

Representations of Facial Identity in the Left Hemisphere Require Right Hemisphere Processing

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Abstract

■ A quintessential example of hemispheric specialization in the human brain is that the right hemisphere is specialized for face perception. However, because the visual system is organized contralaterally, what happens when faces appear in the right visual field and are projected to the nonspecialized left hemisphere? We used divided field presentation and fMRI adaptation to test the hypothesis that the left hemisphere can recognize faces, but only with support from the right hemisphere.

Consistent with this hypothesis, facial identity adaptation was observed in the left fusiform face area when a face had previously been processed by the right hemisphere, but not when it had only been processed by the left hemisphere. These results imply that facial identity information is transferred from the right hemisphere to the left hemisphere, and that the left hemisphere can represent facial identity but is less efficient at extracting this information by itself. ■

INTRODUCTION

Information from the left visual field (LVF) is processed initially by the right hemisphere, whereas information from the right visual field (RVF) is processed initially by the left hemisphere. However, the two hemispheres are specialized for different types of visual information: For example, word processing is lateralized to the left hemisphere (Dehaene & Cohen, 2011; Cohen et al., 2000), and face processing is lateralized to the right hemisphere (Thomas et al., 2009; Yovel, Tambini, & Brandman, 2008; Le Grand, Mondloch, Maurer, & Brent, 2003; De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994; De Renzi, 1986; Gazzaniga & Smylie, 1983). Because information can appear in either the LVF or RVF in the environment, what happens when information appears contralateral to a nonspecialized hemisphere? For instance, in the case of face processing, how are we able to recognize people who appear on our right?

Whereas lower-level visual regions respond almost exclusively to the contralateral visual field, higher-level regions show a weaker preference (Hemond, Kanwisher, & Op de Beeck, 2007). The weaker bias in these regions may result from communication between hemispheres (interhemispheric transfer), whereby regions in one hemisphere receive input from the other hemisphere via commissures along the longitudinal fissure (Seacord, Gross, & Mishkin, 1979). Because objects and people frequently shift between visual fields because of their own motion or eye movements, interhemispheric transfer may help the visual system to track and recognize objects

across such changes and benefit from processing in the other visual field. In the case of lateralized functions, interhemispheric transfer may serve an additional role: it may allow the hemisphere specialized for a particular function to share its output with the nonspecialized hemisphere and facilitate processing there.

In the current study, we used divided field presentation and fMRI adaptation to investigate the interhemispheric transfer of higher-level visual information. Divided field presentation, a technique where images are presented in the periphery of the visual field (Gazzaniga & Smylie, 1983), allowed us to manipulate which hemisphere initially received information about an image. fMRI adaptation, the attenuated BOLD response to repeated versus novel images (Grill-Spector, Henson, & Martin, 2006), allowed us to determine what information was represented in particular brain regions (Turk-Browne, Scholl, & Chun, 2008). We combined these techniques to test the role of each hemisphere in representing facial identity.

Twelve subjects first completed a behavioral training session in which they learned associations between faces and names (Figure 1A). To dissociate facial identity from low-level image properties, subjects were trained to associate each name with multiple views of a face. During a subsequent fMRI session, subjects completed a divided field presentation task while fixating centrally (as verified with eyetracking). Each trial consisted of two faces presented sequentially to either LVF or RVF (Figure 2A), resulting in four spatial location conditions (LVF–LVF, LVF–RVF, RVF–RVF, and RVF–LVF; Figure 2B). The two faces were always shown from different viewpoints and depicted either the same person (same-identity) or different people (different-identity; Figure 2C). Due to the change in viewpoint (and

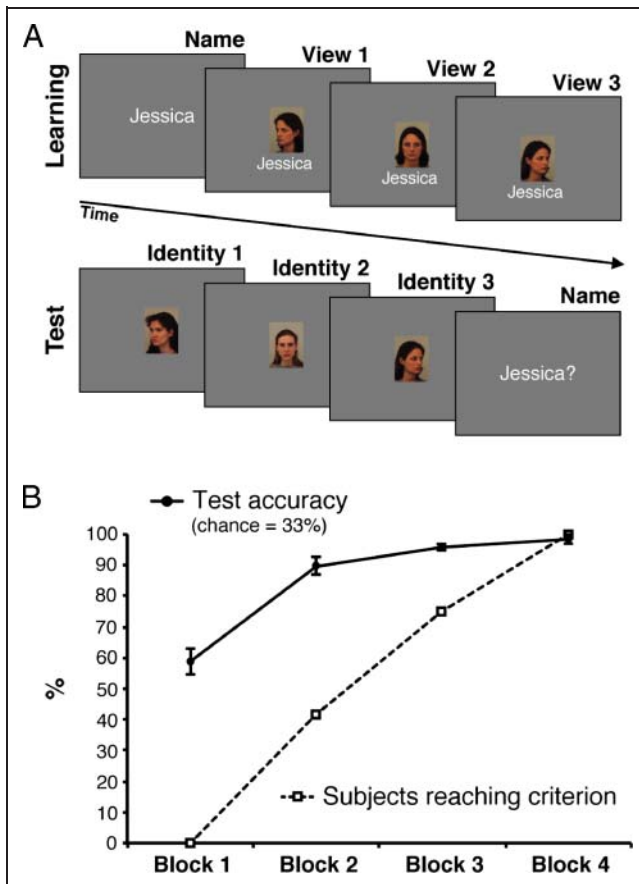


Figure 1. Training task. (A) On each “learning” trial, subjects passively watched a name followed by three views of that facial identity. On each “test” trial, three views of different facial identities were shown followed by a name, and subjects chose which face matched the name. (B) Test performance by block. Black circles indicate mean accuracy across subjects who had not yet reached criterion; white squares indicate percentage of subjects who reached criterion. Error bars depict ± 1 SEM.

corresponding change in image properties), an attenuated BOLD response for same-identity versus different-identity trials reflects viewpoint-independent adaptation of facial identity (Mur, Ruff, Bodurka, Bandettini, & Kriegeskorte, 2010; Ewbank & Andrews, 2008; Fang, Murray, & He, 2007; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005a, 2005b).

