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COGNITIVE NEUROSCIENCE

Personally familiar faces are perceived categorically in face-selective regions other than the fusiform face area

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Abstract

Neuroimaging studies of humans have provided inconsistent evidence with respect to the response properties of the fusiform face area (FFA). It has been claimed that neural populations within this region are sensitive to subtle differences between individual faces only when they are perceived as distinct identities [P. Rotshtein *et al.* (2005) *Nature Neuroscience*, **8**, 107–113]. However, sensitivity to subtle changes of identity was found in previous studies using unfamiliar faces, for which categorical perception is less pronounced. Using functional magnetic resonance adaptation and morph continua of personally familiar faces, we investigated sensitivity to subtle changes between faces that were located either on the same or opposite sides of a categorical perceptual boundary. We found no evidence for categorical perception within the FFA, which exhibited reliable sensitivity to subtle changes of face identity whether these were perceived as distinct identities, or not. On the contrary, both the posterior superior temporal sulcus and prefrontal cortex exhibited categorical perception, as subtle changes between faces perceived as different identities yielded larger release from adaptation than those perceived as the same identity. These observations suggest that, whereas the FFA discriminates subtle physical changes of personally familiar faces, other regions encode faces in a categorical fashion.

Introduction

Over the past years it has been established that the ability of humans to process the various types of information conveyed by faces relies on a distributed neural network of face-preferential cortical regions (e.g. Haxby *et al.*, 2000; Fox *et al.*, 2009). Previous studies have investigated the response properties of these face-preferential regions using repetition suppression, or functional magnetic resonance (fMR) adaptation, which refers to the phenomenon of signal attenuation associated with repetition of a stimulus (for a review see Grill-Spector *et al.*, 2006). The rationale of fMR adaptation is that the shared characteristics of two stimuli (adapting, test) will be associated with decreased activation (adaptation). Consequently, any observed increase in activity (release from adaptation) would indicate a region's sensitivity to the characteristic(s) according to which the two stimuli differ.

Investigations of the response properties of face-preferential regions by means of fMR adaptation have most commonly focused on the fusiform face area (FFA) (Kanwisher *et al.*, 1997), which exhibits release from adaptation upon presentation of different faces, and is therefore considered to be sensitive to changes in facial identity (e.g. Gauthier *et al.*, 2000; Grill-Spector & Malach, 2001; Andrews & Ewbank, 2004). However, the degree of sensitivity of the FFA and other face-preferential regions of the face-processing network to individual faces remains a matter of debate. [Other studies have also demonstrated sensitivity of the FFA to other face-like geometrical properties, e.g. symmetry (Caldara *et al.*, 2006; Caldara & Seghier, 2009).]

Using morph continua between unfamiliar, real faces, Gilaie-Dotan & Malach (2007) parametrically varied the difference in perceived identity between consecutively presented faces. Faces that differed with respect to as little as 30% of identity information were reported to elicit full release from adaptation. The earlier results of Loffler *et al.* (2005) with morphed synthetic faces organized around an average face also suggest that subtle changes of facial identity are sufficient to elicit release from adaptation in the FFA, thereby providing converging evidence of the FFA's sensitivity to subtle changes between individual faces in general.

However, the results of another study by Rotshtein *et al.* (2005) are at odds with the above findings. In their study, participants were presented with stimuli taken from morph continua created from famous faces. When two faces differed by 30% along a morph continuum, and were perceived as the same identity, no release from adaptation was observed in the FFA. Only when the two faces involving the same physical change (30% along the morph continua) were perceived as different identities, i.e. crossed a perceptual categorical boundary along the morph continuum (Beale & Keil, 1995), did the FFA show release from adaptation.

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Thus, investigations of the FFA's sensitivity to subtle changes between faces have yielded conflicting results, which may be related to one critical factor: face familiarity. Although studies reporting sensitivity to subtle changes of facial identity used photographs of synthetic or unfamiliar faces (Loffler *et al.*, 2005; Gilaie-Dotan & Malach, 2007 respectively), Rotshtein *et al.* (2005) used pictures of famous faces. Accordingly, Gilaie-Dotan & Malach (2007) suggested that the discrepancy between their findings and those of Rotshtein *et al.* (2005) may have resulted from representational differences between familiar and unfamiliar faces.

To address this issue, we carried out an experiment similar to that of Rotshtein *et al.* (2005), investigating the sensitivity of the FFA and other face-preferential regions to subtle changes between individual faces in an fMR adaptation experiment, with two notable modifications of paradigm. First, rather than presenting pictures of famous faces, we used photographs of personally familiar ones. This avoids the issue of different levels of familiarity, as even with famous faces an observer could, for instance, conceivably be highly familiar with faces of actors but not politicians, which were mixed in the study of Rotshtein *et al.* (2005).

Moreover, photographs of famous faces are often taken from magazines or from the web and have become typical, 'iconic' pictures of famous people. As these individuals can be recognized based on e.g. the particular pose they have on a given photograph (i.e. the iconic photographs of Marylin Monroe or Che Guevara), it has been suggested that recognizing these pictures of famous faces does not call upon normal face recognition processes as compared with the recognition of personally familiar faces (Tong & Nakayama, 1999; Knappmeyer *et al.*, 2003; Carbon, 2008). To our knowledge, the present study is the first to investigate response properties within face-preferential regions using personally familiar, and thereby ecologically valid, face stimuli.

Second, contrary to the study of Rotshtein *et al.* (2005), we ensured that face stimuli crossing the perceptual boundary between individual faces did not represent 'rare events'. That is, they were not presented less often (than those located on the same side of the perceptual boundary) during our fMR imaging experiment, as this novelty factor may have up-regulated the signal (interpreted as release from adaptation) recorded to these stimuli in the study of Rotshtein *et al.* (2005).

Materials and methods

Participants

Thirteen individuals (eight females; mean age 23 ± 1 years), who were personally familiar with those whose images were presented as stimuli, participated in the present study. The participants were final-year students from the Department of Psychology of the University of Louvain with the same major, attending a number of courses together; three were left-handed (two females) and all had normal or corrected vision. Prior to the experiment, written informed consent was obtained following the procedures approved by the University of Maastricht; all participants were paid for their participation.

Stimuli

Full-frontal high-quality color photographs of 26 Caucasian students from the University of Louvain were taken during a course that all participants of this experiment attended throughout the academic year and served as stimuli. Using Adobe Photoshop, the original photographs were processed to meet the experimental requirements. The faces were cropped along the face contour, so that no hair or external cues were visible, with the resulting images subtending approximately 250 pixels in width and 335 pixels in height ($4.56 \times 6.11^\circ$ visual angle). Slight variations in the stimuli (face size and shape, luminosity) reflected natural differences as all images were obtained under identical conditions (distance, lighting, position). The stimulus height varied between 326 and 335 pixels and the stimulus width between 212 and 268 pixels. The average luminosity value across faces was 131 (SD: 10; range: 113–141). An image of each of the participants was included in the stimulus set, so that each participant was presented with his/her own face, as well as those of 25 other students.

PHOTO MORPHER™ v3.10 (Morpheus, Santa Barbara, CA, USA) was used to create 13 morph continua. Face pairs were selected based on gender, eye color and overall luminosity of the face (average difference in luminosity values of the faces constituting the extremes of the 13 continua was 0.2; SD 0.6). For each face, 350 points were placed on the critical features (encompassing the pupils, iris, eye bulbs, eye lids, eye brows, mouth, nose and overall facial contour) to allow smooth transitions between the 11 stimuli created per morph continuum (two original faces representing the extremes, with consecutive increments of 10%; see Fig. 1A).

