

Face Processing Changes in Normal Aging Revealed by fMRI Adaptation

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Abstract

■ We investigated the neural correlates of facial processing changes in healthy aging using fMRI and an adaptation paradigm. In the scanner, participants were successively presented with faces that varied in identity, viewpoint, both, or neither and performed a head size detection task independent of identity or viewpoint. In right fusiform face area (FFA), older adults failed to show adaptation to the same face repeatedly presented in the same view, which elicited the most adaptation in young adults. We also performed a multivariate analysis to examine correlations between whole-brain activation patterns and behavioral performance in a face-matching task tested outside the scanner. Despite poor neural adaptation in right FFA, high-performing older adults engaged the same face-processing network as high-performing young adults across conditions, except the one pre-

senting a same facial identity across different viewpoints. Low-performing older adults used this network to a lesser extent. Additionally, high-performing older adults uniquely recruited a set of areas related to better performance across all conditions, indicating age-specific involvement of this added network. This network did not include the core ventral face-processing areas but involved the left inferior occipital gyrus, frontal, and parietal regions. Although our adaptation results show that the neuronal representations of the core face-preferring areas become less selective with age, our multivariate analysis indicates that older adults utilize a distinct network of regions associated with better face matching performance, suggesting that engaging this network may compensate for deficiencies in ventral face processing regions. ■

INTRODUCTION

What neural mechanisms account for differences in face perception between old and young adults? It has been widely reported that recognition and perception of familiar and unfamiliar faces decline in normal aging (Habak, Wilkinson, & Wilson, 2008; Boutet & Faubert, 2006; Lott, Haegerstrom-Portnoy, Schneck, & Brabyn, 2005; Searcy, Bartlett, & Menon, 1999; Bartlett, Strater, & Fulton, 1991). Older adults show similar hit rates but more false alarms compared with young adults in face recognition (reviewed in Searcy et al., 1999) and are poor at discriminating a face across viewpoints (Habak et al., 2008). Although the optics of the eye undergo changes with age (Weale, 1982), deficits in visual face processing also are likely to arise at cortical levels (Carp, Park, Polk, & Park, 2011; Goh, Suzuki, & Park, 2010; Park et al., 2004). Neuroimaging evidence has suggested a decrease in occipital and hippocampal activation with age, which is accompanied by poorer performance in face matching and recognition (e.g., Grady, 2000; Grady et al., 1995). In the present study, we used an fMRI adaptation paradigm to identify the neural changes associated with age-related differences in face processing.

Visual representation of faces involves multiple regions (Haxby, Hoffman, & Gobbini, 2000). Haxby and his colleagues have proposed a general model of distributed neural systems for face perception, which consists of a “core” system concerned with the visual analysis of faces, and an “extended” system for extracting person knowledge and emotion (Gobbini & Haxby, 2007; Haxby et al., 2000). The core system includes the fusiform face area (FFA) and surrounding region (Maurer et al., 2007; Kanwisher, McDermott, & Chun, 1997) and occipital face area (OFA; Gauthier, Skudlarski, Gore, & Anderson, 2000) in the occipitotemporal regions. The FFA and OFA interact with each other (e.g., Schiltz & Rossion, 2006; Steeves et al., 2006; Rossion et al., 2003) and are a crucial part of the bottom-up and top-down face processing networks. A right hemisphere dominance is often observed for the FFA in young adults (see Dien, 2009, for meta-analysis of FFA lateralization). The extended system (Gobbini & Haxby, 2007; Haxby et al., 2000) is comprised of areas such as the amygdala, insula, anterior temporal cortex, anterior paracingulate, and precuneus (Gobbini & Haxby, 2007). The core system provides input to the extended system, and in turn the extended system modulates the activation of the core system through feedback. Because face processing is distributed widely over many functionally interacting brain regions, deficiencies at early processing stages could cascade downstream and result in changes in functional brain

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networks (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; Grady, 2000).

Similarly, neuroimaging studies assessing directly the effects of aging on face processing have pointed toward reduced neural function at early stages, including visual striate and extrastriate cortices. Grady et al. (1994) reported reduced activity in the occipital cortex (BA 18) of older adults compared with young adults. In addition, activations were less specific in older adults: A location matching task, which involved dorsal visual areas in young adults, showed greater activation in face-responsive regions of the fusiform gyrus (BA 37) in older adults. Similarly, Park et al. (2004) have shown attenuated neural selectivity with age for stimulus categories (faces, objects, places, words) in the ventral visual cortex (also see Carp et al., 2011). In a subsequent study (Goh et al., 2010), older adults showed greater adaptation in the FFA when two morphed faces within a trial differed by 40%, whereas young adults yielded minimal adaptation to these stimuli. These neuronal effects were reflected in the behavioral data gathered outside the scanner, in that older adults could not distinguish a 40% difference between two morphs whereas younger adults could. Rousselet et al. (2009), using brain ERPs, have assessed the occipito-temporal component N170, which is larger for faces than for objects and related to early perceptual processes (Bentin, Allison, Puce, Perez, & McCarthy, 1996). In their study, older adults exhibited strong N170 amplitude to pure noise, whereas the N170 amplitude in young adults was modulated by the amount of facial information embedded in noise. Interestingly, older adults with stronger N170 response to noise did not perform worse on behavioral tests. In other ERP studies, older adults showed no differential amplitude in N170 to inverted versus upright faces unlike young adults (Daniel & Bentin, 2010; Gao et al., 2009), despite behavioral findings (Boutet & Faubert, 2006) that older adults were affected by face inversion as much as the young group. Moreover, face processing was not lateralized in the older brain: The N170 amplitude was equal for both hemispheres in the older group, whereas it was larger on the right in young adults (Daniel & Bentin, 2010; Gao et al., 2009). These studies clearly demonstrate that neural representations in the ventral visual cortex become less domain-specific with age, although the influence of these neural effects on face processing is not always clear.

The present study used an fMRI-adaptation technique to examine neural selectivity in the ventral occipito-temporal cortex. This technique is based on the assumption that neural activity is attenuated with recurring presentations of a visual stimulus (Grill-Spector & Malach, 2001). Specifically, neuronal populations will show reduced responses (i.e., adaptation) when stimulus features to which they were sensitive are repeated. When these features are varied, the same neurons will no longer habituate but revert to preadaptation levels (i.e., release from adaptation). For example, it has been shown in young adults that the fMRI BOLD signal in the FFA decreases upon successive presen-

tation of an identical face but recovers from adaptation by changes in facial viewpoint. This result suggests that the FFA is sensitive to the degree of perceived differences between facial identities (Fox, Iaria, & Barton, 2009; Gilaie-Dotan & Malach, 2007; Jiang et al., 2006; Rotshtein, Henson, Treves, Driver, & Dolan, 2005) and changes in facial viewpoint (Andrews & Ewbank, 2004; Grill-Spector & Malach, 2001; Grill-Spector et al., 1999).

To date, there has been little research into the effects of aging on adaptation to repetitions of facial identity or viewpoint. Using an fMRI adaptation paradigm, we expected that age-related changes in neural processes would be found locally in the ventral visual areas and globally in the network of face processing areas. We used a block design to obtain a maximum adaptation effect (Grill-Spector, Henson, & Martin, 2006). Each block consisted of a single stimulus condition and presented a series of faces that could vary in either identity, viewpoint, both features, or neither feature (i.e., the faces were identical). In each trial, participants were required to respond to a slightly bigger head, a simple size judgment task that did not require identity or viewpoint recognition, as the FFA is insensitive to size changes of the face (Andrews & Ewbank, 2004; Grill-Spector & Malach, 2001). This procedure was designed to measure stimulus-driven bottom-up adaptation effects in the ventral visual cortex, minimizing decision-based processes, which would provoke top-down signals while maintaining strict attention (e.g., Betts & Wilson, 2010; Davies-Thompson, Gouws, & Andrews, 2009). We used this approach because it has been shown that neural response patterns in ventral face-sensitive areas are influenced by the cognitive strategy demanded by the given task (Kadosh, Henson, Kadosh, Johnson, & Dick, 2010; Bernstein, Beig, Siegenthaler, & Grady, 2002), and we wanted to avoid the influence of task demands where age differences might occur. That is, by adopting a simple task in the scanner yielding equivalent performance between the two groups, instead of identity judgment in which older adults perform more poorly, group differences in brain activity would be attributed to age-related changes in stimulus processing rather than behavior performance. Additionally, we scanned participants in localizer runs containing different categories of stimuli (faces, houses, common objects, scrambled versions of the objects) to localize face- and object-sensitive areas. We obtained an individual measure of the adaptation magnitudes in face- and object-sensitive regions, hypothesizing that face perception deficits in older adults would be reflected by abnormal adaptation in the core face processing areas (e.g., Goh et al., 2010; also as has been found in the auditory system in Grady, Yu, & Alain, 2008) and compared the results between two hemispheres in each group. Moreover, we assessed a functional network of distributed neural regions whose activity covaries with the participant's face matching ability tested outside the scanner, and we hypothesized that older adults would demonstrate a distinct network of brain regions from young adults to support their performance (Grady, 2000, 2008).

Outside the scanner, participants completed a behavioral test, in which they viewed pairs of faces, presented one after another, and were required to specify whether the two faces had the same identity or not. We expected to replicate earlier behavioral studies showing that older adults would be good at matching the same identity shown in the same view but poor when viewpoints changed (Habak et al., 2008; Searcy et al., 1999). We also expected that face discrimination deficits across viewpoints (Habak et al., 2008) would be associated with age differences in the wider face processing network, as view-invariant face representations appear to be established in areas other than the FFA (Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005; Andrews & Ewbank, 2004; Grill-Spector & Malach, 2001).