We focused on a face-selective region of ventral temporal cortex, the fusiform face area (FFA; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997). We used the FFA as a probe of whether facial identity information exists in a given hemisphere because this region has previously been implicated in facial identity processing (Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Grill-Spector, Knouf, & Kanwisher, 2004; Gauthier et al., 2000). To circumvent the anatomical variability of the FFA across subjects and avoid multiple comparisons over voxels, FFA ROIs were defined bilaterally in each subject using an independent localizer task. Percent BOLD signal change was extracted from these ROIs for each condition of the main

task. The second face in each trial allowed us to test whether the identity of the first face had been represented in the FFA. Although the FFA in each hemisphere receives input from both visual fields (directly or via interhemispheric transfer), it responds preferentially to faces in the contralateral visual field (Hemond et al., 2007). Thus, primary analyses were limited to the hemisphere contralateral to where the second face appeared.

We entertained three possible outcomes: First, because the right hemisphere is specialized for face processing, identity adaptation might be limited to when both faces are shown to the right hemisphere (LVF–LVF in the right FFA) or even occur irrespective of the visual field of the first face (RVF–LVF in the right FFA). Second, identity adaptation might occur in both hemispheres, but only when both faces are shown to the same hemisphere and interhemispheric transfer is not required (LVF–LVF in the right FFA and RVF–RVF in the left FFA). Third, our main hypothesis, the right hemisphere might extract identity information and share it with the left hemisphere, such that identity adaptation occurs in both hemispheres when the adapting first face is shown to the right hemisphere (LVF–LVF in the right FFA and LVF–RVF in the left FFA).

METHODS

Participants

Twelve participants (six women; mean age = 23.1 years, range = 18–34 years) participated for monetary compensation. All participants provided informed consent, and the study was approved by the Princeton University Institutional Review Board. All participants were right-handed, had normal or corrected-to-normal vision, and reported no history of neurological or psychiatric disorders.

Stimuli

Images for the main task were color photographs of 15 female facial identities from the Karolinska Directed Emotional Faces set (Lundqvist, Flykt, & Ohman, 1998). There were three photographs of each identity: one facing directly forward and two with the head turned 30° – 40° to the left and right. The individuals always displayed neutral facial expressions and eye gaze matched head direction. Images for the localizer task were a separate set of color photographs of male/female faces and indoor/outdoor scenes.

Procedure

Training Task

Before being scanned, subjects completed a behavioral training task where they learned associations between faces and names. Each of 15 identities was randomly assigned a unique name. The names were selected from the 20 most popular female baby names of 1989 (www.

ssa.gov/oact/babynames/) to ensure that subjects would be familiar with them. The training task served to teach subjects the name of each identity and to familiarize them with the three views of each face. The task consisted of a learning phase and a test phase, which subjects cycled between until reaching a criterion.

During the learning phase, subjects saw 15 identities one at a time. For each identity, a name appeared in the center of the screen. When the subject pressed the spacebar, a sequence of three images appeared in the center of the screen. The first image showed the person facing to the left, the next image showed her facing directly forward, and the last showed her facing right. Each image remained onscreen for 5 sec, with the name underneath.

During the test phase, subjects were tested on which name belonged to each face. On each trial, subjects saw a sequence of three faces in the center of the screen. Each face remained onscreen for 5 sec. After the three faces, a name appeared in the center of the screen. Subjects indicated the serial position of the face that went with the name (the target image) using the number keys 1–3. Subjects received feedback about whether each response

was correct. Each block of the test phase contained 45 trials, such that each view of each face was the target image for one trial. Subjects received an accuracy score for each block, and the training session ended when subjects received greater than 95% correct.

Main Task

During the scanning session, subjects viewed stimuli on a projection screen located at the back of the scanner bore via an angled mirror attached to the head coil. On each trial, subjects saw a sequence of two faces. Each face was shown for 300 msec, separated by a 400-msec ISI. The faces were followed immediately by two names presented above and below fixation: one belonged to the second face, and the other was a foil that did not belong to either face. Subjects were instructed that the identity of the faces in each pair could change or stay the same, but regardless, their task was to choose the name that matched the second face. Subjects pressed a button with their right index finger for the top name and with their right middle finger for the bottom name (name position)