Six stimuli were selected from each morph continuum [as opposed to three in Rotshtein *et al.* (2005)]. For a continuum created from, e.g. faces A and B, the stimuli selected represented each original face by 100, 70 or 40% respectively (see Fig. 1B). We reasoned that, in the light of recent findings indicating that the likelihood of stimulus repetition modulates the magnitude of observed neural adaptation (Summerfield *et al.*, 2008), both identities A and B should be perceived equally often.

Design and procedure

In an event-related fMR adaptation paradigm, participants were required to decide whether test and adapting stimuli were exactly identical or different by pressing one of two buttons on a response box (Gilaie-Dotan & Malach, 2007). The experiment entailed three experimental conditions, each of which commenced by presentation of an adapting stimulus containing 70% of a given identity. These conditions involved either (i) repetition of the adapting face, i.e. no change in physical properties or identity (*same*; 70/70%); (ii) within-category changes between the adapting and test face, i.e. both were located on the same side of the perceptual boundary (*within*; 70/100%); or (iii) between-category changes between the adapting and test faces, which were located on opposite sides of the perceptual boundary (*between*; 70/40%) (see Fig. 1B). As indicated above, all participants were presented with the three conditions derived from the extremes (i.e. identities) of a given morph continuum, to ensure both identities being perceived equally often.

All participants completed three experimental runs, each of which lasted about 15 min and included a total of 78 randomly presented trials (13 morph continua derived from two identities each, and three conditions per identity). Thus, each face pair (representing one of three possible conditions from one side of each morph continuum) was presented three times in total.

On each trial, adapting and probe faces were displayed for 1000 ms each, with an interleaved cross displayed for 250 ms. The probes were presented in the center of the screen and were subsequently replaced by a fixation cross, the duration of which randomly varied between 6750, 9000 and 11 250 ms. This timing ensured that the onsets of any two subsequent trials were separated by 9000–13 500 ms (4–6 TRs), for the purpose of reducing overlapping hemodynamic responses.

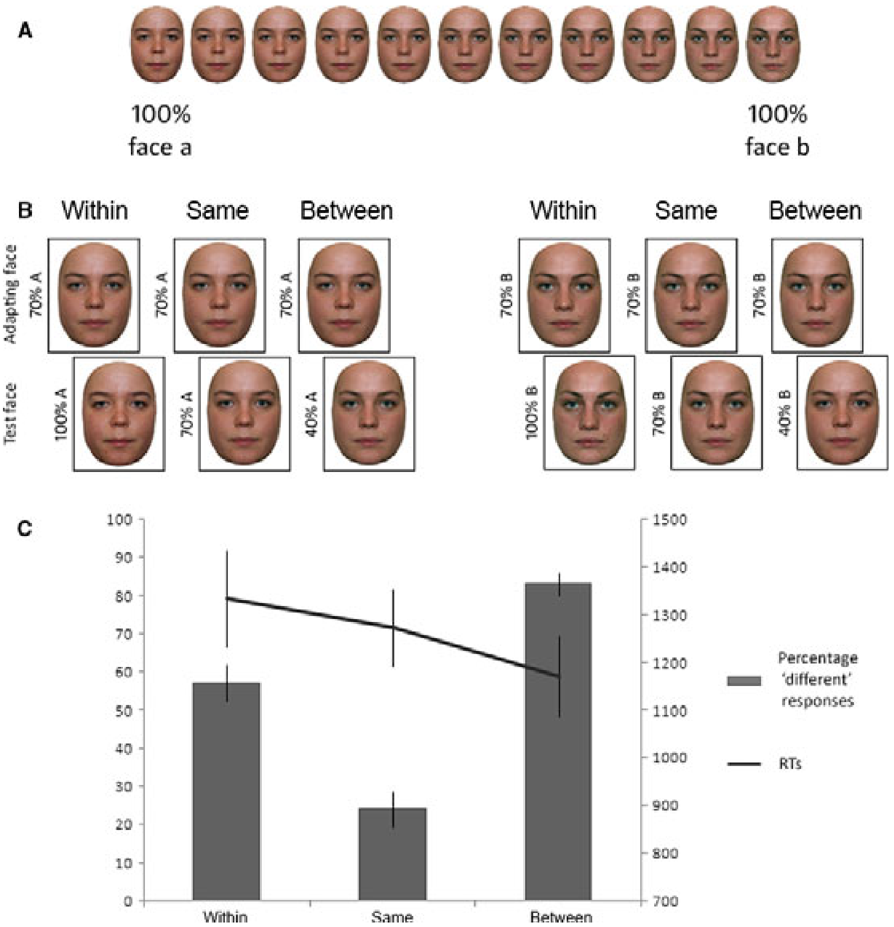

FIG. 1. Stimuli, design and behavioral results for experimental runs. (A) An example of a morph continuum created between faces a and b; extremes represent the respective faces by 100%, with 10% increments. (B) The three types of face pairs created for the three conditions (*within*, *same*, *between*), displayed for both identities representing extremes in the continuum provided in (A). The adapting face was constant across conditions (70%). Test faces could be either slightly different faces located on the same side of the categorical boundary (*within*, 100%), repetitions of the adapting stimulus (*same*, 70%) or slightly different faces that were located on opposite sides of the categorical boundary changes (*between*, 40%). (C) Behavioral results averaged across experimental runs. Displayed are the proportions of different responses (SE) and RTs (SE) in ms for the three conditions (averaged across 13 participants).

Stimuli were presented using E-PRIME 1.1 (Psychology Software Tools, Inc., Pittsburgh, PA, USA) and were back projected onto a screen located over the participant's head. To avoid pixel-wise matching, and to minimize low-level confounds, adapting faces were 10% larger than probes and their location was jittered randomly trial by trial. The range of shift in both the *x*- and *y*-axes was within ±40 pixels (±0.7264 cm/±0.73° visual angle).

Localizer scans

Prior to the experiment described above, each participant completed two runs of an external localizer in order to localize face-preferential areas and verify the response properties of regions derived from the whole-brain analysis. In each run, participants were presented with blocks of faces, cars, phase-scrambled faces and phase-scrambled cars, during which they performed a one-back matching task. Each run lasted 11 min and consisted of 24 alternating blocks (18 s each) separated by 9 s of fixation; 18 images were presented for 750 ms followed by a 250 ms blank screen in each block. All images of faces and cars were presented in color with equalized luminance and their scrambled version was created with Fourier phase randomization (e.g. Sadr & Sinha, 2004).

Image acquisition

Scanning took place at the Maastricht Brain Imaging Center, using a 3T head scanner (Siemens, Erlangen, Germany). Functional data were obtained from 36 transverse slices with a spatial resolution of 3.5 × 3.5 × 3.5 mm (acquisition matrix: 64 × 64), using a repeated single-shot echo-planar imaging sequence (TE = 50 ms; TR = 2250 ms; FA = 90°; FOV = 224 mm). T1-weighted structural images were obtained with 1 × 1 × 1 mm spatial resolution (acquisition matrix: 256 × 256), using ADNI sequence (TE = 2.6 ms; TR = 2250 ms; FA = 9°; FOV = 256 mm). A 25° angle perpendicular to the main magnetic field B_0 was used to reduce magnetic artifacts and signal dropout, allowing us to record up to the anterior inferior temporal lobe (Deichmann *et al.*, 2003) in all functional scans (localizer and subsequently recorded experiment with morph stimuli).

Functional magnetic resonance imaging data analysis

Data were analyzed using BRAIN VOYAGER QX (Version 1.10.4, Brain Innovation, Maastricht, The Netherlands). The first four volumes of each functional dataset were discarded due to saturation effect. Preprocessing steps included slice scan time correction, linear trend removal, high pass filtering (removing frequencies lower than 2 cycles/session, ≈0.003 Hz for experimental runs and 0.005 Hz for localizer runs) and three-dimensional motion correction (with realignment to the respective first volume). The data were spatially smoothed using a Gaussian filter (FHWM = 6 mm). Both anatomical and functional data were transformed into Talairach space (Talairach & Tournoux, 1988). The statistical analysis was based on a general linear model (GLM), in which the predictor time-course was obtained by convolution of a condition time-course with a two-gamma hemodynamic response function.