METHODS

Participants

Fifteen older adults (mean age = 67.7 years, $SD = 4.2$ years, range = 61–75 years; six men) and 15 young adults (mean age = 24.1 years, $SD = 4.9$ years, range = 18–32 years; seven men) were recruited from the Greater Toronto Area. Healthy community-dwelling older adults were carefully screened through a detailed phone interview for general health (e.g., cardiovascular disease, stroke), medications, and normal vision (e.g., cataract, glaucoma, macular degeneration, eye examination within a year from the time of participation). Older adults achieved an average score of 29.3 ($SD = 1.1$) on the minimal state examination (Folstein, Folstein, & McHugh, 1975), and all had undergraduate or graduate-level education. Young adults were undergraduate or graduate students attending the University of Toronto. All participants had normal or corrected-to-normal vision (with their own contact lenses or MRI-compatible corrective eye glasses) and no history of eye disease and neurological or psychiatric problems.

All provided written informed consent to a protocol approved by the Baycrest Centre Research Ethics Board.

Stimuli and Tasks

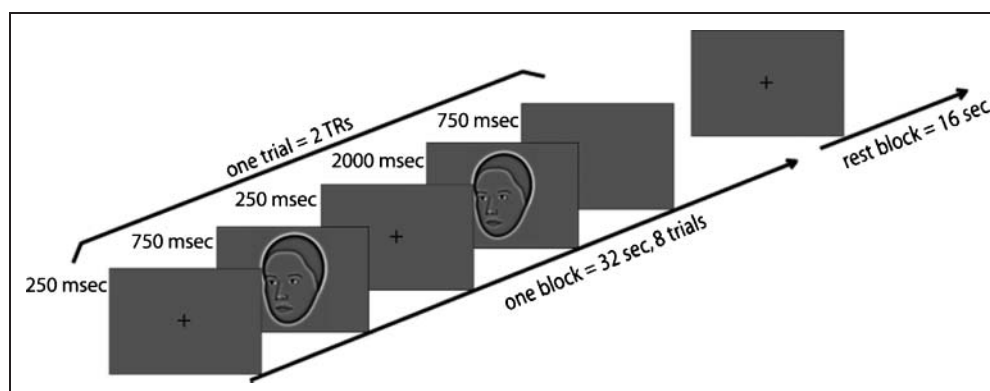
Overview of the Study Design

There were two phases in this study: fMRI and postscan behavioral test. The imaging phase consisted of five runs of the adaptation task and two runs of the face localizer to identify ROIs in each participant. Both adaptation and localizer experiments were conducted in a block design. The two localizer runs were presented between the third and the fourth adaptation runs. The postscan test phase was conducted outside the scanner on a different day (on average, within a month). The postscan test involved sequential matching of unfamiliar faces across identity and/or viewpoints.

Stimuli

During adaptation runs, synthetic faces (Wilson, Loffler, & Wilkinson, 2002) were presented, which allowed for precise control of stimulus properties (see Figure 1). Briefly, synthetic faces are schematic representations of real faces (frontal and 20° side views) with neutral expressions and they activate the same areas in the brain as real faces (Betts & Wilson, 2010; Loffler, Yourganov, Wilkinson, & Wilson, 2005). Each face is defined by 37 geometric measurements indicating positions of facial features and head shape, representing configural information of the face. The head shape and hairline were fitted with a curve composed of radial frequency components (Wilkinson, Wilson, & Habak, 1998). For individual features, generic eye, nose, and mouth templates were used. Images were bandpass filtered with a circular difference of Gaussians. The filter had a bandwidth of 2.0 octaves and was centered at 10.0 cycles per face width,

Figure 1. Block design procedure used in both face localizer and experimental runs. Each stimulus block lasted for 32 sec and presented 16 images across eight trials. In each trial (two TRs), a fixation cross was displayed for 250 msec, followed by a first item for 750 msec, a fixation for 250 msec, a second item for 2000 msec, and a blank screen for 750 msec. The figure shows an example of experimental condition IsVs presenting the same identity synthetic faces in the same view. Blocks of stimulus images were alternated with fixation blocks displaying a fixation cross in a gray background screen for 16 sec.



which was approximately 8.0 cpd at the viewing distance used. This spatial frequency band provides spatial frequency information crucial for face identification (Gold, Bennett, & Sekuler, 1999; Näsänen, 1999). Stimulus contrast was held at 100% for all faces used. For these reasons, synthetic faces are optimal for testing older adults whose face perception and recognition are affected by age differences in aspects of spatial vision such as contrast and spatial frequency (Lott et al., 2005; Owsley, Sekuler, & Boldt, 1981; also see Delahunt, Hardy, & Werner, 2008; Owsley, Sekuler, & Siemen, 1983). The synthetic faces were used to examine older adults in Habak et al. (2008): Older adults performed as well as young adults in matching the same facial identity when there was no viewpoint change, but they were poor at matching the same face across different viewpoints.

For each gender, mean faces for frontal and 20° side view were constructed from averaging 40 individual faces in the database. All synthetic faces were scaled to equal size by normalizing face measurements of individual faces relative to those of the mean face of that gender. The geometric difference between two faces is determined by the Euclidean distance between their 37-dimensional vectors.

To control for incidental similarities among faces presented in the same block, the individual faces were normalized to have a 12% geometric variation from the mean after subtracting a mean face and orthogonalized by removing cross-correlations among faces using the Gram-Schmidt procedure (Diamantaras & Kung, 1996). Recent evidence has shown that the mathematically orthogonal synthetic faces are perceptually orthogonal as well (Yotsumoto, Kahana, Wilson, & Sekuler, 2007). These orthogonal faces always have a constant difference between any two faces: When they are distanced 12% from the mean, any two faces differ by $12 \cdot \sqrt{2} = 17\%$. Facial views were morphed following the same procedure as previously described (see Lee, Matsumiya, & Wilson, 2006). Four views, 0°, 6.7°, 13.3° and 20°, and their mirror images were used in the condition presenting different views.

Stimuli for localizer runs included gray-scaled photographs of natural faces (frontal, 20° side views), houses (frontal, 20° side views), common household objects and scrambled textures of the objects (created by scrambling patches of the intact objects to obscure any discernible features). These localizer stimuli were previously employed in fMRI studies using synthetic faces (Betts & Wilson, 2010; Loffler et al., 2005).

For a postscan face matching task that examined the participant's face perception ability, novel faces that were not presented during the fMRI experiment were used (i.e., pictures of real people). This postscan testing was carried out on a different day from the scan because adaptation effects can last up to several days (Henson, 2003). Moreover, we considered that matching performance of real faces would be more representative of face recognition in real life as we have tested face discrimination using syn-

thetic faces in a larger group of older adults (see Habak et al., 2008). Unfamiliar faces (40 women and 40 men) were downloaded from the Max-Planck Institute for Biological Cybernetics in Tuebingen, Germany (faces.kyb.tuebingen.mpg.de/). These facial images were trimmed to remove hair and clothing and had neutral expressions. They were displayed in the frontal and/or 30° side views (to the right). Each face was converted to a 256-gray-level format and fit a 200-pixel high window (6.2° of visual angle at the viewing distance of 60 cm).

Experimental Procedure

The adaptation experiment included four conditions: same identity–same viewpoint (IsVs), same identity–different viewpoint (IsVd), different identity–same viewpoint (IdVs), and different identity–different viewpoint (IdVd). Procedures for adaptation and localizer runs were the same. During a run, each stimulus condition was repeated twice in a counterbalanced order, which produced a total of eight blocks per run. Each stimulus block lasted for 32 sec and presented 16 images (Figure 1). In each trial, a fixation cross was displayed in a uniform gray field for 250 msec, followed by a first stimulus displayed for 750 msec, a fixation cross for 250 msec, a second stimulus for 2000 msec, and a gray blank screen for 750 msec. The participant's task was to indicate which of the two stimulus intervals contained a 6% smaller head during an adaptation experiment or whether the two presentations have the same image during a localizer scan (three repetitions per block). The FFA response to faces is invariant up to a threefold linear size change (Andrews & Ewbank, 2004). The 6% size difference was large enough to yield equally good performance in both old and young groups (see Table 1) and sufficiently small to require strict attention. We used a size judgment that was independent of the experimental variables, identity, and view to prevent attention from being tuned to individual identity or viewpoint, which might modulate the BOLD signal (Henson, 2003). Blocks of stimulus images were alternated with fixation blocks displaying a fixation cross in a gray background screen for 16 sec, such that each run lasted 404 sec.