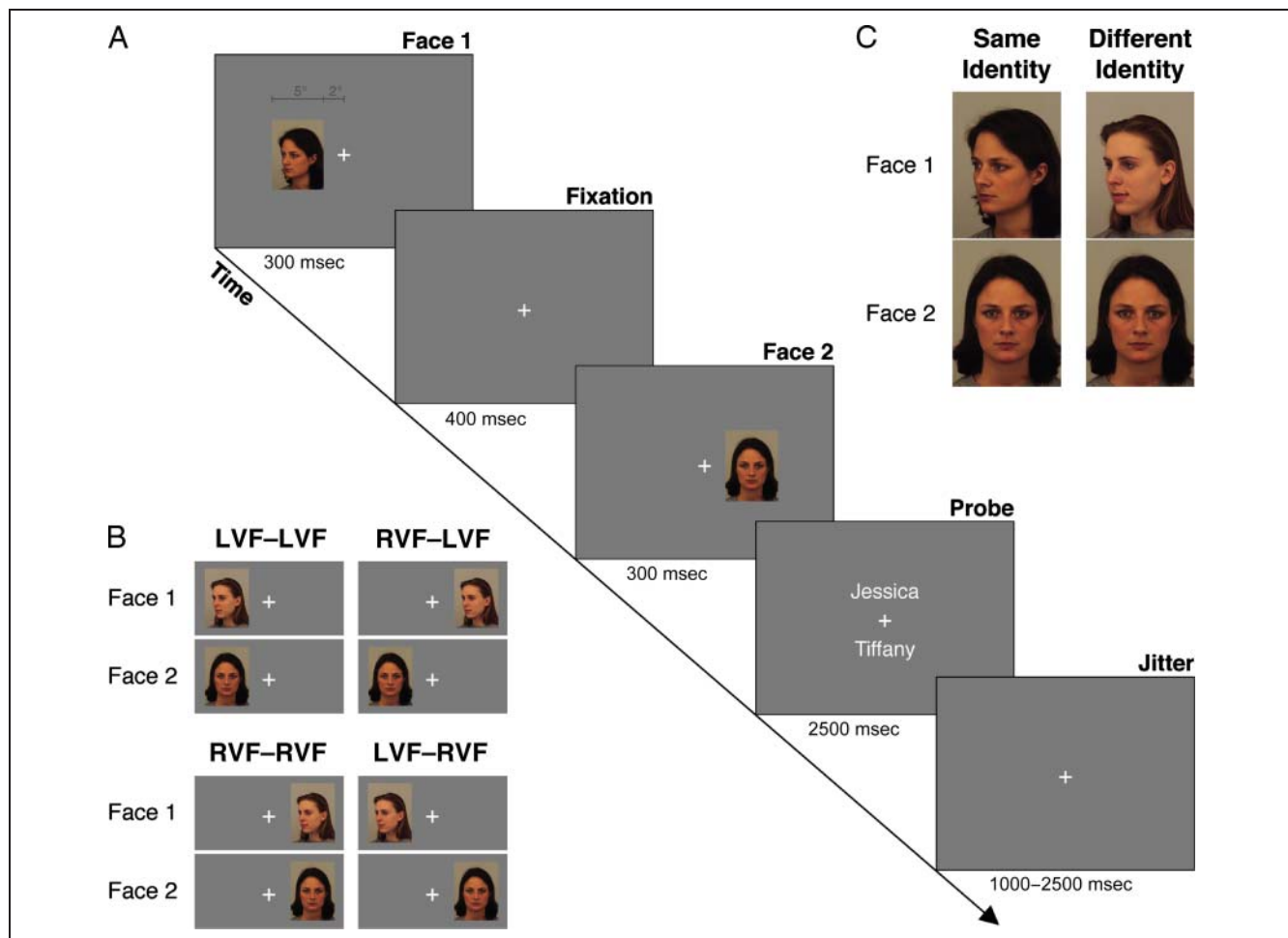


Figure 2. Main task. (A) On each trial, two faces were shown sequentially followed by two names. Subjects chose which name matched the second face. (B) The first and second faces each appeared in either LVF or RVF. (C) The first and second faces depicted the same person (same-identity) or different people (different-identity).

was randomized). The two names remained onscreen for 2.5 sec irrespective of when subjects responded. There was a jittered intertrial interval of 1.0 or 2.5 sec between trials, resulting in an overall trial onset asynchrony of 4.5 or 6.0 sec.

Identity adaptation was measured by comparing fMRI responses for pairs of faces depicting the same person (same-identity) versus different people (different-identity). Whether or not the identity repeated, there was always a change in viewpoint to isolate adaptation for facial identity from adaptation for low-level image properties. The viewpoint change was limited to less than 45°, resulting in four types of change: left–center, right–center, center–left, and center–right. For each viewpoint change, the same-identity condition depicted the same person from each viewpoint, and the different-identity condition depicted different people from each viewpoint. Thus, the same-identity and different-identity conditions were matched in terms of the frequency of each viewpoint and viewpoint change. The 15 identities appeared with equal probability at each viewpoint. Although the majority of trials contained a viewpoint change, we also included trials in which the same viewpoint and same identity were repeated to reduce the predictability of the task. These trials are not considered because repeating the same viewpoint could elicit adaptation for low-level image properties and because the frequency of particular viewpoints was not matched to the conditions of interest.

Because behavioral responses depended only on the second face, subjects could have, in principle, ignored the first face on each trial. We chose this task, rather than the one in which both faces were task relevant, precisely because responses were orthogonal to identity repetition. This was a conservative design decision because it worked against finding differences between identity conditions: If a subject did not attend to the first face, then the same-identity and different-identity conditions would be identical, and we would not be able to detect differences in behavior or the brain.

Divided field presentation was used to manipulate which hemisphere initially processed each image. Faces subtended 5.0° (*w*) × 6.8° (*b*), presented such that the inner edge of the image was 2.0° to the left or right of fixation. This distance away from the fovea helped ensure that images were processed by the contralateral hemisphere. There were four spatial location conditions: LVF–LVF and RVF–RVF, where both images were projected to the right and left hemisphere, respectively, and RVF–LVF and LVF–RVF, where the first image was projected to the left and right hemisphere, respectively, and the second image to the right and left hemisphere, respectively. There were eight conditions of interest: 2 (same-identity, different-identity) × 4 (LVF–LVF, RVF–RVF, RVF–LVF, LVF–RVF). Collapsing across the four viewpoint changes, there were four trials per condition per run. Eight functional runs lasting 259.5 sec were collected, resulting in 32 trials per condition.

Eye position was monitored to ensure that subjects maintained central fixation throughout each trial, since saccades to the images presented in the LVF or RVF would disrupt our manipulation of visual field. In the behavioral session before scanning, subjects were trained to fixate during a divided field presentation task: Images were presented in the periphery, and subjects were given real-time feedback about their eye position until they could fixate reliably. During the behavioral training session, eye-tracking was performed with a desktop system (Pan/Tilt 504, Applied Science Laboratories, Bedford, MA). During the scanning session, eye-tracking was performed with a 60-Hz long-range optics system (Model LRO, Applied Science Laboratories, Bedford, MA). Eye position was recorded through an aperture in the display screen, from a reflection of the subject's right eye in the head coil mirror. We focused on eye movements in the horizontal (vs. vertical) plane. To eliminate eyetracker drift, the data from each trial were centered around the mean coordinate from a baseline period at the start of the trial. The number of time points recorded during the baseline period varied across trials, with a mean length of 372 msec (~22 samples). For the first two subjects, the length of the baseline period was not recorded, and thus data from these subjects were centered around a baseline period of the group mean length.

