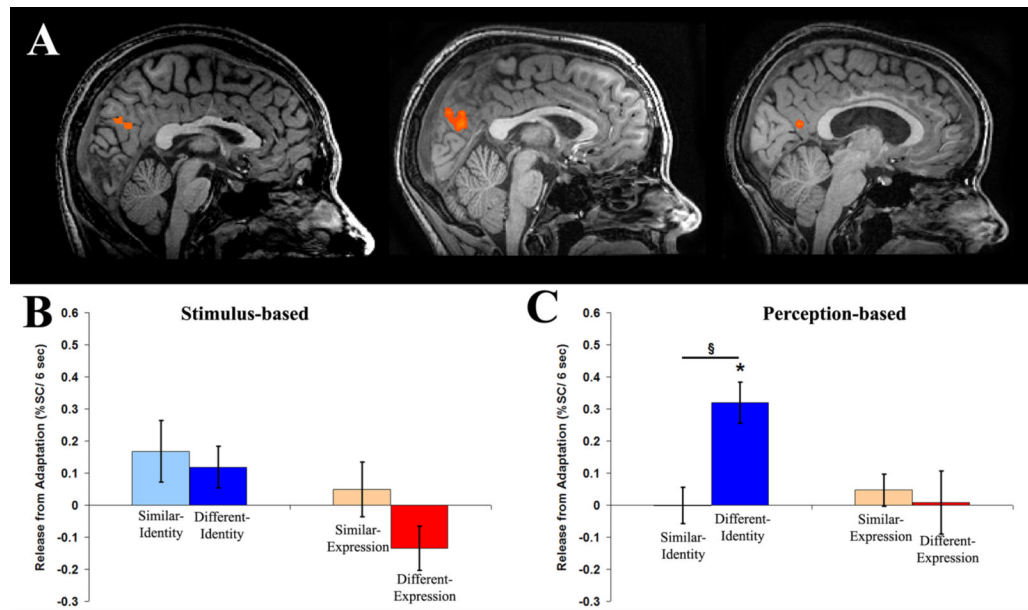


Figure 7.

(A) Examples of the precuneus in three subjects (sagittal slices). (B) The stimulus-base analysis does not reveal a significant release from adaptation in any experimental condition. (C) However, the perception-based analysis demonstrates a significant release from adaptation in the *different-identity perception* condition as compared to the *identical condition* (indicated with an *) and to the *similar-identity perception* condition (indicated with an §), evidence for precuneus involvement in the perception of facial identity only.

Average results from the functional localizer. The t-value of the peak voxel and number of voxels are reported from regions-of-interest localized in native non-standardized space, and all analyses were performed on these regions-of-interest. Mean Talairach coordinates are reported for comparison with other studies only.

Table 1

Region-of-Interest	# of subjects (/15)	t-value of Peak Voxel	# of Voxels (FDR; $q < 0.05$)	X	Y	Z
OFA	13	6.85 ± 0.74	510 ± 163	38 ± 2	-78 ± 3	-12 ± 2
FFA	15	7.54 ± 0.62	794 ± 217	37 ± 1	-47 ± 2	-19 ± 1
pSTS	15	6.05 ± 0.36	382 ± 68	52 ± 1	-50 ± 2	8 ± 1
mSTS	13	4.49 ± 0.19	78 ± 17	52 ± 2	-8 ± 2	-10 ± 2
precuneus	10	5.20 ± 0.30	665 ± 240	1 ± 1	-61 ± 2	27 ± 3