Because the task in the scanner did not assess face perception per se, we conducted an additional face matching test so that we could correlate brain activity with a sensitive measure of behavioral performance. As noted above, the in-scanner task was used to maintain attention and avoid age differences in performance. Previous fMRI adaptation studies also have used different tasks in and outside the scanner (Davies-Thompson et al., 2009; Ewbank & Andrews, 2008); similar to our study, these earlier ones used detection of a small red dot superimposed on the face to maintain attention in the scanner and then an identity matching task was performed outside the scanner (also see Rotshtein, Geng, Driver, & Dolan, 2007). In the present study, some participants did not return for this test, resulting in 14 older adults and 12 young adults with behavioral measures. In

Table 1. Behavioral Performance (Outside and Inside the Scanner)

| | Older Adults | | Younger Adults | |
|---|--------------|-----------------|----------------|-----------------|
| | Accuracy | RT | Accuracy | RT |
| <i>Face-matching performance (outside the scanner)</i> | | | | |
| IsVs | 0.97 (0.01) | 797.50 (47.94) | 0.98 (0.01) | 708.87 (42.58) |
| IsVd | 0.77 (0.06) | 1059.16 (59.72) | 0.88 (0.02) | 867.79 (55.04) |
| IdVs | 0.78 (0.05) | 1037.73 (66.22) | 0.88 (0.04) | 853.66 (62.65) |
| IdVd | 0.77 (0.04) | 1133.05 (98.14) | 0.86 (0.03) | 871.15 (45.54) |
| <i>Head size detection performance (inside the scanner)</i> | | | | |
| IsVs | 0.92 (0.11) | 751.70 (168.41) | 0.95 (0.05) | 774.34 (102.41) |
| IsVd | 0.91 (0.11) | 807.91 (150.24) | 0.92 (0.08) | 814.30 (94.16) |
| IdVs | 0.90 (0.11) | 818.19 (146.79) | 0.93 (0.07) | 812.52 (137.32) |
| IdVd | 0.88 (0.11) | 870.08 (136.53) | 0.90 (0.09) | 838.68 (123.64) |

RT (in msec) included correct trials only. *SEs* are in parentheses.

each trial, a first face was displayed for 500 msec, followed by a mask (random noise patterns) for 500 msec, and a second face was shown for 4 sec or until the participant responded. Identity and/or viewpoint were manipulated in the four conditions: IsVs, IsVd, IdVs, and IdVd. Repetitions were run for each condition, and all conditions were randomly interleaved from trial to trial. Participants had to determine whether the identity of the second face matched that of the first one regardless of viewpoint change; accuracy and RTs were recorded.

fMRI Data Acquisition

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

Stimuli were presented using E-Prime software version 1.2 (Psychology Software Tools). Images were back-projected onto a screen behind the scanner and shown to the participant using a mirror mounted on the head coil. The display had a spatial resolution of 1024 × 768 pixels and a visual angle of approximately 14.8° × 12.1° at a view-

ing distance of 132 cm. Frontal synthetic faces subtended, on average, 2.9° × 4.3° of visual angle.

fMRI Data Analysis

Data preprocessing was carried out using the Analysis of Functional Neuroimages package (AFNI; Cox, 1996). The first 10 scans in each run, during which participants saw the experimental instructions on the screen and then maintained fixation, were excluded to allow for brain magnetization to reach a steady state. Further preprocessing of functional scans involved physiological noise correction, slice timing correction, and 3-D motion correction (using a 3-D Fourier transform interpolation). Any individual run, in which the peak range of the participant's head motion exceeded 1.5 mm, was discarded.

ROI Analysis

We used the general linear model (GLM) in AFNI for assessing activity in functionally defined regions. In the GLM analysis, the shape of the hemodynamic response functions was modeled as a gamma function convolved with a boxcar function of width equal to the duration of the block. The resultant fit coefficients (β -coefficients) represent activity from baseline averaged within the block. Statistical maps were converted into MNI space (the Montreal Neurological Institute 152 template) and smoothed with a Gaussian filter with an FWHM value of 6 mm in the adaptation experiment and with a 4-mm Gaussian filter in the localizer experiment. A smaller filter was used for localizer data to facilitate the localization of the FFA, which had a relatively small volume in each participant. Face-preferring ROIs

such as the FFA and OFA were functionally defined in each participant using GLM to determine the voxels that sustained greater responses to faces compared with houses, or to objects in the lateral/middle fusiform gyrus (Kanwisher et al., 1997) and the inferior or middle occipital gyrus (Gauthier et al., 2000).

Univariate Analysis (GLM): Age Differences

A voxel-wise mixed-effects ANOVA was conducted with two fixed factors, condition (IsVs, IsVd, IdVs, IdVd) and group (old, young), and a random factor, participants. The p values for cluster reports were corrected using AFNI AlphaSim with 1000 Monte Carlo simulations.

Multivariate Analysis: Whole-brain and Behavior Correlations

We employed a multivariate method to assess brain-behavior correlations, partial least squares (PLS; McIntosh, Chau, & Protzner, 2004; McIntosh, Bookstein, Haxby, & Grady, 1996). PLS measures distributed signal changes across time and space and reveals brain regions that covary with behavior performance (called behavior PLS). It examines the coordinated activity of a set of brain regions showing similar activity patterns rather than the independent activity of a single brain region. The output of PLS analysis is a set of latent variables (LVs) that account for maximum covariance between regional activity changes and a behavioral measure.

For PLS analysis, all motion-corrected images of each run and each participant were resampled to 2-mm isotropic voxel resolution, transformed into MNI space and smoothed with a 6-mm Gaussian filter. In the current study, behavior PLS examined the correlations between brain activity and RTs (correct trials only) and between brain activity and accuracy measured across participants in the face-matching test for each condition and then contrasted these correlations across conditions. A brain score is calculated for each participant, which is the product of the weighted value (salience) of each voxel and BOLD signals summed across the entire brain for each condition on a given LV. Salience indicates the degree to which a voxel is related to the LV and can be positive or negative depending on the voxel's relation with the pattern of behavior-dependent differences identified by the LV. Hence, a brain score is an index of how strongly each participant expresses the particular pattern of activity seen in each LV. Behavior PLS reports the correlation between this summary measure of brain activity and the behavioral measure. The significance of each LV was determined by 700 permutation tests and the standard error of each voxel's salience on each LV was estimated by 100 bootstrap resampling steps (McIntosh et al., 1996). Peak voxels with a bootstrap ratio (salience/standard error, BSR) >3.0 are considered to be reliable, approximating $p < 0.005$ (Sampson, Streissguth, Barr, & Bookstein, 1989). In the present study, cluster re-

ports are based on local maxima of BSR > 3.0 and contiguous clusters of ≥ 60 voxels (480 mm^3). The bootstrap also calculates confidence intervals (CIs) for each correlation between RTs and brain scores as a measure of reliability, and the 95% CI was used in the current study.

RESULTS

Behavioral Results

Face Matching Performance Outside the Scanner

Data from the postscan face-matching task of both accuracy and RTs are shown in Table 1. The data were examined by a 2×4 repeated measures ANOVA (Group \times Condition), and Greenhouse–Geisser estimates were used to correct for violations of sphericity. For accuracy measures, the effects of Group [$F(1, 24) = 6.47, p = .018, \eta_p^2 = 0.21$] and Condition [$F(1.72, 41.18) = 9.38, p = .001, \eta_p^2 = 0.28$] were significant, but the interaction was not [$F(1.72, 41.18) = 0.78, p = .45, \eta_p^2 = 0.03$]. Pairwise comparisons with Bonferroni corrections revealed better performance in the IsVs condition compared with IsVd, IdVs, or IdVd conditions ($p < .001$ in all three comparisons). The analysis of RT data revealed similar results: significant effects of Group [$F(1, 24) = 5.29, p = .03, \eta_p^2 = 0.18$], Condition [$F(1.84, 44.07) = 19.36, p < .001, \eta_p^2 = 0.45$], and no interaction [$F(1.84, 44.07) = 1.99, p = .15, \eta_p^2 = 0.08$]. The difference between conditions was due to faster RTs in IsVs compared with the other conditions ($p < .001$ in all three comparisons).

Size Detection Performance in the Scanner

During scanning, the size judgment task produced equivalent performance between the two groups (see Table 1). In RTs (for correct trials), a 2×4 mixed-factors ANOVA revealed no effect of Group [$F < 1$], no interaction between Group \times Condition [$F(2.28, 63.71) = 2.08, p = .13, \eta_p^2 = 0.07$] and only an effect of Condition [$F(2.28, 63.71) = 22.47, p < .001, \eta_p^2 = 0.45$]. Similarly, in accuracy, there were no effect of Group [$F < 1$], no interaction [$F < 1$] but an effect of Condition [$F(3, 84) = 7.14, p < .001, \eta_p^2 = 0.20$].

In summary, older adults were worse in face identity matching than young adults (measured outside the scanner), consistent with the literature suggesting face perception and recognition deficits in aging. Although the older adults exhibited significant deficits overall, they performed as well as young adults in matching the same-view faces. In contrast, there were no age differences on the task of head size detection carried out in the scanner. Next, we examined the fMRI data to see whether the magnitude of adaptation in face-sensitive ROIs would reflect the face recognition reductions of the older adults in each condition, and if the whole brain activity would differ between the groups.

fMRI Results

Activity in ROIs Identified in Each Participant (Localizer Scans)

Table 2 shows the ROI coordinates and BOLD signals averaged across individual participants of each group. One young adult's localizer data were discarded because of noise (but this participant's adaptation scans were included for group analysis). The FFA and OFA were identified by either a face versus house or face versus object contrast to identify all ROIs reliably (see issues of traditional face localizer in Fox, Iaria, & Barton, 2009). When corrected for $p < .05$ (using AFNI AlphaSim with 1000 Monte Carlo simulations), all young adults and 10 of 15 older adults showed activation of the right FFA. Accordingly, all ROIs in Table 2 were determined using a more liberal threshold of uncorrected $p = .005$ which now included 13 of 15 older adults. ROIs in one of the two remaining two older adults were with uncorrected $p = .01$ (included in Table 2; e.g., Goh et al., 2010 used uncorrected $p < .05$). The other older adult did not show right FFA activation even with these liberal p values, although this participant demonstrated the left FFA and bilateral OFAs with uncorrected $p = .005$.

Adaptation Magnitudes in ROIs

Figure 2 shows signal levels (β -weights) across four conditions in each of the ROIs. The figure suggests that older adults show no decrease in BOLD response to IsVs in all face-preferring regions, whereas young adults show signal decrease in the FFA bilaterally and right OFA. A 2×4 mixed-factors ANOVA (Group \times Condition) was performed with β -coefficient values in each ROI. Subsequently, one-way repeated measures ANOVAs and Bonferroni tests were conducted for each group separately to compare conditions.