Localizer Task

After the main experiment, subjects completed three runs of a functional localizer. Each run contained faces and scenes in separate blocks. For faces, subjects indicated whether each face depicted a male or female person; for scenes, subjects indicated whether each scene depicted an indoor or outdoor place. The blocks contained 12 images (5° square), each presented for 500 msec and separated by an ISI of 1000 msec. Each block lasted 18 sec, followed by 12 sec of fixation. Runs lasted 249 sec and consisted of four face blocks and four scene blocks, shown in alternating order (starting category was counterbalanced). The location of images differed across runs, such that all images in a given run were presented in LVF, RVF, or at fixation. The order of the three locations/runs was counterbalanced across subjects. For the runs with peripheral stimuli, the inner edge of images was 2° to the left or right of fixation. As in the main task, eye-tracking was used to ensure that subjects maintained central fixation.

fMRI Acquisition

Neuroimaging data were collected on a Siemens 3T Allegra head-only scanner using a Nova Medical NM-011 Head Transmit Coil with receive-only array system. Functional images were acquired using a T2*-weighted EPI sequence (echo time = 28 msec, repetition time = 1500 msec, flip angle = 64°, matrix = 64 × 64). Twenty-six interleaved oblique axial slices aligned parallel to the anterior commissure/

posterior commissure were used to achieve whole-brain coverage (3.5×3.5 mm in-plane, 5 mm thick). Two T1-weighted structural images were acquired for registration: a coplanar FLASH sequence and a high-resolution MPRAGE sequence.

fMRI Preprocessing

The first six volumes (9 sec) of each functional run were discarded to allow for T1 equilibration. Preprocessing and analyses were conducted with FEAT in FSL (www.fmrib.ox.ac.uk/fsl). Data were corrected for slice acquisition time and head motion, spatially smoothed (5 mm FWHM), detrended, and high-pass filtered (128-sec period cutoff). Functional runs were registered to the coplanar anatomical scan and to the high-resolution anatomical scan. Data were normalized into Montreal Neurological Institute (MNI) space and interpolated to 2-mm isotropic voxels.

fMRI Analysis

For the main task, we compared responses to pairs of faces where identity changed versus remained the same. Due to the rapid presentation of the two images in each trial and the sluggishness of the BOLD response, we examined the combined response to the pair of images. This is a standard approach for assessing adaptation in paired-pulse designs (Summerfield, Monti, Trittschuh, Mesulam, & Egner, 2008; Turk-Browne, Yi, Leber, & Chun, 2007; Kourtzi & Kanwisher, 2001). In particular, the first image in the pair is unadapted for all conditions, and thus differences

between conditions in the combined response must reflect differential amounts of adaptation for the second image.

Separate regressors were used to predict the response in each condition, along with an additional regressor for trials with incorrect or missed responses. For each regressor, a delta function was placed at the onset of every trial and convolved with a double-gamma canonical hemodynamic response function. A temporal derivative was included in the model for each regressor to account for variability in the latency of the BOLD response. Parameters from motion correction were included as covariates of no interest.

ROI Analyses

For every subject, the FFA ROI in each hemisphere was defined using the localizer run in which images appeared peripherally in the contralateral visual field (e.g., right FFA was defined using the localizer with images in LVF). We used the peripheral runs to mirror how images were presented in the main task, and the contralateral runs more specifically because the FFA has a contralateral bias (Hemond et al., 2007) and our analyses of the main task focused on ROIs contralateral to the second face in a pair. Boxcar functions lasting 18 sec were placed at the onset of face and scene blocks, and convolved with a double-gamma hemodynamic response function. To determine FFA coordinates, parameter estimates for face blocks were contrasted with those for scene blocks, and the peak voxel in an anatomically restricted region of the fusiform gyrus was selected (all $ps < .001$; Table 1).

Table 1. FFA Coordinates

Subject	Contralateral (Used for Analyses)		Central	
	Right FFA	Left FFA	Right FFA	Left FFA
1	38, -40, -16	-38, -46, -22	42, -42, -22	-38, -46, -24
2	36, -50, -24	-36, -46, -22	44, -48, -18	-36, -46, -22
3	38, -60, -20	-40, -60, -16	44, -60, -20	-40, -60, -16
4	38, -42, -32	-40, -48, -20	38, -42, -30	-40, -46, -26
5	42, -44, -22	-40, -52, -20	40, -50, -18	-40, -52, -20
6	44, -40, -20	-40, -48, -20	44, -40, -24	-40, -52, -18
7	52, -56, -14	-42, -48, -24	52, -56, -14	-46, -38, -30
8	46, -50, -32	-44, -56, -26	46, -50, -32	-48, -60, -26
9	50, -52, -24	-38, -54, -26	50, -56, -14	-38, -54, -26
10	44, -54, -24	-42, -54, -24	42, -54, -22	-42, -54, -28
11	40, -56, -12	-36, -48, -24	40, -50, -12	-36, -48, -24
12	44, -50, -18	-34, -48, -28	42, -62, -26	-34, -48, -30

Chosen from the contrast of faces > scenes in an independent functional localizer task where the images appeared peripherally in the contralateral visual field or centrally at fixation (all $ps < .005$).

The peak voxels in the right and left FFA are provided for each subject in MNI space.

Because there has not been much work investigating the variability of the FFA for faces at different spatial locations, we chose a second set of FFA coordinates using the localizer run in which images appeared at fixation (all $ps < .005$). As seen in Table 1, the peak of the FFA remains relatively stable irrespective of whether faces are presented peripherally or centrally. Although not our primary focus, occipital face area (OFA) ROIs were also defined for each subject to help assess the level at which facial identity is processed. The localizer run in which images appeared in the contralateral visual field was used to select the peak voxel in the right and left inferior occipital gyrus in the contrast of faces versus scenes (all $ps < .005$; Table 2).

Percent BOLD signal change for each condition in the main task was extracted from a 4-mm-radius spherical ROI centered on the peak voxel (Turk-Browne, Scholl, Johnson, & Chun, 2010). A standard adaptation index was calculated for each spatial location condition.

$$\frac{(\text{different-identity} - \text{same-identity})}{(\text{different-identity} + \text{same-identity})}$$

The second face in each trial provided a probe of whether the identity of the first face had been represented, and thus, we focus on the hemisphere contralateral to the location of this face (right FFA: LVF–LVF, RVF–LVF; left FFA: RVF–RVF, LVF–RVF). For completeness, we also present the results for each condition in the hemisphere ipsilateral to the location of the second face.

Table 2. OFA Coordinates

Subject	Right OFA	Left OFA
1	34, -78, -22	-38, -86, -18
2	36, -78, -8	-32, -80, -6
3	42, -72, -16	-44, -84, -14
4	48, -80, -6	-32, -76, -14
5	44, -86, -18	-42, -72, -14
6	36, -92, -14	-36, -78, -18
7	38, -84, -8	-34, -90, -12
8	44, -76, -16	-40, -78, -16
9	48, -68, -18	-32, -74, -14
10	48, -68, -26	-38, -74, -20
11	36, -74, -12	-34, -70, -12
12	46, -82, -10	-40, -82, -16

Chosen from the contrast of faces > scenes in an independent functional localizer task where images appeared in the contralateral visual field (all $ps < .005$).