The areas responding preferentially to faces were defined independently for each individual participant from localizer scans, using the contrast [faces − cars] in conjunction with the contrast [faces − scrambled faces]. This conjunction analysis ensured that the activation in all regions of interest (ROIs) was not related to low-level features of faces. Before identifying regions individually, we first performed a GLM on localizer scans at the group level. Clusters that showed significant effects [*p*(Bonferroni corrected for multiple comparisons) < 0.005] were identified and used as a guideline for the selection of individual ROIs. At the group level, numerous regions within the face-processing network were identifiable by means of the face localizer (see Table 1, Fig. 2). These included (bilaterally) the FFA, occipital face area (OFA), superior temporal sulcus (STS), amygdala, precentral gyrus (PrG) and a right lateral region within the anterior inferior temporal gyrus/temporal pole. We selected those clusters that were consistently identifiable for the majority of participants ($n \geq 8$ in the right hemisphere) as our ROIs, and attempted to identify homologous regions when possible. Thereby, we included bilateral FFA, OFA, STS and PrG (note that the left PrG was only identifiable for five participants; see Table 2, Fig. 3).

For each participant, all contiguous voxels in the middle fusiform gyrus, inferior/middle occipital gyrus, STS and PrG that were significant at *q*(false discovery rate)< 0.001 were selected. We raised the statistical threshold for three participants to separate their overlapping fusiform and inferior occipital activation. We also lowered the *q*(false discovery rate) to 0.005 for one, to 0.05 for two and to 0.1 for two participants in order to be able to localize the OFA, due to the relatively smaller size of their respective regions (see Table 2 for individual ROIs). Note that this is performed independently of the scans used to test the hypothesis of this study, and is required given the overlap in activation in face-preferential regions (see e.g. Dricot *et al.*, 2008).

TABLE 1. Mean Talairach coordinates of face-preferential ROIs obtained by contrasting [faces − cars] in conjunction with [faces − scrambled faces] for two external localizer runs, across 13 participants

	Mean coordinates (±SD)			
ROI	*x*	*y*	*z*	No. of voxels
rFFA	40 ± 3	−45 ± 7	−16 ± 4	3574
lFFA	−40 ± 3	−45 ± 5	−16 ± 3	1867
rOFA	31 ± 4	−85 ± 4	−7 ± 5	2407
lOFA	−28 ± 2	−87 ± 2	−10 ± 3	368
rSTS	50 ± 6	−45 ± 6	9 ± 5	4969
lSTS	−47 ± 3	−48 ± 2	8 ± 2	556
rPrG	31 ± 1	7 ± 2	25 ± 2	180
lPrG	−36 ± 3	6 ± 2	27 ± 2	560
rAmg	19 ± 4	−7 ± 4	−9 ± 3	1508
lAmg	−20 ± 4	−8 ± 3	−9 ± 3	1222
rAIT/temporal pole	28 ± 3	−3 ± 2	−27 ± 3	453

Reported clusters [*p*(Bonf) < 0.005] were used as a guideline for the selection of individual ROIs. *x*, *y*, *z*, Talairach coordinates in mm. lAmg, left amygdala; lFFA, left FFA; lOFA, left OFA; lPrG, left PrG; lSTS, left STS; rAIT, right anterior inferior temporal gyrus; rAmg, right amygdala; rOFA, right OFA; rPrG, right PrG; rSTS, right STS.

To test our hypothesis, we investigated fMR adaptation effects in each of the individually defined ROIs. To this end, only half of the trials could be analyzed as, due to technical error for 10 subjects on one side of each morph continuum, the *within* condition erroneously involved presentation of stimuli differing by 20% as opposed to 30%. These trials were therefore omitted for all 13 participants in order to have an equal number of trials across subjects. Note that this did not affect the ratio with which both identities of a given continuum were presented. However, given their potential importance to the research question addressed, we analyzed these data for the subsample of 10 participants (see later). As was the case in the study of Rotshtein *et al.* (2005), the analysis was time locked to the onset of the test (i.e. second) stimulus for each trial. Specifically, for each subject and each ROI, the beta weights associated with experimental conditions (i.e. the coefficients of predictor time-course) were estimated. To examine and compare the magnitude of the release from adaptation, we conducted paired *t*-tests for random effects, as well as independent sample *t*-tests with unequal variances assumed for fixed effects. In the following, both analyses will be referred to as random and fixed effects analyses, respectively.

It has been established that increasing the number of subjects is desirable to elevate the statistical power in fMR imaging studies [as opposed to increasing the number of scans per subject; see e.g. Tanabe *et al.* (2002)]. However, especially in the light of the nature of the present investigation, the number of participants testable was limited (only students of the same class could participate, participation was voluntary). Although, strictly speaking, only tests of random effects allow population-related inferences, we note that tests of fixed effects analyses can indeed be meaningful in terms of allowing inferences about typical characteristics at the population level, via the use of conjunction (separate subject) analyses for relatively small numbers of subjects (see Friston *et al.*, 1999).

Using the *same* condition as a baseline, we compared the difference in beta weights to illustrate the magnitude of release from adaptation induced by *between* or *within* conditions, respectively.

To show that the effects that we report here are reflected in the hemodynamic response function, we computed the condition-related average time-courses within each ROI. Specifically, for each ROI, a mean time-course was extracted across all included voxels for each of the three experimental conditions, for each participant separately. These time-courses were then averaged across participants for each condition and ROI, respectively. Note that we present the time-course plots for illustration purposes only, not for statistical inference.

We also performed a whole-brain analysis to highlight brain regions that are sensitive to *within* and *between* category changes, without prior external localization. A multi-subject fixed-effects GLM was carried out independently for each voxel. Brain regions sensitive to *within* and/or *between* category differences were then identified given the appropriate contrasts. Clusters that showed a significant effect (one-tailed *t*-test, postcorrected by cluster size thresholding > 5 voxels; for contrast-dependent *P*-values see Table 3) were reported. We further examined the face selectivity of the resulting clusters using the contrasts [faces − cars] and [faces − scrambled faces] with the time-course data extracted from localizer scans. A cluster was considered face-preferential only if both contrasts yielded significant results.

Behavioral data analysis

The behavioral performance of the participants was collected throughout the fMR imaging experiment. The accuracy and mean correct response time were computed for each of the three conditions

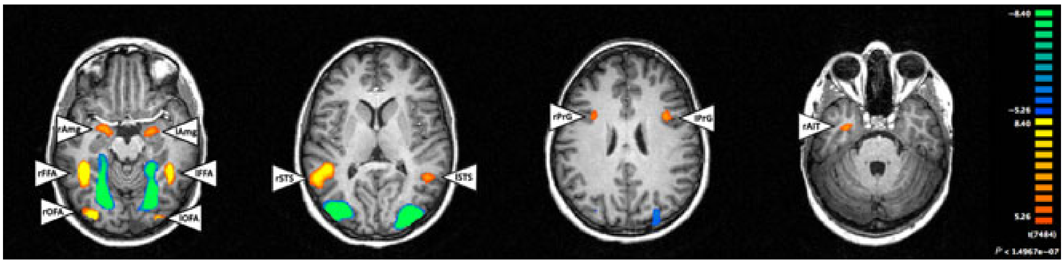

FIG. 2. Face-preferential regions identified at the group level for $N = 13$ subjects in an external localizer (axial planes, radiological convention). Clusters displayed here responded significantly more to faces as compared with cars and scrambled faces, respectively [p(Bonf) < 0.005], and served as a guideline for individual ROI selection. These included the bilateral FFA, OFA, amygdala (Amg), STS and PrG, as well as a right lateral region within the anterior inferior temporal gyrus/temporal pole (rAIT; for coordinates see Table 1). Clusters that were individually identified and subject to ROI analyses included the bilateral FFA, OFA, STS and PrG (see Table 2, Fig. 3). r, right; l, left.