In right FFA, a significant effect was found for Condition [$F(2.06, 53.42) = 3.29, p = .04, \eta_p = 0.11$] and Group \times Condition [$F(2.06, 53.42) = 5.25, p = .008, \eta_p = 0.17$], but not for group [$F < 1$]. Although the level of activation was similar in both groups, older adults and young adults demonstrated different patterns of BOLD responses across

conditions. In one-way repeated measures ANOVA, older adults did not show a difference among the conditions [$F(1.37, 17.77) = 1.50, p = .25, \eta_p = 0.10$], confirming no adaptation. Young adults showed a significant effect [$F(1.74, 22.59) = 8.0, p = .003, \eta_p = 0.38$]. Post-hoc comparisons were subsequently conducted in young adults. A difference in IsVs versus IdVs [$MD = 0.17, p = .002$] indicates a significant recovery from adaptation by identity changes in the same view. A difference between IsVs versus IdVd was also significant [$MD = 0.21, p = .001$].

In left FFA, a 2×4 mixed ANOVA found no effect of group [$F(1, 25) = 1.41, p = .25, \eta_p = 0.05$], no effect of condition [$F(3, 75) = 1.96, p = .13, \eta_p = 0.08$], and no interaction [$F(3, 75) = 1.78, p = .16, \eta_p = 0.07$]. Although the pattern of results resembles that in right FFA, it was not significant, consistent with observations that the left FFA is less specialized in processing faces (e.g., Dien, 2009).

In the OFA, a 2×4 mixed ANOVA for each hemisphere showed only a significant effect of Condition on the right [$F(2.15, 45.15) = 3.41, p = .04, \eta_p = 0.14$].

The age differences in right FFA raise the question of whether the magnitude of adaptation in ROIs would be related to the observer's performance on face matching outside the scanner. Partial correlations, controlled for participants' age, were assessed between the adaptation index for IsVs and performance in the face-matching test. The adaptation index (0 = no adaptation) was calculated by $(\text{IdVd} - \text{IsVs})/(\text{IdVd} + \text{IsVs})$ with β -coefficient values. In one YA, a signal value in IsVs was negative and resulted in an exponentially large index; thus, this participant's β value was rounded to 0 and the adaptation index was capped to 1 (see Avidan & Behrmann, 2009). Three measures of accuracy and RT were examined, one representing the average between IdVd and IsVs (relating to fMRI adaptation conditions), one averaged across all conditions, and one representing the difference between IdVd and IsVs. No significant correlations were found: with accuracy of IdVd and IsVs [$r = 0.24, p = .27$], accuracy of all conditions [$r = 0.09, p = .68$], accuracy difference of IdVd - IsVs [$r = 0.33, p = .12$], RT of IdVd and IsVs [$r = -0.03, p = .90$], RT of all conditions [$r = 0.05, p = .81$], RT difference of IdVd - IsVs [$r = -0.26, p = .23$].

Table 2. Regions of Interest (Localizer Scans)

| ROI | Hem | Older Adults | | | | | Younger Adults | | | | |
|-----|-----|---------------------------|---------|--------|-------|---------------------------|----------------|--------|-------|--|--|
| | | MNI Coordinates | β | Volume | n | MNI Coordinates | β | Volume | n | | |
| FFA | R | 43 (5), -58 (9), -18 (4) | .62 | 437 | 14/15 | 42 (5), -56 (5), -18 (5) | .84 | 1311 | 14/14 | | |
| | L | -40 (5), -57 (9), -21 (4) | .82 | 309 | 14/15 | -41 (4), -53 (7), -20 (3) | .92 | 1596 | 13/14 | | |
| OFA | R | 46 (6), -73 (7), -5 (6) | .64 | 966 | 13/15 | 45 (6), -78 (8), -8 (6) | .51 | 1022 | 11/14 | | |
| | L | -40 (6), -78 (7), -6 (10) | .48 | 478 | 13/15 | -41 (8), -79 (9), -8 (5) | .50 | 740 | 11/14 | | |

Hem = hemisphere; R = right; L = left; MNI Coordinates = averaged MNI coordinates [x, y, z] for a peak voxel with 1 SD in parentheses; β = averaged β -coefficient (activity from baseline) of each group; Volume = averaged cluster size (mm^3); n = the number of participants who showed the region/the total number of participants. The voxel resolution $3 \times 3 \times 5$ was used.

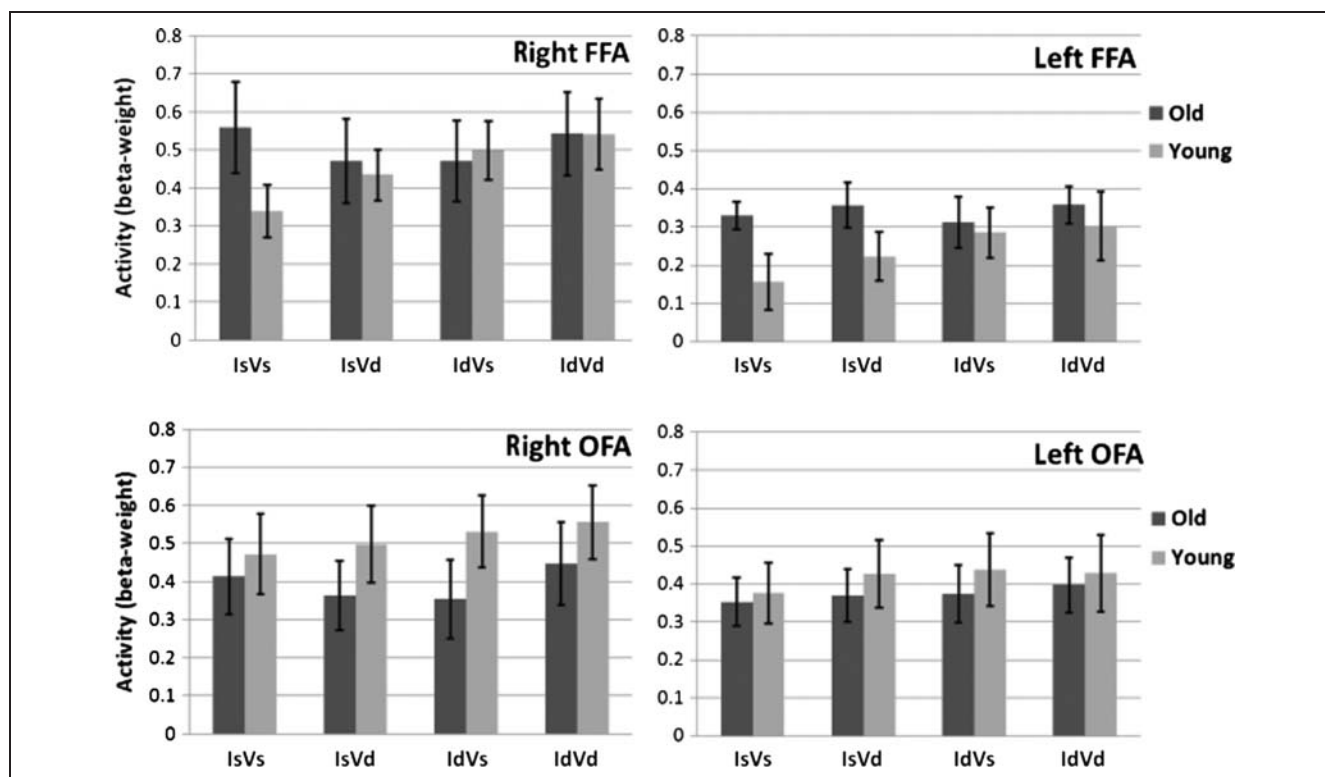


Figure 2. Activation profiles across conditions in FFA and OFA.

In summary, older adults failed to reduce neural responses to repeated facial stimuli in right FFA. Despite deficient neural representations in this core face area, older adults' behavioral data clearly demonstrated 97% successful hits in perceiving faces as the same at a given viewpoint. This suggests that other regions contribute to face matching and compensate deficiencies in the core face processing areas. In contrast, young adults had reduced responses to repeated faces or views in right FFA. Despite the age differences observed in adaptation patterns, overall BOLD activation levels did not differ between the two groups in any of the face ROIs, so absence of adaptation in older adults may not be attributed to weak BOLD signals. The next analysis contrasted whole brain activity in the two groups to examine brain regions that were unique to each group.

Hemispheric Differences in ROIs

A 2×4 repeated measures ANOVA (Hemisphere \times Condition) assessed hemispheric differences in ROIs for each group. In the FFA, no effect was significant in older adults: Hemisphere [$F(1, 12) = 2.35, p = .15, \eta_p = 0.16$], Condition [$F < 1$], Hemisphere \times Condition [$F(3, 36) = 2.08, p = .12, \eta_p = 0.15$]. In young adults, a significant effect was found for Hemisphere [$F(1, 12) = 17.34, p = .001, \eta_p = 0.59$] and Condition [$F(1.68, 20.13) = 6.07, p = .01, \eta_p = 0.34$], but not for Hemisphere \times Condition [$F < 1$]. Young adults showed a stronger activity in right than left

FFA. In the OFA, none of the effects was significant in older as well as in young adults.