The peak voxels in the right and left OFA are provided for each subject in MNI space.

Voxelwise Analyses

Our primary analyses relied on individually defined ROIs because the location of the FFA is variable across subjects and because this approach eliminates multiple comparisons across voxels. However, we also conducted exploratory voxelwise analyses to examine regions beyond our ROIs. Group-level statistical maps were generated from permutation tests conducted with *randomize* in FSL. For each contrast, the sample of paired differences within each voxel was permuted 5000 times by randomly flipping the sign of each subject's difference, resulting in a null distribution to which the actual contrast value could be compared nonparametrically. Threshold Free Cluster Enhancement (TFCE) was used to identify clusters that reached significance ($p < .05$) controlling for the family-wise error rate (Smith & Nichols, 2009).

RESULTS

Training Results

Test performance during the training session is depicted in Figure 1B. During the first test block of the training session (i.e., after one round of training), accuracy in identifying which face went with which name was significantly above chance ($t(11) = 6.06, p < .001$). During the second test block (i.e., after another round of training), accuracy improved against chance ($t(11) = 20.30, p < .001$). Five of 12 subjects reached the criterion of 95% correct during this block and thus did not complete any more training. During the third block, accuracy improved further against chance ($t(6) = 61.28, p < .001$), and four more subjects reached criterion. During the fourth block, the three remaining subjects reached criterion.

Behavioral Results

Accuracy

Behavioral data were analyzed with a 2 (identity change: same-identity, different-identity) \times 2 (field of first presentation: LVF, RVF) \times 2 (field of second presentation: LVF, RVF) repeated-measures ANOVA. Accuracy in choosing which name matched the identity of the second face was near ceiling ($M = 97.2\%$, $SD = 2.0\%$). Nonetheless, there was a main effect of Identity Change, with higher accuracy for same-identity trials ($M = 98.0\%$, $SD = 2.1\%$) than different-identity trials ($M = 96.3\%$, $SD = 2.0\%$; $F(1, 11) = 20.72, p = .001$); this difference provides a behavioral measure of facial identity priming. There was also a main effect of Visual Field of First Presentation, such that subjects were more accurate when the first face was presented in LVF ($M = 97.8\%$, $SD = 1.6\%$) versus RVF ($M = 96.5\%$, $SD = 2.5\%$; $F(1, 11) = 7.71, p = .018$); this is consistent with a right hemisphere advantage in face processing. The amount of facial identity priming did not differ as a function of visual field, as revealed by a nonsignificant interaction between identity change and field of first presentation ($F < 1$). Whereas behavioral priming can accompany fMRI

adaptation in ventral temporal cortex, there is no necessary relationship between the two measures (because other brain regions may be responsible for behavioral priming; Xu, Turk-Browne, & Chun, 2007). There was no main effect of Field of Second Presentation ($F < 1$), nor were any other interactions reliable ($F_s < 1$).

Response Time

There was a main effect of Identity Change, with marginally faster RTs for same-identity trials ($M = 808.7$ msec, $SD = 134.5$ msec) than different-identity trials ($M = 829.3$ msec, $SD = 122.5$ msec; $F(1, 11) = 4.00, p = .071$). For correct responses alone, RTs were numerically faster for same-identity trials ($M = 802.5$ msec, $SD = 132.4$ msec) than different-identity trials ($M = 821.3$ msec, $SD = 122.7$ msec), although the difference was no longer marginally significant ($F(1, 11) = 3.08, p = .107$). These results rule out a speed-accuracy tradeoff: Responses in same-identity trials were both faster and more accurate than in different-identity trials. There were no main effects of Visual Field of First or Second Presentation ($F_s < 1$) nor were any interactions reliable ($F_s < 1$).

Eyetracking

As a result of isolated technical issues or shifts of pupil position in the head coil mirror (due to head motion), the eyetracker was occasionally unable to track eye position accurately. Thus, analysis of eyetracking data was limited to trials in which eye position data were collected for at least 95% of samples. Across subjects, the mean percentage of such trials was 86.91% ($SD = 14.29\%$). Eye position was reliably maintained within $\pm 2^\circ$ of central fixation (i.e., between the inner edges of where images could appear in LVF and RVF) throughout these trials ($M = 96.49\%$ of samples, $SD = 4.49\%$). When fixation was broken, peripheral images were rarely the target: Breaks

included blinks, missing data (up to 5%), and eye movements before or after the images were presented. Given that fixation breaks were extremely rare, we included all trials in our fMRI analyses to maximize statistical power. This was a conservative decision: If a subject fixated a peripheral image, the mapping of its location to a (retinotopic) visual field would have been destroyed, diluting differences between spatial location conditions.

fMRI Results

Contralateral FFA Analyses

A 2 (identity change: same-identity, different-identity) \times 2 (field of first presentation: LVF, RVF) \times 2 (field of second presentation: LVF, RVF) repeated-measures ANOVA was conducted on percent BOLD signal change from the FFA (Figure 3). Because this analysis was limited to the hemisphere that initially processed the second face (i.e., contralateral to where the second face appeared), the Field of Second Presentation factor also codes for the Hemisphere from which data were extracted. In particular, data were extracted from the right FFA when the second face was presented in LVF and from the left FFA when the second face was presented in RVF. According to our main hypothesis, Identity Change (adaptation) should interact with the Field of First Presentation. This interaction should be driven by stronger adaptation when the first face appeared in LVF, irrespective of the field of second presentation.

Mean percent BOLD signal change for each condition is reported in Table 3. There was a main effect of identity change ($F(1, 11) = 9.84, p = .009$), with greater signal change for different-identity trials than same-identity trials; this reflects overall fMRI adaptation for facial identity in the FFA. There was a main effect of Visual Field of First Presentation ($F(1, 11) = 7.68, p = .018$), with greater signal change when the first face was presented in LVF versus RVF, but no main effect of Field of Second Presentation ($F < 1$). There was an interaction between Field of First

Figure 3. FFA Results. Percent BOLD signal change for same-identity (white) and different-identity (black) trials when the second face was presented to (A) the right FFA and (B) the left FFA. Insets: individual subject ROIs shown in unique colors (Table 1). Error bars depict ± 1 within-subject SEM; $*p < .05$.