(for one side of each continuum; see above) and tested with a repeated-measures ANOVA. *Post hoc* comparisons were conducted to investigate the differences between conditions.

Results

Behavioral results

For both accuracy and reaction times (RTs), individual performance was determined by combining the available data from all three experimental runs; individual averages were then subject to a repeated-measures GLM, with condition as a within-subject factor. On average, participants obtained 72% correct responses, and showed significant differences between conditions as revealed by a significant main effect ($F_{2,24} = 8.64$, $P = 0.001$). *Post hoc* comparisons indicated that participants were significantly more accurate for the *between* as compared with the *within* condition ($P < 0.001$); the remaining comparisons (*between* vs. *same* and *within* vs. *same*) did not yield significant differences ($P = 0.62$ and $P = 0.10$, respectively).

Parallel findings were obtained for the analyses of RTs. We found a main effect of condition ($F_{2,24} = 5.31$, $P = 0.012$), and *post hoc* comparisons revealed that RTs were significantly prolonged for *within* as compared with *between* trials ($P = 0.03$). As for accuracy scores, the remaining comparisons (*between* vs. *same* and *within* vs. *same*) did not yield significant differences ($P = 0.07$ and $P = 0.66$, respectively).

Thus, we found categorical perception for our personally familiar face stimuli in that *within* trials were associated with fewer ‘different’ responses and higher RTs as compared with *between* trials (see Fig. 1C).

Region of interest-based imaging analysis

In the following, the results of the ROI-based analysis are reported. As indicated above, we performed paired t-tests for random effects, and independent sample t-tests with unequal variances assumed for fixed effects (given that some ROIs had a smaller number of subjects included for the analysis) on the beta weights extracted from the ROIs of the participant, as shown in Fig. 3. For illustration purposes, time-course plots (see above) of a subset of ROIs are provided in Fig. 4.

Right fusiform face area

As demonstrated in Figs 3 and 4, the response in the right FFA (rFFA) (Talairach coordinates in millimeters along left-right (x), anterior-posterior (y), and superior-inferior (z) axes, (mean ± SD), voxel size ± SD, 37 ± 3, −44 ± 8, −15 ± 3, 933 ± 502 voxels, $n = 13/13$) was significantly larger for the *between* and *within* as compared with the *same* condition [$t_{12} = 3.80$, $P = 0.001$ and $t_{12} = 3.19$, $P = 0.004$], thus indicating a general release from adaptation. There was no difference in the magnitude of release from adaptation between these two conditions either when analyzing for random [$t_{12} = 0.88$, ns] or fixed [$t_{116} = -1.34$, $P = 0.182$] effects.

Left fusiform face area

The results within the left FFA (−37 ± 3, −46 ± 7, −16 ± 2, 681 ± 291 voxels, $n = 13/13$) paralleled those found for the rFFA; a general effect of adaptation was found along with no differences between the two conditions involving stimulus changes (see Figs 3 and 4). The *within* condition elicited a larger response as compared with the *same* condition [$t_{12} = 3.66$, $P = 0.002$]. Although the responses for *between* trials were larger than those for *same* trials when analyzing for random effects, this comparison did not yield significant differences [$t_{12} = 1.55$, $P = 0.073$]; however, both conditions differed significantly when analyzed for fixed effects [$t_{116} = 2.90$, $P = 0.004$]. There was no significant difference between the *within* and *between* conditions either when analyzing for random [$t_{12} = 0.21$, ns] or fixed [$t_{116} = 0.29$, ns] effects.

Right occipital face area

In the right OFA (33 ± 8, −83 ± 7, −9 ± 4, 579 ± 413 voxels, $n = 13/13$), neither the *between* nor the *within* condition differed significantly from the *same* condition [$t_{12} = -0.75$, ns and $t_{12} = 0.32$, ns, respectively] (Fig. 3); this was also true when analyzing for fixed effects [$t_{116} = -0.87$, ns and $t_{116} = 0.42$, ns, respectively]. Beyond this, although responses for the *within* condition were larger than those obtained for the *between* condition, this difference did not reach significance, either when analyzed for random [$t_{12} = 1.52$, $P = 0.077$] or fixed [$t_{116} = 1.74$, $P = 0.081$] effects.

Left occipital face area

The random effects analysis within the left OFA (−30 ± 9, −84 ± 7, −9 ± 6, 237 ± 160 voxels, $n = 10/13$) revealed significantly larger responses for the *between* as compared with the *same* condition [$t_9 = 1.84$, $P = 0.049$]. The responses associated with the *within* and *same* conditions did not differ significantly [$t_9 = 1.23$, $P = 0.25$ and $t_{89} = 1.49$, $P = 0.137$]. Furthermore, we found no difference between the *between* and *within* conditions [$t_9 = 0.25$, ns and $t_{89} = 0.16$, ns] (see Fig. 3).

Right superior temporal sulcus

Within the right STS (−49 ± 4, −44 ± 10, −10 ± 7, 408 ± 479 voxels, $n = 12/13$), *between* trials elicited larger responses than

TABLE 2. Talairach coordinates and cluster sizes of ROIs of individual participants

	rFFA				lFFA				rOFA				lOFA			
	x	*y*	*z*	Voxels	*x*	*y*	*z*	Voxels	*x*	*y*	*z*	Voxels	*x*	*y*	*z*	Voxels
S01‡	43	−59	−11	892	−41	−46	−16	726	27	−86	−12	1219	−23	−89	−9	58
S02*	37	−44	−17	762	−34	−43	−18	637	28	−87	−12	702	−33	−85	−10	242
S03‡	39	−40	−13	75	−35	−50	−15	454	19	−95	1	992	−30	−93	0	345
S04¶	33	−32	−17	592	−35	−38	−17	555	45	−78	−9	460	−27	−78	−18	76
S05†	40	−45	−16	1321	−39	−43	−14	797	42	−70	−13	1152	−45	−74	−12	334
S06‡	39	−36	−17	310	−43	−38	−19	483	31	−85	−10	885	−19	−97	−11	130
S07‡	38	−42	−16	1374	−34	−50	−18	1399	41	−88	−4	721				
S08**	36	−45	−16	1223	−40	−49	−15	986	41	−82	−10	175	−39	−81	−10	379
S09¶	35	−60	−7	800	−36	−39	−14	325	26	−80	−7	695	−21	−83	−11	127
S10†	38	−40	−12	840	−39	−57	−13	495	30	−74	−10	104				
S11**	37	−39	−20	563	−37	−57	−17	539	35	−78	−15	154				
S12§	36	−49	−15	1609	−37	−40	−17	508	35	−86	−12	66	−21	−86	−7	548
S13‡	35	−46	−12	1772	−37	−47	−16	949	28	−88	−6	198	−40	−76	1	127
Average	37 ± 3	−44 ± 8	−15 ± 3	933 ± 502	−37 ± 3	−46 ± 7	−16 ± 2	681 ± 291	33 ± 8	−83 ± 7	−9 ± 4	579 ± 413	−30 ± 9	−84 ± 7	−9 ± 6	237 ± 160

	rSTS				lSTS				rPrG				lPrG			
	x	*y*	*z*	Voxels	*x*	*y*	*z*	Voxels	*x*	*y*	*z*	Voxels	*x*	*y*	*z*	Voxels
S01‡	50	−37	8	1500					35	0	30	572	−35	−1	33	104
S02*	50	−46	2	418	−51	−48	5	208	38	0	20	161	−36	−2	25	56
S03‡	48	−36	4	269												
S05†	57	−48	9	118	−53	−48	13	352	30	5	22	170	−35	10	23	85
S06‡	46	−35	12	68	−50	−65	14	567					−56	8	24	222
S07‡	46	−66	22	135	−40	−63	21	251								
S08**	48	−43	19	80					33	10	25	162				
S09¶	42	−31	5	117					40	22	27	116				
S10†	52	−53	13	344	−45	−44	7	198	33	9	28	80	−40	7	27	136
S11**	51	−47	4	1027	−50	−55	8	127								
S12§	52	−55	15	470					31	21	22	75				
S13‡	46	−44	8	734	−51	−52	5	232	49	12	21	169				
Average	49 ± 4	−44 ± 10	10 ± 7	408 ± 479	−49 ± 5	−54 ± 8	10 ± 6	276 ± 145	36 ± 6	10 ± 8	24 ± 4	188 ± 160	−40 ± 9	4 ± 6	26 ± 4	121 ± 64