Univariate Analysis (GLM): Age Differences

Age differences were examined by contrasting the two groups in each condition as well as all conditions collapsed. In each condition, older adults engaged more brain areas than young adults. There were only two areas that showed greater activity in young adults: left middle frontal gyrus ($x = -39, y = 27, z = 45.5$) found in IsVd and left superior frontal gyrus ($x = -12, y = 33, z = 50.5$) in IdVd. With all conditions combined, older adults showed significantly more activations in left fusiform and left middle occipital, bilateral frontal, and parietal regions (Table 3 and Figure 3), whereas no area showed greater activations for young adults. To examine whole-brain activation patterns correlated with behavioral performance, the following analyses used behavior PLS.

Multivariate Analysis (PLS): Whole-brain and Behavior Correlations

Behavior PLS was conducted with face matching RTs independently measured outside the scanner to examine whole-brain correlations (for accuracy, see Supplementary Data) because stimulus-driven adaptation levels were not positively associated with face matching performance in right FFA. The results of FFA correlation analyses imply that

Table 3. Age Differences across All Conditions: Older Adults > Younger Adults

| Gyrus or Region | Hem | MNI Coordinates | | |
|---------------------------------|-----|-----------------|-----|-------|
| | | x | y | z |
| Fusiform | L | -39 | -42 | -24.5 |
| Middle occipital | L | -24 | -78 | 20.5 |
| Superior temporal | L | -54 | -39 | 20.5 |
| Middle temporal | R | 60 | -39 | -9.5 |
| Precuneus | R | 15 | -75 | 45.5 |
| Supramarginal | L | -57 | -24 | 15.5 |
| | L | -63 | -45 | 25.5 |
| Inferior parietal | R | 48 | -45 | 40.5 |
| Superior orbital frontal | L | -24 | 45 | -14.5 |
| Superior medial frontal | R | 9 | 30 | 40.5 |
| Inferior frontal (triangularis) | L | -45 | 48 | 5.5 |
| Thalamus | L | -9 | -6 | 5.5 |
| Cerebellum | L | -6 | -81 | -19.5 |
| | L | -27 | -36 | -39.5 |
| | L | -12 | -69 | -49.5 |
| | L | -33 | -54 | -29.5 |
| | L | -21 | -48 | -24.5 |
| | L | -33 | -54 | -44.5 |
| | R | 24 | -36 | -39.5 |
| | R | 33 | -60 | -54.5 |

All clusters are $\geq 405 \text{ mm}^3$, $p < .05$ (corrected). All clusters have significantly increased activity in older adults compared with younger adults. No region was found to show more activity in younger adults. Coordinates indicate a peak voxel location. Hem = hemisphere; L = left; R = right; x = right/left; y = anterior/posterior; z = superior/inferior.

successful performance in this type of task does not solely rely upon a core face processing area but involves additional regions.

Behavior PLS with RTs from the face matching task yielded two significant LVs, and behavior PLS with face matching accuracy yielded one significant LV (29.06% of covariance, $p < .001$), in which correlation patterns were similar to LV1 of behavior PLS with RT (see Supplementary Data). Hence, the PLS results based on RT data were reported here. It should be noted that because in-scanner RTs from the size detection task were equivalent between the two groups, the results of PLS with outside-scanner RTs would not be ascribed to differences in motor speed between the two groups during the scan.

Behavior PLS identified two sets of brain regions where activity covaried with performance across conditions in older and young adults. The first LV accounted for 44.5% of the covariance in the data and was highly significant at $p < .001$ (Figure 4). In three conditions, IsVs, IdVs and

IdVd, faster older adults activated a similar network of regions as faster young adults (Table 4). These regions are typically involved in face processing and include fusiform, middle occipital, middle temporal, middle cingulate on the right, and superior temporal gyri, insula, middle and inferior frontal cortices bilaterally (Figure 4). The cluster found in right fusiform gyrus does not appear to overlap the right FFA (see Table 2). For the older adults in the IsVd condition, there was not a reliable correlation between the pattern of activity seen in Figure 4 and RT, and no other regions were found to be correlated with RT in this condition. This indicates that activity in the same set of brain regions was associated with faster responding in young adults across all conditions, whereas older adults using this same network did not necessarily perform more quickly in IsVd. These PLS results may reflect older adults' difficulty in detecting facial identity when viewpoints differ.

The second LV differentiated older adults from young adults across all the conditions (17% of covariance, $p < .021$; Figure 5 and Table 5). Faster older adults activated a number of regions to a greater extent than slower older adults, including left occipital and left inferior frontal areas (colored in blue in Figure 5). Interestingly, these also were areas where older adults also had more activation than the young (see Table 3). The correlations were in the opposite direction in young adults, so activity was greater in these regions (Table 5) in young adults who responded more

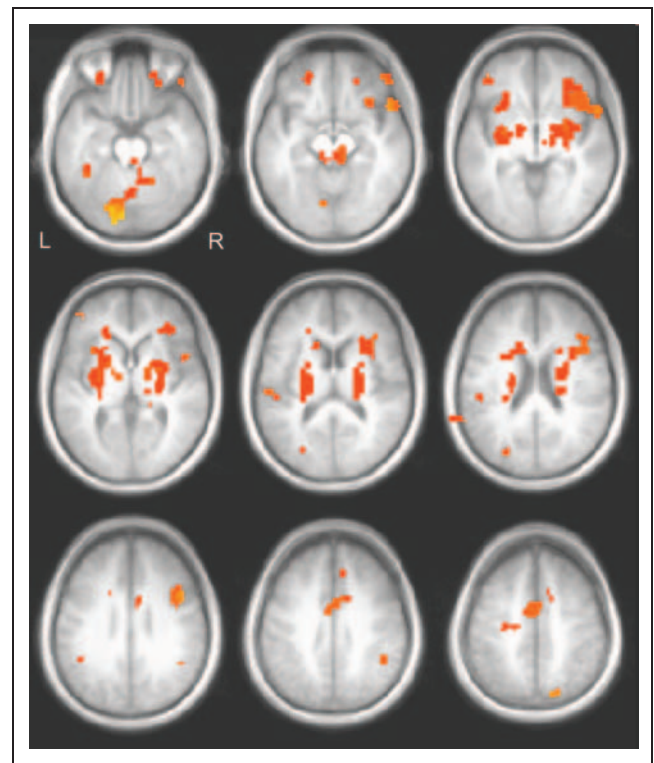


Figure 3. Univariate ANOVA results showing age effects. Older adults elicited greater activity than YAs across all conditions collapsed (Table 3). Clusters are corrected at $p < .05$ and volume $\geq 405 \text{ mm}^3$. Top left corner slice $z = -18$, slice space = 8 mm.

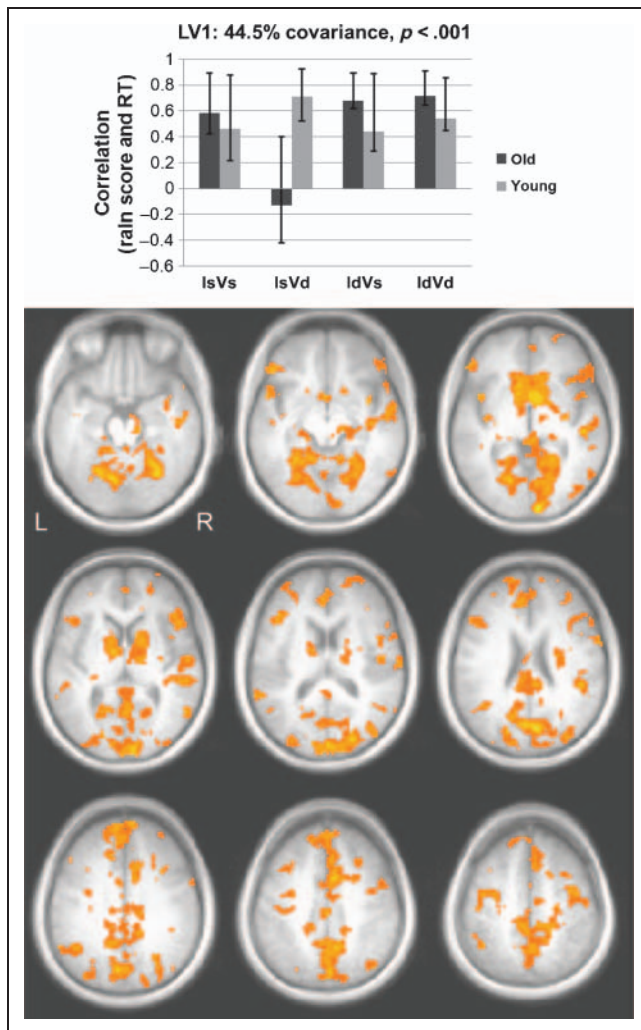


Figure 4. Multivariate analysis of brain-behavior correlations (LV1 from behavior PLS). The LV profile plot summarizes brain score and behavior correlations across conditions (error bar = 95% CI from bootstrapping). Brain regions show the pattern of correlated activity. All maxima have BSR ≥ 3.0 , cluster volume $\geq 480 \text{ mm}^3$ and are reported in Table 4. In IsVs, IdVs, and IdVd, faster older adults activated a similar network of regions (in red and yellow) as faster YAs. Top left corner slice $z = -16$, slice space = 8 mm.

slowly. In contrast, slower older and faster young adults had more activity in left middle orbital frontal ($x = -2, y = 48, z = -10$), left cuneus ($x = -14, y = -58, z = 18$), and right calcarine gyrus ($x = 20, y = -58, z = 16$). Thus, the results of LV2 indicate that a network of regions that is helpful for older adults does not support fast performance in young adults, whereas the opposite is true for regions which support fast performance in young adults, suggesting that some regions recruited for processing faces are different in old and young adults.