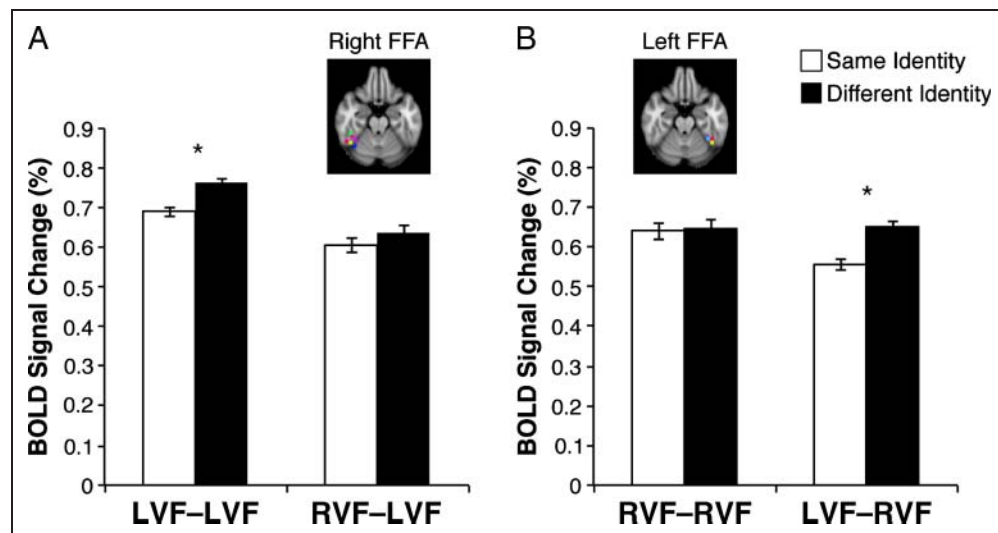


Table 3. Contralateral FFA Results

	<i>Right FFA</i>		<i>Left FFA</i>	
	<i>LVF–LVF</i>	<i>RVF–LVF</i>	<i>RVF–RVF</i>	<i>LVF–RVF</i>
Same-identity	.69 (.25)	.60 (.22)	.64 (.20)	.56 (.21)
Different-identity	.76 (.27)	.64 (.23)	.65 (.25)	.65 (.25)

Mean (and standard deviation) percent bold signal change in the FFA by spatial location from the hemisphere contralateral to the location of the second face.

Presentation and Field of Second Presentation ($F(1, 11) = 34.17, p < .001$), with greatest signal change when both faces appeared contralaterally (LVF–LVF in the right FFA, RVF–RVF in the left FFA); this provides evidence of a contralateral bias in the FFA (Hemond et al., 2007). There was no interaction between Identity Change and Field of Second Presentation ($F < 1$), indicating that facial identity adaptation did not vary by hemisphere.

Critically, there was an interaction between Identity Change and Field of First Presentation ($F(1, 11) = 7.40, p = .020$), with stronger adaptation (different-identity vs. same-identity) when the first face was presented in LVF and projected to the right hemisphere than when it was presented in RVF and projected to the left hemisphere. Further exploring this interaction, adaptation occurred when the first face appeared in LVF ($F(1, 11) = 17.68, p = .001$), but not when it appeared in RVF ($F < 1$). Planned comparisons revealed that this was true in both right and left hemispheres: in the right FFA, adaptation occurred for LVF–LVF ($t(11) = 3.04, p = .011$), but not RVF–LVF ($t < 1$); in the left FFA, adaptation occurred for LVF–RVF ($t(11) = 3.50, p = .005$), but not RVF–RVF ($t < 1$). The interaction between identity change and field of first presentation did not further interact with field of second presentation (three-way interaction, $F < 1$), indicating that the stronger adaptation observed when the first face appeared in LVF did not vary by hemisphere. These findings support our conclusion that facial identity adaptation can occur in both hemispheres, but only when faces are initially processed by the right hemisphere.

To quantify adaptation in each spatial location condition, we computed an adaptation index. In the right FFA, adaptation occurred for LVF–LVF ($M = .05, SD = .06$; one-sample t test; $t(11) = 3.22, p = .008$), but not RVF–LVF ($M = .02, SD = .09; t < 1$). In the left FFA, adaptation occurred for LVF–RVF ($M = .08, SD = .10; t(11) = 2.61, p = .024$), but not RVF–RVF ($M = .00, SD = .12; t < 1$). Thus, two methods of defining adaptation produced an identical pattern of results: Adaptation was observed in both right and left FFA, but only when the first face was presented to the right hemisphere.

Ipsilateral FFA Analyses

We decided a priori to focus on the hemisphere contralateral to the second face on each trial because it pro-

vided a direct probe of whether the first face had been represented in a region (via bottom–up input or transfer) without requiring additional transfer for the second face. In contrast, the ipsilateral ROIs did not provide as direct or incisive a test of our hypothesis that prior processing in the right hemisphere is needed for adaptation in the left hemisphere because information about a second face in LVF could only reach the left FFA via interhemispheric transfer. Although more difficult to interpret, we report results from the ipsilateral hemisphere for completeness.

Mean percent BOLD signal change for each condition is reported in Table 4. There was no main effect of Identity Change ($F(1, 11) = 1.87, p = .198$), indicating no overall identity adaptation for ipsilateral faces in the FFA. There was a main effect of Visual Field of First Presentation ($F(1, 11) = 4.97, p = .048$), with greater signal change when the first face was presented in LVF versus RVF, but there was no main effect of Field of Second Presentation ($F < 1$). There was an interaction between Field of First and Second Presentation ($F(1, 11) = 4.91, p = .049$), with greater signal change when one face was presented in the contralateral visual field (LVF–RVF in the right FFA, RVF–LVF in the left FFA) versus both in the ipsilateral visual field; this provides further evidence of a contralateral bias in the FFA. There was no interaction between Identity and Field of Second Presentation ($F < 1$), indicating that the effect of identity did not vary by hemisphere. Unlike FFA, there was no interaction between Identity and Visual Field of First Presentation ($F(1, 11) = 1.23, p = .291$), indicating that adaptation did not vary depending on whether the first face was presented in LVF versus RVF (although note that there was no overall adaptation effect to begin with).