Superscript symbols indicate the statistical threshold applied for individual ROI definition: *p(Bonf) < 0.000; $^{\dagger}p$(Bonf)<0.002; $^{\ddagger}q$[false discovery rate (FDR)] < 0.001; $^{\S}q$(FDR) < 0.005; $^{\P}q$(FDR) < 0.05; **q(FDR) < 0.1. *x*, *y*, *z*, Talairach coordinates in mm. lFFA, left FFA; lOFA, left OFA; lPrG, left PrG; lSTS, left STS; rOFA, right OFA; rPrG, right PrG; rSTS, right STS.

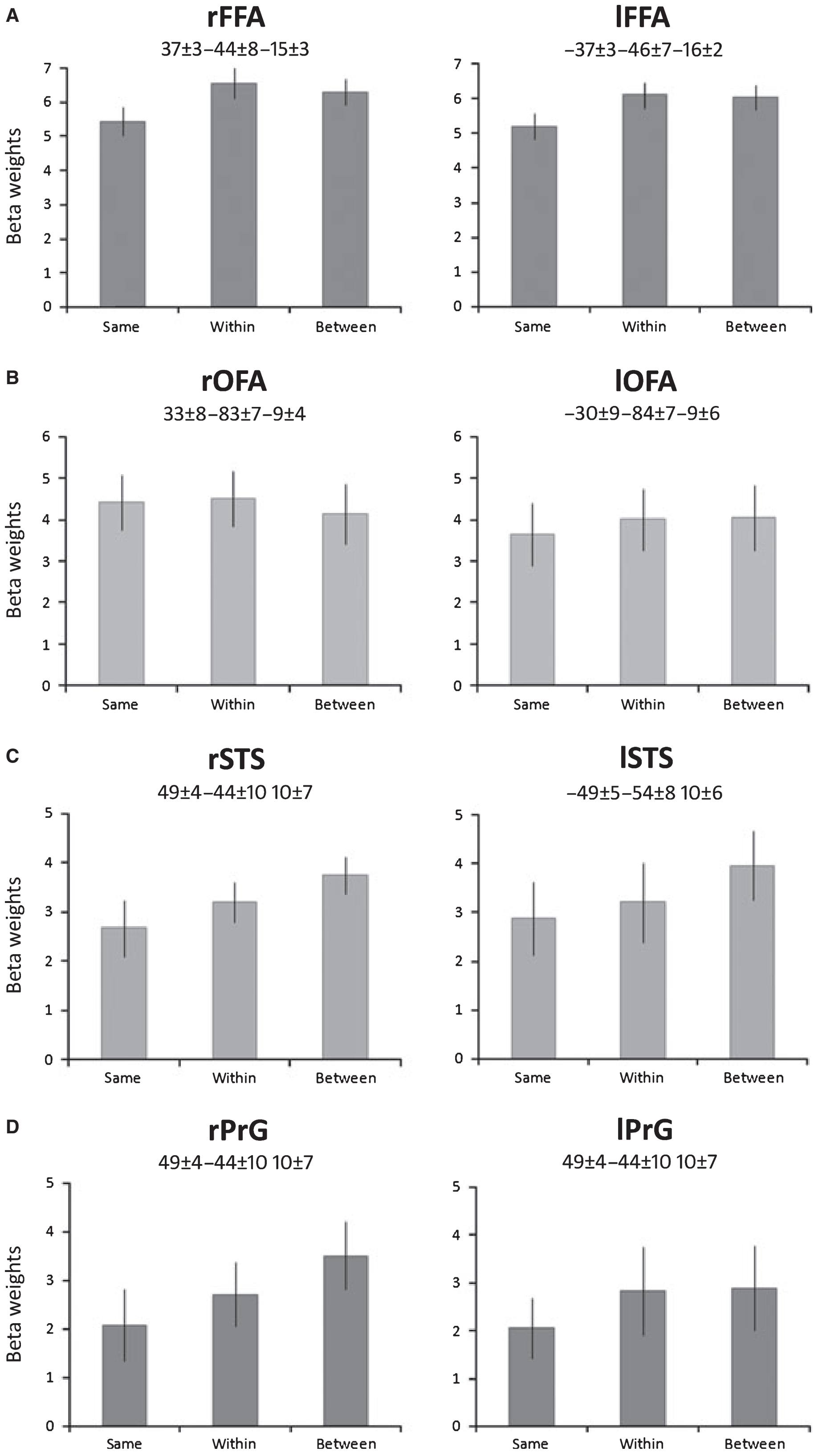

FIG. 3. Results of analyses for externally identified ROIs. Displayed are the beta weights obtained for stimulus repetition (*same*) and test faces differing from the adapting face by 30% that were located on either the same or opposite side of the categorical boundary (*within* or *between* conditions, respectively). Histograms depict beta weights within left and right ROIs. (A) FFA, (B) OFA, (C) STS and (D) PrG. r, right; l, left.

TABLE 3. Clusters revealed by the whole-brain analysis: location, coordinates, size and face selectivity

Contrast	Cluster location	Hemisphere	*x*	*y*	*z*	No. of voxels	Face selectivity	
							F>O	F>ScrF
[W + B] − S	Lateral OcG	R	37 ± 4	−61 ± 4	−11 ± 2	1108	ns	***
	Middle FuG	R	32 ± 4	−41 ± 3	−17 ± 2	857	*	***
	Middle FuG	L	−37 ± 2	−52 ± 5	−15 ± 2	314	***	***
[B − W] and [B − S]	*STG*	L	*−52 ± 5*	*−53 ± 3*	*27 ± 7*	*1764*	+	**
	SFGM	L	−5 ± 5	39 ± 4	39 ± 2	658	ns	**
	STS (lower bank)	L	*−59 ± 2*	*−38 ± 5*	*2 ± 2*	*357*	*ns*	**
	MFG	L	*−25 ± 3*	*7 ± 3*	*47 ± 2*	*240*	*ns*	**
	Genu of the CC	L	−5 ± 2	18 ± 2	12 ± 2	223	+	ns
	IFGTr	L	−52 ± 2	37 ± 3	7 ± 2	207	**	ns
	MFPG	L	−30 ± 2	59 ± 1	6 ± 2	168	ns	ns
	MFG	L	−33 ± 2	14 ± 2	27 ± 2	151	**	*
	Lateral ITG/temporal pole	R	49 ± 1	15 ± 2	−27 ± 1	111	ns	$P = 0.03$
	STS (inferior branch)	R	51 ± 1	−51 ± 1	13 ± 2	93	***	***
[W − S] and [W − B]	ITG	R	46 ± 2	−36 ± 2	−21 ± 2	366	***	***
	Anterior FuG	R	25 ± 3	−4 ± 1	−31 ± 2	229	***	***
	Medial ITG	R	35 ± 3	12 ± 2	−20 ± 2	149	$P = 0.02$	*

Reported clusters are significant at p(uncorrected) < 0.001. W, *within*; B, *between*; S, *same*; F>O, [faces − objects]; F>ScrF, [faces − scrambled faces]; R, right hemisphere; L, left hemisphere. Symbols indicating extent of face selectivity: $*P < 0.01$, $**P < 0.001$, $***P < 0.000001$, $+P < 0.01$ for $F<O$. Italics indicate significantly deactivated clusters. x, y, z, Talairach coordinates in mm. CC, corpus callosum; FuG, fusiform gyrus; IFGTr, inferior frontal gyrus, triangular part; ITG, inferior temporal gyrus; MFG, middle frontal gyrus; MFPG, middle frontopolar gyrus; OcG, occipital gyrus; SFGM, superior frontal gyrus, medial part; STG, superior temporal gyrus.