DISCUSSION

Summary of the Results

The degree of adaptation to a particular stimulus is presumed to provide an index of the extent to which stimulus

specific information is coded by the different populations of neurons and is placed in the service of tasks utilizing that information. In view of this widely held assumption, it was surprising to discover that old adults, who performed similarly to young adults in matching the same facial identity shown in the same view outside the scanner (also consistent with previous behavioral data of Habak et al., 2008; Searcy et al., 1999), showed no adaptation to faces in right FFA, a region that is crucial for face-recognition. Consistent with the role assigned to right FFA in face recognition, young adults showed adaptation effects in that

Table 4. Brain Areas Correlated with Face-Matching Performance (Behavior PLS, LV1)

| Region | Hem | MNI Coordinates | | | BSR | Volume |
|--|-----|-----------------|----------|----------|-------|--------|
| | | <i>x</i> | <i>y</i> | <i>z</i> | | |
| <i>Face-processing network used by both Older and Younger Adults groups, except for IsVd in Older Adults</i> | | | | | | |
| Middle occipital | R | 40 | -80 | 2 | 4.01 | 992 |
| Fusiform | R | 30 | -62 | -16 | 8.82 | 2224 |
| Middle temporal | R | 58 | -60 | 8 | 5.52 | 2216 |
| Superior temporal | R | 50 | -24 | 2 | 7.39 | 7784 |
| | L | -58 | -42 | 14 | 4.97 | 1248 |
| Inferior parietal | L | -40 | -52 | 50 | 5.03 | 592 |
| Supramarginal | R | 48 | -34 | 26 | 6.52 | 1984 |
| Angular | L | -42 | -54 | 30 | 6.06 | 2128 |
| Middle cingulate | R | 8 | 8 | 36 | 8.31 | 29984 |
| Insula | R | 38 | 4 | -8 | 5.98 | 496 |
| | R | 48 | 8 | 2 | 5.17 | 632 |
| | L | -42 | 8 | 0 | 6.65 | 1072 |
| Inferior frontal (p. orbitalis) | L | -22 | 12 | -20 | 7.77 | 584 |
| | L | -48 | 32 | -8 | 6.59 | 1472 |
| (p. triangularis) | R | 50 | 22 | 10 | 6.21 | 5000 |
| | L | -44 | 24 | 18 | 6.67 | 2456 |
| Middle frontal | R | 42 | -6 | 52 | 8.05 | 4112 |
| | R | 38 | 46 | 22 | 4.63 | 888 |
| | L | -36 | 18 | 42 | 5.81 | 792 |
| | L | -32 | 44 | 22 | 4.44 | 984 |
| Putamen | R | 34 | -12 | 4 | 8.79 | 18744 |
| Precentral | R | 64 | 8 | 24 | 5.43 | 1496 |
| | L | -32 | -8 | 52 | 6.00 | 3744 |
| Cerebellum | L | -10 | -66 | -18 | 10.00 | 131600 |
| | L | -24 | -38 | -40 | 5.45 | 800 |

Hem = hemisphere; R = right; L = left. All reported activations are from LV1, BSR > 3.0 , cluster volume $> 480 \text{ mm}^3$.

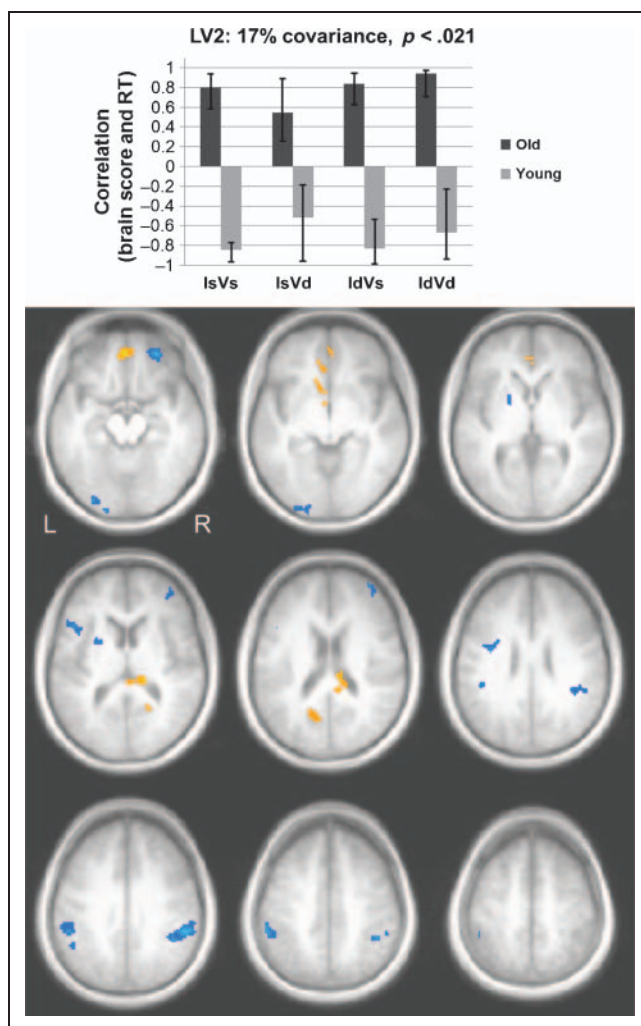


Figure 5. Multivariate analysis of brain–behavior correlations (LV2 from behavior PLS). The LV profile plot summarizes brain score and behavior correlations across conditions (error bar = 95% CI from bootstrapping). Brain regions show the pattern of correlated activity. All maxima have BSR ≥ 3.0 , cluster volume $\geq 480 \text{ mm}^3$ and are reported in Table 5. Fast older adults activated the regions colored in blue to a greater extent than slow older adults. Top left corner slice $z = -12$, slice space = 8 mm.

region to repetition of facial identity in the same view. Unlike young adults, older adults failed to show neural adaptation to repetition even when facial identity and view were kept constant. In analysis of correlation between the adaptation magnitude in right FFA and behavioral performance, no significant correlation was found in both groups when the effect of age was removed. Such findings suggest that adaptation levels in right FFA alone do not provide an accurate index of performance.

Comparing young and old adults across all conditions (univariate GLM results), we found that older adults showed greater activation in left fusiform, left middle occipital, bilateral frontal and parietal regions compared with young adults. Importantly, we eliminated age differences in behavioral performance during scanning by adopting a task that yielded equivalent performance in older and young

adults so that age differences in brain activity could be attributed to changes in neural processing, and not to performance difference.

Such overrecruitment of brain regions found in older adults compared with young adults could be interpreted either as less efficient use of brain resources by older adults (Grady, 2008; Morcom, Li, & Rugg, 2007; Zarahn, Rakitin, Abela, Flynn, & Stern, 2007) or that those regions are recruited to compensate for the deficiencies of the non-adapted fusiform region (Davis et al., 2008; Grady, 2002, 2008; Cabeza, Anderson, Locantore, & McIntosh, 2002). The latter interpretation was supported by results from multivariate PLS analyses, which examined whole brain–behavior correlations. The first network identified in PLS showed that the same face-processing network was engaged in older adults and in younger adults as a function of how well they performed in all conditions, except the one presenting a same facial identity across different viewpoints. The network included fusiform, middle occipital, middle temporal on the right, and superior temporal gyri, insula, frontal cortices bilaterally. The area found in right fusiform gyrus does not appear to overlap with the right FFA. Hence, even with deficient neural adaptation in right FFA, older adults recruited similar other regions as young in three conditions, suggesting that regions other than right FFA contributed to performance in matching the same face shown in the same view. Moreover, a second network of regions was identified that was correlated with performance in older adults but not young adults, indicating age-specific involvement of this network across all conditions. These regions included the left occipital, bilateral frontal and parietal areas. These results suggest that older adults utilize a different network of regions and activate

Table 5. Brain Areas Correlated with Matching Performance (Behavior PLS, LV2)

| Region | MNI Coordinates | | | | | BSR | Volume |
|---|-----------------|-----|-----|-----|------|------|--------|
| | Hem | x | y | z | | | |
| <i>Better performance in Older Adults (worse performance in Younger Adults)</i> | | | | | | | |
| Inferior occipital | L | -28 | -84 | -10 | 5.81 | 592 | |
| | | -18 | -96 | -12 | 4.35 | 592 | |
| Supramarginal | R | 52 | -36 | 36 | 5.84 | 3080 | |
| Inferior parietal | L | -54 | -36 | 42 | 5.35 | 2696 | |
| Middle orbital frontal | R | 30 | 44 | -14 | 6.80 | 904 | |
| Middle frontal | R | 38 | 56 | 20 | 4.26 | 544 | |
| Inferior frontal (triangularis) | L | -48 | 20 | 10 | 4.71 | 624 | |
| Putamen | L | -24 | 6 | 12 | 4.75 | 512 | |

The table shows only the regions colored in blue (Figure 5) because only a few participants demonstrated brain scores corresponding to red areas. All reported activations are from LV2, BSR > 3.0 , cluster volume $> 480 \text{ mm}^3$. Hem = hemisphere; R = right; L = left.

more areas to compensate for deficient neural function of the ventral visual areas. We now discuss implications of these results with regards to aging in more detail.