There was a three-way interaction between Identity, Field of First Presentation, and Field of Second Presentation ($F(1, 11) = 5.59, p = .038$). This interaction was supported by a numerically greater effect of Field of First Presentation on adaptation in the right versus left FFA. However, this interaction should again be interpreted with caution, because the main effect of Identity Change did not reach significance and neither did the interactions between Field of First Presentation and Identity Change in the right FFA ($F(1, 11) = 2.95, p = .114$) or left FFA ($F < 1$). Moreover, adaptation was not statistically reliable in any spatial location condition: in the right FFA, RVF–RVF ($t < 1$)

Table 4. Ipsilateral FFA Results

	<i>Left FFA</i>		<i>Right FFA</i>	
	<i>LVF–LVF</i>	<i>RVF–LVF</i>	<i>RVF–RVF</i>	<i>LVF–RVF</i>
Same-identity	.53 (.17)	.55 (.22)	.59 (.24)	.62 (.24)
Different-identity	.56 (.22)	.59 (.25)	.56 (.22)	.68 (.27)

Mean (and standard deviation) percent bold signal change in the FFA by spatial location from the hemisphere ipsilateral to the location of the second face.

and LVF–RVF ($t(11) = 1.64, p = .130$); in the left FFA, LVF–LVF ($t(11) = 1.08, p = .304$) and RVF–LVF ($t(11) = 1.98, p = .074$). The marginal effect for RVF–LVF is intriguing but is not readily interpretable given the post hoc nature of these tests and the lack of adaptation in other conditions. Lack of adaptation in the LVF–LVF condition demonstrates that contralateral input about the second face (as in the LVF–RVF condition of the contralateral analyses) is needed to reveal identity adaptation in the left FFA.

OFA Analyses

As in the main FFA analyses, mean percent BOLD signal change was extracted for each condition from the hemisphere contralateral to the second face (Table 5). There was no main effect of Identity Change ($F(1, 11) = 3.15, p = .103$), consistent with past findings (Rotshtein et al., 2005). There were no main effects of Visual Field of First Presentation ($F(1, 11) = 1.47, p = .250$) or Second Presentation ($F(1, 11) = 2.35, p = .153$). However, there was an interaction between Field of First and Second Presentation ($F(1, 11) = 55.22, p < .001$), with greater signal change when both faces were presented in the contralateral visual field (LVF–LVF in the right OFA, RVF–RVF in the left OFA); this indicates a robust contralateral bias in the OFA. There was no interaction between Identity Change and Field of Second Presentation ($F < 1$), indicating that identity adaptation did not vary by hemisphere.

As in the FFA, there was an interaction between Identity Change and Field of First Presentation ($F(1, 11) = 5.06, p = .046$), with stronger adaptation (different-identity vs. same-identity) when the first face was presented in LVF and projected to the right hemisphere than when it was presented in RVF and projected to the left hemisphere (although note that there was no overall adaptation effect). Further exploring this interaction, adaptation occurred when the first face appeared in LVF ($F(1, 11) = 5.32, p = .042$), but not when it appeared in RVF ($F < 1$). Moreover, this interaction did not further interact with field of second presentation ($F < 1$), indicating that the stronger adaptation observed when the first face appeared in LVF did not vary by hemisphere. Nevertheless, the effect of First Presentation in LVF was numerically stronger in the left hemisphere: in the right OFA, adaptation was not reliable for either LVF–LVF ($t(11) = 1.35, p = .203$) or RVF–LVF

($t < 1$); in the left OFA, marginally significant adaptation was found for LVF–RVF ($t(11) = 2.20, p = .050$), but not RVF–RVF ($t < 1$).

Voxelwise Analyses

Although our primary analyses relied on individually defined ROIs, we also conducted exploratory voxelwise analyses to examine regions outside of the FFA. We conducted two contrasts for facial identity adaptation (different-identity > same-identity): one collapsing across conditions where the first face appeared in LVF (LVF–LVF, LVF–RVF) and the other collapsing across conditions where the first face appeared in RVF (RVF–RVF, RVF–LVF). No clusters survived correction for multiple comparisons (TFCE corrected, $p < .05$) in either contrast.

Because multiple face patches have been identified in the ventral visual cortex (Pinsk et al., 2009), we also examined these contrasts with a small-volume correction based on an anatomical mask covering bilateral fusiform gyrus and surrounding cortex. When the first face appeared in LVF and was projected to the right hemisphere, four clusters showed identity adaptation (TFCE-corrected $p < .05$, MNI center-of-gravity, Harvard-Oxford labels): bilateral occipital fusiform gyrus (right: 38, –62, –12; left: –34, –81, –14) and bilateral temporal fusiform gyrus (right: 42, –53, –18; left: –33, –59, –9). When the first face appeared in RVF and was projected to the left hemisphere, no regions showed identity adaptation at the same corrected threshold or even a much more liberal threshold (uncorrected $p < .01$). No regions, in either the whole-brain or small-volume-corrected analyses, showed the opposite effect (same-identity > different-identity). These findings support our conclusion that facial identity adaptation in both the right and left hemispheres requires initial processing by the right hemisphere. Moreover, these analyses demonstrate that the results from our ROIs were not widespread beyond the fusiform gyrus.

DISCUSSION

The right hemisphere is specialized for face processing (Thomas et al., 2009; Yovel et al., 2008; Le Grand et al., 2003; De Renzi et al., 1994; De Renzi, 1986; Gazzaniga & Smylie, 1983), as shown in our data by robust adaptation in the right FFA but not in the left FFA when two faces appeared in their preferred contralateral visual field. On the basis of how they were defined, both right and left FFA were face selective, and so the right hemisphere advantage we observed reflects superior facial identity processing per se. We discovered that the FFA can show facial identity adaptation, however, but only when the adapting face is initially processed by the right hemisphere. In other words, the left FFA showed adaptation when an identity moved from LVF to RVF, but not when it repeated in the same RVF location.

Table 5. Contralateral OFA Results

	Right OFA		Left OFA	
	LVF–LVF	RVF–LVF	RVF–RVF	LVF–RVF
Same-identity	.87 (.29)	.69 (.31)	.99 (.40)	.81 (.36)
Different-identity	.93 (.33)	.72 (.27)	.98 (.46)	.90 (.42)

Mean (and standard deviation) percent bold signal change in the OFA by spatial location from the hemisphere contralateral to the location of the second face.