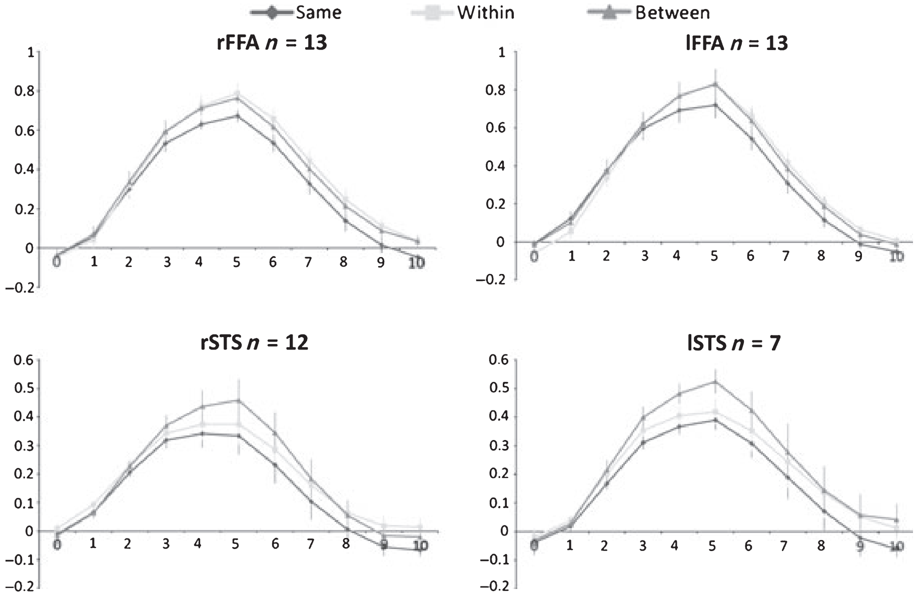

FIG. 4. Average time-courses extracted for the bilateral FFA and STS. Displayed are average time-courses for each of the three experimental conditions (*same*, *within*, *between*). In both the right and left FFA the *within* and *between* conditions elicited equivalent levels of signal increase as compared with stimulus repetition (*same*). In the right and left STS the magnitude of signal change was modulated by the degree of perceived changes in identity (*between* > *within* > *same*). x- and y-axes represent the time in volumes and amount of signal percent change, respectively. r, right; l, left.

same trials [$t_{11} = 3.66$, $P = 0.002$] (Figs 3 and 4). Responses for *between* trials were also significantly larger than those associated with *within* trials [$t_{11} = 1.91$, $P = 0.041$], but the *within* condition did not differ from the *same* condition [$t_{11} = 1.41$, $P = 0.093$]. However, this latter comparison reached significance when analyzed for fixed effects [$t_{116} = 2.37$, $P = 0.018$].

Left superior temporal sulcus

The left STS (−49 ± 5, −54 ± 8, 10 ± 6, 276 ± 145 voxels) was identified in 7 of 13 participants. Analyzing for random effects revealed a significantly larger response in the left STS for the *between* as compared with the *same* [$t_6 = 3.03$, $P = 0.011$] and *within* [$t_6 = 2.02$, $P = 0.045$] condition, despite the small sample size. Responses on *within* trials did not differ from those obtained for the *same* condition [$t_6 = 0.72$, ns]; this also held when investigated for fixed effects [$t_{62} = 1.12$, ns] (see Figs 3 and 4).

Right precentral gyrus

The right PrG (36 ± 6, 10 ± 8, 24 ± 4, 188 ± 160 voxels) was also identified in only 7 of 13 participants. Despite the small sample size, the *between* condition elicited a larger response within this ROI as compared with the *same* condition [$t_6 = 3.88$, $P = 0.004$]. Contrasting the *between* and *within* conditions yielded significantly larger responses in the prior condition [$t_6 = 2.31$, $P = 0.030$]. *Within* trials elicited larger responses than *same* trials; although this difference was not significant when tested for random effects [$t_6 = 1.51$, $P = 0.092$], it reached significance in a fixed effect analysis [$t_{62} = 2.12$, $P = 0.034$] (see Fig. 3).

Left precentral gyrus

The left PrG (−40 ± 9, 4 ± 6, 26 ± 4, 121 ± 64 voxels) was identified in an even smaller number of participants ($n = 5/13$). Contrasting both the *between* as well as the *within* with the *same* condition revealed that *between* trials elicited larger responses. Although these contrasts failed to reach significance when analyzed for random effects [$t_4 = 2.02$, $P = 0.057$ and $t_4 = 1.69$, $P = 0.083$], they differed significantly in the fixed effects analysis [$t_{44} = 2.40$, $P = 0.016$ and $t_{44} = 2.21$, $P = 0.027$]. However, there was no indication of differential responses for *between* compared with *within* conditions [$t_4 = 0.11$, ns], which was also true for the fixed effects analysis [$t_{44} = 0.20$, ns] (see Fig. 3).

To summarize, investigating the magnitude of release from adaptation in individually defined ROIs, we found differential, region-dependent effects of *within* and *between* category changes. In both the right and left FFA, *within* and *between* category changes elicited an equivalent signal increase as compared with stimulus repetition (*same*), indicating a general effect of adaptation in the absence of categorical perception within these ROIs. [We also conducted analyses on the trials omitted due to technical error to establish whether within-category changes that involved 20% differences were associated with less recovery from adaptation than those involving 30% differences. Specifically, we first investigated whether '20%-*within*' trials elicited recovery from adaptation as compared with stimulus repetition (*same*). In both the right and left FFA, separate subject random effects GLMs revealed significant recovery from adaptation for 20%-*within* trials [$t_9 = 3.25$, $P = 0.001$ and $t_9 = 2.69$, $P = 0.007$]. Contrasting 20%-*within* and 30%-*within* trials using the same approach yielded no significant differences, either in the right or left FFA [$t_9 = 0.28$, ns and $t_9 = 1.06$, ns, respectively]. These results thus indicate that 20% changes between faces located on the same side of the perceptual boundary were sufficient to elicit full recovery from adaptation (as reported above for 30%-*within* trials) in the FFA bilaterally.]

On the contrary, categorical perception was found within the right lateral STS and PrG. Beyond finding a general effect of adaptation (i.e. both conditions involving physical changes eliciting a signal increase compared with stimulus repetition), the largest signal increase was found for *between* category changes, which was larger than that observed for *within* category changes.

The results within the *left* STS and PrG were somewhat different. In the prior ROI, we found that only *between* category changes elicited a signal increase; *within* category changes were associated with signal changes similar to those associated with stimulus repetition. In the left PrG, both types of physical changes (*within*, *between*) led to equivalent signal changes, which were elevated as compared with that associated with stimulus repetition (*same*).