Adaptation Is Reduced in the FFA with Age

Neuronal adaptation indicates that the populations of neurons underlying a representation are sensitive to the repeated property of the stimulus. It is still poorly understood how the adaptation magnitude would be linked to behavioral performance (Grill-Spector et al., 2006; Krekelberg, Boynton, & van Wezel, 2006). Deficiencies in adaptation (i.e., either no adaptation or too much adaptation) to face or object repetitions have been reported in normal aging (Goh et al., 2010; Chee et al., 2006; also see Grady et al., 2008 for auditory domain). Significant adaptation may occur only when older participants attend to the relevant stimulus dimension as spatially directed attention facilitates stimulus selection in the visual scene and suppresses unwanted information (Desimone & Duncan, 1995). Chee et al. (2006) found that adaptation effects in the lateral occipital complex to repeated objects in a changing background were observed in older adults only when they were instructed to attend to the objects. Likewise, Goh et al. (2010) found greater adaptation in the FFA bilaterally with age to a pair of morphed faces that differed by 40%, and a significant relationship between FFA adaptation and behavioral performance in the scanner. By requiring their participants to make a same or different identity judgment in the scanner, they effectively directed their participants' attention to facial identity (e.g., Henson & Mouchlianitis, 2007; Eger, Henson, Driver, & Dolan, 2004). By contrast, in our study, the participant's attention was directed to head size, a stimulus attribute irrelevant to identity, and we found no adaptation effects to facial identity in older adults and no correlation with behavioral performance outside the scanner, in both older and younger adults. Thus, when considered in context with other findings, our results suggest that adaptation effects to facial identity in older adults do not occur unless attention is directed to the stimulus dimensions that distinguish one face from another. In young adults, mere repetition is sufficient to induce adaptation effects (also see similar discussion in Daniel & Bentin, 2010; Gao et al., 2009).

Current theories posit that adaptation or reduction in neural response is due to "tuning" or "sharpening" of the internal stimulus representation through reductions in firing rates (Grill-Spector et al., 2006). It is possible that subtle differences between two faces is sufficient to activate different neuronal populations in young adults even when attention is not directed at the relevant stimulus dimensions—that is, neurons are narrowly tuned and the representation of a face is achieved by a unique response profile among the populations of neurons (Gilaie-Dotan & Malach, 2007) that can be achieved relatively automatically. By comparison, neurons in the brains of older adults may be broadly tuned to facial identity with

overlapping representations, such that neuronal populations respond less selectively to any particular stimulus face and instead respond to a greater number of faces, resulting in less distinctive brain responses to faces in general (e.g., Carp et al., 2011). Studies of old monkeys provide evidence for broadly tuned neurons in the middle temporal area (Liang et al., 2010) and in V1 perhaps due to reductions in GABA-mediated lateral inhibition (Leventhal, Wang, Pu, Zhou, & Ma, 2003). Such studies observed decreases in neuronal selectivity accompanied by increases in neural noise. A neural model based on human psychophysical data (Wilson, Mei, Habak, & Wilkinson, 2011) also has suggested broadening of cortical bandwidths for facial orientation in older adults. Future study should examine the selectivity of responses to facial identities in older adults.

Viewpoint Representation Is Less Reliable with Age

The results of behavior PLS indicated older adults' difficulty in representing facial identity across viewpoints (Habak et al., 2008). Behaviorally, older adults were similarly poor in the three conditions involving a change in identity or viewpoint (IsVd, IdVs, IdVd), yet those who engaged the same face processing network utilized by young adults were able to perform better in IdVs and IdVd but not in IsVd. These results suggest that viewpoint-independent representation in older adults does not reliably involve the face-processing network, leading to poor performance.

Face-processing Network Changes with Age

Our results demonstrate that older adults could perform as well as young adults in identifying faces as the same given the same viewpoint despite deficient FFA adaptation. This is in line with Rousselet et al. (2009), who showed that older adults exhibited strong N170 amplitude to pure noise while performing well on behavioral tests. This suggests that FFA activity per se does not predict face-matching performance, perhaps due to an involvement of additional regions required for face processing.

Deficiencies at early processing stages such as the FFA could cascade downstream and result in changes in functional brain networks (Davis et al., 2008; Grady, 2000, 2008). Our results are consistent with aging studies reporting reduced activity in occipito-temporal regions coupled with an increased engagement of prefrontal areas (Davis et al., 2008; Madden, Whiting, Provenzale, & Huettel, 2004; Grady, 2002; Grady, Bernstein, Beig, & Siegenthaler, 2002; Schiavetto, Kohler, Grady, Winocur, & Moscovitch, 2002; Grady et al., 1994); that is, older observers seem to compensate for processing deficits associated with decreased activity in the occipital lobe by increasing frontal activity. In our study, OFAs were not less active in older adults, but they did activate less selectively, suggesting that frontal regions sharpen the response to particular faces and lead to better differentiation. Most importantly, we found a network of regions that was uniquely associated

with performance in older adults but not in young adults. Consistent with the compensation hypothesis, this network included frontal areas, such as the left inferior frontal cortex, which was previously shown to be associated with improved face recognition following deep encoding (Grady et al., 2002), and the OFC, which had been shown to increase its connectivity with the OFA in young adults during detection of a face embedded in noise (Li et al., 2010; also see Ishai, 2008). If one considers that reduced selectivity of processing in occipito-temporal regions in older adults can be tantamount to adding noise to the system (Wilson et al., 2011), the recruitment of OFC might help to boost or clean up the signal, making faces more recognizable. In addition to OFC, the insula, anterior/middle cingulate cortex, and dorsolateral pFC can be involved in performance monitoring and response selection during challenging task conditions (Eckert et al., 2009; Taylor, Seminowicz, & Davis, 2009), so may have been recruited by our older adults for this reason. In addition to frontal regions, this unique network for high-performing older adults included the inferior parietal lobule implicated in bottom-up stimulus-driven attention (reviewed in Ciaramelli, Grady, & Moscovitch, 2008), the supramarginal gyrus implicated in visual and verbal working memory (Danckert & Ferber, 2006; Cohen et al., 1997), and the putamen involved in learning (reviewed in Packard & Knowlton, 2002). Thus, our results are consistent with the compensation account, such that engaging the frontal and parietal cortex is a general phenomenon associated with aging and assists older adults in performance (Park & Reuter-Lorenz, 2009; Davis et al., 2008; Reuter-Lorenz & Cappell, 2008; Rajah & D'Esposito, 2005; Grady et al., 1994).

The compensation account is further supported by evidence of decreased or altered lateralization with aging. In the FFA, young adults showed a stronger activity on the right than on the left, but older adults showed similar activity in the two hemispheres (e.g., Daniel & Bentin, 2010; Gao et al., 2009). Older adults also showed more activity compared with young adults in left fusiform gyrus and left middle occipital gyrus (Table 3), although face recognition is typically right-lateralized in young adults (see Dien, 2009). Moreover, these findings parallel those of other reports of decreased or altered lateralization in older adults in various domains, including face recognition (Daniel & Bentin, 2010; Gao et al., 2009; Grady et al., 1994, 2002; Grady, McIntosh, Horwitz, & Rapoport, 2000; Meudell & Greenhalgh, 1987; for reviews, see Grady, 2008; Reuter-Lorenz & Lustig, 2005; Cabeza, 2002). Together, these findings, including ours, suggest that, in older adults, regions in the left hemisphere are recruited to help the corresponding right hemisphere face-processing regions in face recognition.

Acknowledgments

This study was supported by a Canadian Institutes of Health Research grant to M. M. and C. L. G. (MOP106301) and the Canada

Research Chairs program, the Ontario Research Fund, and the Canadian Foundation for Innovation to C. L. G.

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REFERENCES

- Andrews, T. J., & Ewbank, M. P. (2004). Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe. *Neuroimage*, *23*, 905–913.
- Avidan, G., & Behrmann, M. (2009). Functional MRI reveals compromised neural integrity of the face processing network in congenital prosopagnosia. *Current Biology*, *19*, 1146–1150.
- Bartlett, J. C., Strater, L., & Fulton, A. (1991). False recency and false fame of faces in young adulthood and old age. *Memory and Cognition*, *19*, 177–188.
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, *8*, 551–565.
- Bernstein, L. J., Beig, S., Siegenthaler, A. L., & Grady, C. L. (2002). The effect of encoding strategy on the neural correlates of memory for faces. *Neuropsychologia*, *40*, 86–98.
- Betts, L. R., & Wilson, H. R. (2010). Heterogenous structure in face-selective human occipito-temporal cortex. *Journal of Cognitive Neuroscience*, *22*, 2276–2288.
- Boutet, I., & Faubert, J. (2006). Recognition of faces and complex objects in younger and older adults. *Memory and Cognition*, *34*, 854–864.
- Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: The HAROLD model. *Psychology and Aging*, *17*, 85–100.
- Cabeza, R., Anderson, N. D., Locantore, J. K., & McIntosh, A. R. (2002). Aging gracefully: Compensatory brain activity in high-performing older adults. *Neuroimage*, *17*, 1394–1402.
- Carp, J., Park, J., Polk, T. A., & Park, D. C. (2011). Age differences in neural distinctiveness revealed by multi-voxel pattern analysis. *Neuroimage*, *56*, 736–743.
- Chee, M. W. L., Goh, J. O. S., Venkatraman, V., Tan, J. C., Gutchess, A., Sutton, B., et al. (2006). Age-related changes in object processing and contextual binding revealed using fMR adaptation. *Journal of Cognitive Neuroscience*, *18*, 495–507.
- Ciaramelli, E., Grady, C. L., & Moscovitch, M. (2008). Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia*, *46*, 1828–1851.
- Cohen, J. D., Perlstein, W. M., Braver, T. S., Nystrom, L. E., Noll, D. C., Jonides, J., et al. (1997). Temporal dynamics of brain activation during a working memory task. *Nature*, *386*, 604–608.
- Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research*, *29*, 162–173.
- Danckert, J., & Ferber, S. (2006). Revisiting unilateral neglect. *Neuropsychologia*, *44*, 987–1006.
- Daniel, S., & Bentin, S. (2010). Age-related changes in processing faces from detection to identification: ERP evidence. *Neurobiology of Aging*, doi:10.1016/j.neurobiolaging.2010.09.001.
- Davies-Thompson, J., Gouws, A., & Andrews, T. J. (2009). An image-dependent representation of familiar and unfamiliar faces in the human ventral stream. *Neuropsychologia*, *47*, 1627–1635.