We interpret these results as evidence of interhemispheric transfer: in particular, that the right hemisphere computed the facial identity of the first face and shared this information with the left hemisphere, resulting in adaptation in the left FFA for the second face. The lack of adaptation in the left FFA when both faces were presented in RVF suggests that this region cannot compute facial identity on its own. Perhaps as a result, the transfer of facial identity information was asymmetric: there was no adaptation in the right FFA when the first face appeared in RVF and the second face appeared in LVF.

How is it possible for left FFA to represent facial identity (as indicated by adaptation for LVF–RVF) but not be able to compute facial identity (as indicated by the lack of adaptation for RVF–RVF)? One potential explanation is that the left FFA is less efficient at computing facial identity than the right FFA (Moscovitch, 1986). For example, left FFA may be capable of limited identity processing but require additional processing time or longer stimulus durations to reach a threshold at which identity can be recognized. When the more efficient right hemisphere transfers facial identity information to the left hemisphere, this threshold may be reached more quickly. If adaptation occurs only after the threshold has been reached, the boost in speed afforded by transfer may increase the likelihood that this has occurred by the time that the second face arrives. Another potential explanation is that identity processing in the left FFA is noisier than in the right FFA, and that input from the right hemisphere may help reduce this noise. If adaptation only occurs when the second face is perceived to be the same identity as the first, the more veridical representation of the first face afforded by transfer may increase the likelihood that the second face matches the first.

Our results show that identity adaptation in the left FFA depends on right hemisphere processing. However, because we measured the consequences of transfer rather than the transfer itself, our results do not speak directly to how the underlying interhemispheric transfer happens. Nevertheless, our findings may still provide some initial insights about this process. Specifically, we can consider the interhemispheric transfer of two different kinds of information: low-level sensory information and high-level identity information.

The results from ipsilateral ROIs highlight the transfer of low-level information: The FFA in each hemisphere was strongly activated even when both faces appeared in the ipsilateral visual field. This demonstrates that a substantial amount of sensory input had already been transferred from the contralateral hemisphere by this stage of processing. Early regions such as V1 are almost completely contralaterally selective, and this bias persists but decreases moving anteriorly in the brain through LO, OFA, posterior fusiform, and FFA (Hemond et al., 2007). This gradual decrease suggests that lateral and feedforward interhemispheric transfer might occur at every stage of processing, compounding across subsequent

stages to reduce the contralateral bias in higher-level areas.

For present purposes, however, we are mainly interested in high-level identity information. Indeed, the activation of a brain region to faces does not imply that this region has represented anything about facial identity. For example, the left FFA was activated maximally when both faces appeared in the contralateral RVF, but this activation did not lead to any identity adaptation. Although the exact manner in which identity information was transferred from the right hemisphere to the left FFA remains beyond the scope of this study, our findings and the previous literature place some constraints on where in the right hemisphere identity information might originate. In particular, it seems reasonable to assume that a region can only transfer identity information if it can represent this information on its own to begin with.

Keeping this assumption in mind, our results suggest one candidate source of facial identity information, the right FFA, which shows robust adaptation for contralateral faces. This may be the earliest level at which transfer could originate in the right hemisphere, because the right OFA did not show identity adaptation for contralateral faces. These results replicate an earlier study that found identity adaptation in the right FFA but not in the right OFA (Rotshtein et al., 2005). Indeed, the OFA is thought to play a role in processing structural properties of faces, including face parts (Pitcher, Walsh, & Duchaine, 2011), rather than identity per se. Beyond the FFA, the right anterior temporal lobe (ATL) is another candidate source of facial identity information: Distributed patterns of activity in the right ATL can discriminate between identities (Nestor, Plaut, & Behrmann, 2011; Kriegeskorte, Formisano, Sorger, & Goebel, 2007). There are several possible ways in which high-level identity information could propagate from these putative sources in the right FFA and in the right ATL to the left FFA, including: laterally from the right FFA, via feedback from the right ATL, or via feedback from control regions in pFC that might have been involved in implementing the name–identity matching task (see Miller & Cohen, 2001). Despite not being able to adjudicate between these possibilities, our study provides a first step toward establishing a more concrete model that can explain transfer-dependent facial identity adaptation.

Several studies have sought to characterize how face-selective regions interact but have focused mostly on within-hemisphere interactions along the posterior–anterior axis of the brain (Turk-Browne, Norman-Haignere, & McCarthy, 2010; Fairhall & Ishai, 2007). Our results suggest that between-hemisphere interactions along the lateral axis may also prove important for understanding how facial identity is recognized (cf. Nestor et al., 2011; Moeller, Freiwald, & Tsao, 2008). We provide some initial material for this endeavor: left and right FFA do not process facial identity in parallel, but rather, left FFA requires initial processing by the right hemisphere.

More generally, we found clear evidence for viewpoint-independent facial identity adaptation in the FFA. Previous evidence for such adaptation has been mixed: Some studies failed to find viewpoint-independent adaptation in object-selective (Grill-Spector et al., 1999) and face-selective regions (Pourtois et al., 2005a; Andrews & Ewbank, 2004), whereas others have at least partly succeeded in face-selective regions (Mur et al., 2010; Ewbank & Andrews, 2008; Pourtois et al., 2005b). Several factors seem to be important across these studies, including whether faces were familiar (Eger, Schweinberger, Dolan, & Henson, 2005; Pourtois et al., 2005a; see also Johnston & Edmonds, 2009), whether short- or long-term adaptation was examined (Fang et al., 2007), and how much faces were rotated (Ewbank & Andrews, 2008). We observed robust identity adaptation across viewpoint changes in the FFA, and whole-brain analyses further indicated that this adaptation was limited to fusiform cortex. The training task, in which different views of each face were familiarized and associated with a name, and the main task, which required attending to identity information for making name judgments, may have contributed to our ability to find this adaptation. Future work is needed to explore these factors more directly.

In sum, we found evidence that the right hemisphere supports facial identity processing in the left hemisphere. This provides a case study in how interhemispheric transfer might distribute the output of lateralized processes, helping to reconcile hemispheric specialization with the contralateral organization of the visual system.

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