Whole-brain imaging analysis

Without prior localization, a whole-brain fixed-effect (separate-subject) GLM analysis was performed to identify brain regions showing adaptation in general, and furthermore those sensitive to *within* as opposed to *between* category changes. The clusters reported here are based on uncorrected P-values < 0.001 (see Table 3) in combination with cluster size thresholding (5 voxels for all contrasts). Face selectivity was confirmed for these clusters by means of contrasting [faces − objects] and [faces − scrambled faces], respectively; clusters were considered as face-preferential if both contrasts yielded significant P-values (see Table 3). The results of the whole-brain analysis are largely consistent with our reported ROI-based results.

First, in order to identify areas showing general adaptation, we combined both conditions involving a stimulus change (*within* and *between*) in comparison to the baseline (*same*). This comparison yielded three ventral clusters, two of which were face-preferential (Table 3), located in the (right middle and left posterior) fusiform gyri. The coordinates of these clusters show close correspondence with the group's rFFA and left FFA, as found for the localizer scans (see Table 1). Despite the partial overlap between the group-based rFFA and the cluster identified within the lateral occipito-temporal sulcus, the latter exhibited significantly increased activation for faces as compared with scrambled faces, but not objects.

Next, the comparison of [*between* − *same*] in conjunction with [*between* − *within*] was performed with the aim of identifying regions sensitive to *between* category changes. Of the 10 identified clusters, three (located in the superior temporal gyrus, lower bank of the STS and middle frontal gyrus) exhibited signal *decrease* across all conditions. We report these clusters, but do not further discuss them, as we were interested in activation-related signal changes. Of the remaining seven clusters, two [located in the middle frontal gyrus and inferior branch of the STS, respectively (see Table 3)] were found to be face preferential. Interestingly, these show close correspondence with two regions defined as ROIs based on the localizer scans, with one located within the posterior part of the right STS and the other proximal to the left PrG.

Lastly, we identified regions exhibiting a larger response to subtle changes between faces located on the same side of the categorical boundary, i.e. the *within* condition, as compared with the remaining ones (contrast: [*within* − *same*] in conjunction with [*within* − *between*]). This comparison gave rise to three face-preferential clusters (Table 3). The first cluster, located in the inferior temporal gyrus, showed partial overlap with the group-based rFFA, located slightly lateral to this ROI (furthermore, it lay just lateral to the face-preferential left mid-fusiform cluster found to display release from adaptation for stimulus changes in general, i.e. [(*within* + *between*) − *same*], see above). The second cluster, located in the right anterior fusiform gyrus, corresponded to a region identified in the localizer scans on the group level, which, however, could not be identified for each subject in order to conduct ROI analyses (see Table 1). The last cluster identified as sensitive to the *within* condition was located in the right inferior temporal polar region, and was the only cluster found in the whole-brain analysis that lacked a localizer-based analog.

Discussion

Sensitivity to subtle changes between faces in the fusiform face area – even for personally familiar faces

We found that the FFA was sensitive to subtle changes of facial identity of personally familiar faces, irrespective of whether the face stimuli were located on the same or opposite side of a categorical boundary. Our findings thus contradict those obtained using famous faces, for which the FFA showed sensitivity to *between* category changes only (Rotshtein *et al.*, 2005). However, they are in line with previous studies that have used synthetic (Loffler *et al.*, 2005) and unfamiliar (Gilaie-Dotan & Malach, 2007) faces.

The present results thus indicate that it is not the nature of the underlying face representations (familiar vs. unfamiliar) that determines the degree of sensitivity of the FFA to face identity. Rotshtein *et al.* (2005) reported that, in the anterior temporal pole (bilaterally) and right anterior hippocampus, familiarity ratings correlated with the difference in activity for the *between* as compared with *within* condition – however, this was not true for the FFA. Thus, although face familiarity modulates the response to faces in the FFA (e.g. Gobbini *et al.*, 2004; Rossion *et al.*, 2003; for a review see Gobbini & Haxby, 2007), categorical perception in the FFA is not modulated by familiarity, as supported by an increasing body of evidence. Although, theoretically, it could be that only iconic face (and/or non-face) representations (as opposed to familiar or unfamiliar ones) render categorical perception within the FFA, there are other potential factors that may explain why the results reported by Rotshtein *et al.* (2005) differ from ours, and those of others (Loffler *et al.*, 2005; Gilaie-Dotan & Malach, 2007). Rotshtein *et al.* (2005) presented participants with face stimuli taken exclusively from one side of each morph continuum. As not all identities were presented, and thus perceived with equal likelihood, the *between* condition involved presentation of a 'rare' or 'novel' event (i.e. identity). Thus, as stimulus probability influences the magnitude of neural adaptation observed (Summerfield *et al.*, 2008), and new faces give rise to larger responses in the FFA (e.g. Dubois *et al.*, 1999; Mur *et al.*, 2010), the relatively larger release from adaptation for *between* as opposed to *within* changes reported by Rotshtein *et al.* (2005) may have been confounded by a novelty effect associated with the prior (rare) condition.

In addition, the nature of the task that subjects engaged in in the respective studies is likely to modulate the magnitude of adaptation observed within the FFA. Both Rotshtein *et al.* (2005) and Loffler *et al.* (2005) employed orthogonal tasks, whereas subjects in the study of Gilaie-Dotan & Malach (2007) had to indicate whether they noticed *any* difference between the face stimuli presented, as was the case in our experiment. Recent evidence suggests that the extent of repetition suppression is directly task-related. Goh *et al.* (2009) compared levels of adaptation when subjects performed a target task [similar to that of Rotshtein *et al.* (2005)], as compared with a discrimination task [as applied here and in Gilaie-Dotan & Malach (2007)]. Their findings indicate that, in the realm of target tasks, repetition suppression is greater than in discrimination tasks. This adds to the findings of attentional/task-dependent modulation of the magnitudes of adaptation observed within this region (Henson *et al.*, 2002; Kadosh *et al.*, 2010), which have further been shown to vary as a function of age (Goh *et al.*, 2010).

To summarize, we suggest that observed insensitivity to subtle facial changes within the FFA, as reported by Rotshtein *et al.* (2005), is more likely to arise due to methodological factors, such as stimulus likelihood and/or task type.

Categorical perception in other face-preferential regions – superior temporal sulcus and precentral gyrus

Another finding of the present study is that in other face-preferential regions (the right STS and PrG), release from adaptation was greater for faces located on the opposite as compared with the same side of the categorical boundary, despite equivalent physical changes (i.e. categorical perception was observed). This observation was made both in the whole-brain and ROI analysis.

Although several studies suggest that these regions are involved in other aspects of face processing (see Haxby *et al.*, 2000), some studies have reported identity adaptation within these regions. For instance, Winston *et al.* (2004) showed repetition suppression for identity in the FFA and right STS, although the effect was modulated by expression repetition in the latter region. Fox *et al.* (2009) also found sensitivity to identity and expression in both the FFA and posterior STS, with the latter being dependent on the subjects' attention to expression. Thus, it appears that there is evidence for a role of the posterior STS in face identity processing. Although, in both cases, processing facial expression was a precondition, flexible use of regions within the multifunctional STS seems plausible. Task- and stimulus-dependent modulation through co-activated (face-preferential) structures via bidirectional connections (Hein & Knight, 2008) may well enable processing of other facial information not related to expression or gaze perception, for instance. Although face identification may not represent the primary function of this region, it may be facilitated by re-entrant functional connections with other face preferential regions. However, this does not mean that subtle within identity changes are discriminated to the same extent as in other regions more directly involved in the processing of face identity information.

A further region that demonstrated categorical perception was the functionally defined PrG. Interestingly, the whole-brain analysis revealed a cluster proximal to this ROI (see Table 3) that displayed a larger signal to subtle changes between faces located on the opposite as compared with the same side of the categorical boundary (*between* vs. *within* and *same*, respectively). Another recent neuroimaging study (Rajimehr *et al.*, 2009) also identified a face-selective region within the PrG. Furthermore, the location of our face-selective prefrontal ROI is proximal to that identified by, e.g. Kelley *et al.* (1998) during intentional encoding of previously unfamiliar faces. The strong right hemisphere lateralization reported by Kelley *et al.* (1998) led Tsao *et al.* (2008a) to suggest that this area may represent the human homolog to one of the three prefrontal face patches found in macaques (namely a prefrontal lateral area (PL), located in the inferior convexity). Single-cell recordings (O Scalaidhe *et al.*, 1997) of face-selective neurons within regions that are identical to those reported by Tsao *et al.* (2008a) have identified functional parallels between frontal face-selective cells and those within regions from which their afferents originate, namely face-selective neurons in the ventral STS and inferior temporal gyrus.

Given the nature of the task in our experiment, the present results corroborate previously suggested functions of prefrontal face-selective regions and furthermore correspond closely with respect to anatomical location. Note that both the right hemisphere bias and the differences in location across animals reported by Tsao *et al.* (2008b) are consistent with our findings. Frontal face-selective ROIs were identified more frequently in the right than left hemisphere and their location varied inter-individually (see Table 2). This has also been reported elsewhere for primates and humans (Tsao *et al.*, 2008b; Rajimehr *et al.*, 2009), and may account for the fact that these ROIs could not be identified consistently for all subjects (Tsao *et al.*, 2008b). The lower statistical power, given the smaller number of individual ROIs identified for both the left STS and PrG, may explain why the results within these regions [despite resembling those in the right hemisphere homologs (see Fig. 3C and D)] failed to reach significance.

Involvement of anterior ventral regions in discrimination of subtle changes between faces perceived as the same identity

The results of our whole-brain analysis revealed three face-selective regions in the anterior part of the ventral cortex that exhibited signal increase for changes between faces on the same side of the categorical boundary (i.e. for *within* as compared with *same* or *between* changes).

Previous fMR imaging studies have generally failed to identify such face-related anterior regions. However, signal drop-out effects in the infero-temporal cortex caused by ear canal and sinus susceptibility artifacts (absent in PET studies; e.g. Sergent *et al.*, 1992; Rossion *et al.*, 2001; Sigiura *et al.*, 2001) may explain the lack of reports of these areas. Furthermore, some studies investigating the function of face-selective regions may simply not have covered the entire temporal lobe (e.g. Kanwisher *et al.*, 1997). Nevertheless, in both humans and primates, similar patterns of up to six distinct face-selective regions can be identified using both familiar and unfamiliar face stimuli (Tsao *et al.*, 2008a). These include anterior regions of similar location to those found here for *within* category changes between faces. Both the anterior fusiform cluster and the one located within the medial inferior temporal gyrus may correspond to the anterior face patches AFP1 and AFP2 of Tsao *et al.* (2008b) identified in 9 and 2 of 13 human subjects, respectively. An anterior fusiform cluster has also been reported as showing a larger response to unfamiliar than familiar faces in a PET study with morphed faces (Rossion *et al.*, 2001).

The present finding of sensitivity to *within* category face changes in these anterior regions suggests that face-selective regions within the ventral cortex may serve the fairly difficult task of discriminating subtle changes between familiar faces. Representations of the latter have been associated with anterior regions, potentially receiving inputs from and sending afferents to posterior regions.

Lack of adaptation in the occipital face area

In this study we did not find adaptation in response to stimulus repetition within the OFA. The nature of our stimuli may have had an impact on the activation patterns observed within this region. Recent findings from our laboratory suggest that the right OFA (defined functionally in the realm of an external localizer) is sensitive to changes of face shape, as opposed to surface reflectance (Jiang *et al.*, 2009). In the present study, stimuli were cropped and then carefully selected (same eye color, overall luminosity) to create best matches, so the faces representing the extremes of morph continua were morphologically extremely similar (see Fig. 1). The relatively small degree of changes in properties to which neural populations in this region are predominantly tuned may explain the observed lack of release from adaptation in the OFA.

The larger inter-individual variability in the OFA (as compared with the FFA) across subjects, as well as its proximity to lower-level visual and non-face-preferential areas, may also influence the extent to which adaptation can be observed in this region. These factors may render a relatively larger variability in terms of the pattern of signal increase/decrease observed across conditions on average. Note that the whole-brain analysis revealed a cluster in the right lateral occipital gyrus that showed general adaptation, i.e. a larger signal decrease for stimulus repetition than for both subtle and perceptually more distinct facial changes ([*within* + *between*] − *same*; see Table 3). The coordinates of this cluster (37 ± 4, −61 ± 4, −11 ± 2) are extremely close to those of right OFA ROIs reported elsewhere [see, e.g. Schiltz *et al.* (2010): 38 ± 5, −68 ± 5, −11 ± 6; block design experiment in Gilaie-Dotan & Malach (2007): 39 ± 2, −64 ± 3, −10 ± 2; Rotshtein *et al.* (2005) (authors reported MNI coordinates, corresponding Talairach coordinates are): 38, −65, −17 for the ROI analysis, 39, −57, −18 for the whole-brain analysis]. However, this lateral occipital cluster identified as showing repetition suppression in the whole-brain analysis did not respond significantly more to faces than objects (see Table 3). We assume that our failure to find adaptation in the OFA may be at least partly due to the conjunction analysis applied with the aim of identifying highly face-preferential ROIs in the localizer scans. If face and object preferential regions are partially overlapping, excluding object preferential areas may lead to a dramatic decrease of adaptation observed if adaptation is most pronounced in the overlapping regions.

It is worth noting that recent neuroimaging investigations have also observed generally lower effects of adaptation within the OFA (e.g. Betts & Wilson, 2010; Goh *et al.*, 2010). Gilaie-Dotan & Malach (2007) reported a gradual growth of adaptation from intermediate to high-order visual areas and, beyond this, that adaptation was 'less consistent' across subjects within the OFA (i.e. adaptation was observed for 6/12 subjects in the block design experiment and 5/8 in the event-related experiment, respectively). This is in line with our data, as six subjects did not show repetition suppression within this ROI, which can account for the overall lack of adaptation observed at the group level.

Again, we would like to offer the suggestion that task factors may also have been responsible for the lack of adaptation observed in the OFA. Kadosh *et al.* (2009) reported that the profile of activation within the FFA and OFA varied as a function of task type. Although they found highly similar response profiles across tasks, this similarity was obtained in the realm of a target detection task, similar to those used elsewhere (Loffler *et al.*, 2005; Rotshtein *et al.*, 2005). The subtle nature of changes to be actively detected in the present study (see stimuli) may partially account for the lack of adaptation observed here and may also have led to less pronounced adaptation in other studies (e.g. Gilaie-Dotan & Malach, 2007).

Conclusion

We demonstrated that the FFA is, in general, sensitive to subtle changes between personally familiar faces, regardless of their location with regard to the perceptual identity boundary. On the contrary, other face-preferential regions (STS, PrG) showed release from adaptation to changes between faces that varied as a function of perceived identity changes: the more different that faces looked, the higher the observed signal change, indicating categorical perception within these regions.

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Abbreviations

ADNI, Alzheimer's Disease Neuroimaging Initiative; FA, flip angle; FHWM, full width at half-maximum; FFA, fusiform face area; fMR, functional magnetic resonance; FOV, field of view; GLM, general linear model; MNI, Montreal Neurological Institute; OFA, occipital face area; PET, positron emission tomography; PrG, precentral gyrus; rFFA, right fusiform face area; ROI, region of interest; STS, superior temporal sulcus; TE, echo time; TR, repetition time.

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