- Davis, S. W., Dennis, N. A., Daselaar, S. M., Fleck, M. S., & Cabeza, R. (2008). Que PASA? The posterior-anterior shift in aging. *Cerebral Cortex*, *18*, 1201–1209.
- Delahunt, P. B., Hardy, J. L., & Werner, J. S. (2008). The effect of senescence on orientation discrimination and mechanism tuning. *Journal of Vision*, *8*, 1–9.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222.
- Diamantaras, K. I., & Kung, S. Y. (1996). *Principal component neural networks*. Toronto: Wiley.
- Dien, J. (2009). A tale of two recognition systems: Implications for the fusiform face area and the visual word form area for lateralized object recognition models. *Neuropsychologia*, *47*, 1–16.
- Eckert, M. A., Menon, V., Walczak, A., Ahlstrom, J., Denslow, S., Horwitz, A., et al. (2009). At the heart of the ventral attention system: The right anterior insula. *Human Brain Mapping*, *30*, 2530–2541.
- Eger, E., Henson, R. N. A., Driver, J., & Dolan, R. J. (2004). BOLD repetition decreases in object-responsive ventral visual areas depend on spatial attention. *Journal of Neurophysiology*, *92*, 1241–1247.
- Ewbank, M. P., & Andrews, T. J. (2008). Differential sensitivity for viewpoint between familiar and unfamiliar faces in human visual cortex. *Neuroimage*, *40*, 1857–1870.
- Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). Mini-mental state: A practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research*, *12*, 189–198.
- Fox, C. J., Iaria, G., & Barton, J. J. S. (2009). Defining the face processing network: Optimization of the functional localizer in fMRI. *Human Brain Mapping*, *30*, 1637–1651.
- Gao, L., Xu, J., Zhang, B. W., Zhao, L., Harel, A., & Bentin, S. (2009). Aging effects on early-stage face perception: An ERP study. *Psychophysiology*, *46*, 970–983.
- Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, *3*, 191–197.
- Gilaie-Dotan, S., & Malach, R. (2007). Sub-exemplar shape tuning in human face-related areas. *Cerebral Cortex*, *17*, 325–338.
- Gobbini, M. I., & Haxby, J. V. (2007). Neural systems for recognition of familiar faces. *Neuropsychologia*, *45*, 32–41.
- Goh, J. O. S., Suzuki, A., & Park, D. C. (2010). Reduced neural selectivity increases fMRI adaptation with age during face discrimination. *Neuroimage*, *51*, 336–344.
- Gold, J., Bennett, P. J., & Sekuler, A. B. (1999). Identification of band-pass filtered letters and faces by human and ideal observers. *Vision Research*, *39*, 3537–3560.
- Grady, C. L. (2000). Functional brain imaging and age-related changes in cognition. *Biological Psychology*, *54*, 259–281.
- Grady, C. L. (2002). Age-related differences in face processing: A meta-analysis of three functional neuroimaging experiments. *Canadian Journal of Experimental Psychology*, *56*, 208–220.
- Grady, C. L. (2008). Cognitive neuroscience of aging. *Annals of the New York Academy of Sciences*, *1124*, 127–144.
- Grady, C. L., Bernstein, L. J., Beig, S., & Siegenthaler, A. L. (2002). The effects of encoding task on age-related differences in the functional neuroanatomy of face memory. *Psychology and Aging*, *17*, 7–23.
- Grady, C. L., Maisog, J. M., Horwitz, B., Ungerleider, L. G., Mentis, M. J., Salerno, J. A., et al. (1994). Age-related changes in cortical blood flow activation during visual processing of faces and location. *Journal of Neuroscience*, *14*, 1450–1462.
- Grady, C. L., McIntosh, A. R., Horwitz, B., Maisog, J. M., Ungerleider, L. G., Mentis, M. J., et al. (1995). Age-related reductions in human recognition memory due to impaired encoding. *Science*, *269*, 218–221.
- Grady, C. L., McIntosh, A. R., Horwitz, B., & Rapoport, S. I. (2000). Age-related changes in the neural correlates of degraded and nondegraded face processing. *Cognitive Neuropsychology*, *17*, 165–186.
- Grady, C. L., Yu, H., & Alain, C. (2008). Age-related differences in brain activity underlying working memory for spatial and nonspatial auditory information. *Cerebral Cortex*, *18*, 189–199.
- Grill-Spector, K., Henson, R. N., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, *10*, 14–23.
- Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzhak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron*, *24*, 187–203.
- Grill-Spector, K., & Malach, R. (2001). fMR-adaptation: A tool for studying the functional properties of human cortical neurons. *Acta Psychologica*, *107*, 293–321.
- Habak, C., Wilkinson, F., & Wilson, H. R. (2008). Aging disrupts the neural transformations that link facial identity across views. *Vision Research*, *48*, 9–15.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*, 223–233.
- Henson, R. N. A. (2003). Neuroimaging studies of priming. *Progress in Neurobiology*, *70*, 53–81.
- Henson, R. N., & Mouchlianitis, E. (2007). Effect of spatial attention on stimulus-specific haemodynamic repetition effects. *Neuroimage*, *35*, 1317–1329.
- Ishai, A. (2008). Let's face it: It's a cortical network. *Neuroimage*, *40*, 415–419.
- Jiang, X., Rosen, E., Zeffiro, T., VanMeter, J., Blanz, V., & Riesenhuber, M. (2006). Evaluation of a shape-based model of human face discrimination using fMRI and behavioral techniques. *Neuron*, *50*, 159–172.
- Kadosh, K. C., Henson, R. N., Kadosh, R. C., Johnson, M. H., & Dick, F. (2010). Task-dependent activation of face-sensitive cortex: An fMRI adaptation study. *Journal of Cognitive Neuroscience*, *22*, 903–917.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.
- Krekelberg, B., Boynton, G. M., & van Wezel, R. J. A. (2006). Adaptation: From single cells to BOLD signals. *Trends in Neurosciences*, *29*, 250–256.
- Lee, Y., Matsumiya, K., & Wilson, H. R. (2006). Size-invariant but viewpoint-dependent representation of faces. *Vision Research*, *46*, 1901–1910.
- Leventhal, A. G., Wang, Y., Pu, M., Zhou, Y., & Ma, Y. (2003). GABA and its agonists improved visual cortical function in senescent monkeys. *Science*, *300*, 812–815.
- Li, J., Liu, J., Liang, J., Zhang, H., Zhao, J., Rieth, C. A., et al. (2010). Effective connectivities of cortical regions for top-down face processing: A dynamic causal modeling study. *Brain Research*, *1340*, 40–51.
- Liang, Z., Yang, Y., Li, G., Zhang, J., Wang, Y., Zhou, Y., et al. (2010). Aging affects the direction selectivity of MT cells in rhesus monkeys. *Neurobiology of Aging*, *31*, 863–873.
- Loffler, G., Yourganov, G., Wilkinson, F., & Wilson, H. R. (2005). fMRI evidence for the neural representation of faces. *Nature Neuroscience*, *8*, 1386–1390.
- Lott, L. A., Haegerstrom-Portnoy, G., Schneck, M. E., & Brabyn, J. A. (2005). Face recognition in the elderly. *Optometry and Vision Science*, *82*, 874–881.

- Madden, D. J., Whiting, W. L., Provenzale, J. M., & Huettel, S. A. (2004). Age-related changes in neural activity during visual target detection measured by fMRI. *Cerebral Cortex*, *14*, 143–155.
- Maurer, D., O'Craven, K. M., Le Grand, R., Mondloch, C. J., Springer, M. V., Lewis, T. L., et al. (2007). Neural correlates of processing facial identity based on features versus their spacing. *Neuropsychologia*, *45*, 1438–1451.
- McIntosh, A. R., Bookstein, F. L., Haxby, J. V., & Grady, C. L. (1996). Spatial pattern analysis of functional brain images using partial least squares. *Neuroimage*, *3*, 143–157.
- McIntosh, A. R., Chau, W. K., & Protzner, A. B. (2004). Spatiotemporal analysis of event-related fMRI data using partial least squares. *Neuroimage*, *23*, 764–775.
- Meudell, P. R., & Greenhalgh, M. (1987). Age related differences in left and right hand skill and in visuo-spatial performance: Their possible relationships to the hypothesis that the right hemisphere ages more rapidly than the left. *Cortex*, *23*, 431–445.
- Morcom, A. M., Li, J., & Rugg, M. D. (2007). Age effects on the neural correlates of episodic retrieval: Increased cortical recruitment with matched performance. *Cerebral Cortex*, *17*, 2491–2506.
- Näsänen, R. (1999). Spatial frequency bandwidth used in the recognition of facial images. *Vision Research*, *39*, 3824–3833.
- Owsley, C., Sekuler, R., & Boldt, C. (1981). Aging and low-contrast vision: Face perception. *Investigative Ophthalmology & Visual Science*, *21*, 362–365.
- Owsley, C., Sekuler, R., & Siemsen, D. (1983). Contrast sensitivity throughout adulthood. *Vision Research*, *23*, 689–699.
- Packard, M. G., & Knowlton, B. J. (2002). Learning and memory functions of the basal ganglia. *Annual Review of Neuroscience*, *25*, 563–593.
- Park, D. C., Polk, T. A., Park, R., Minear, M., Savage, A., & Smith, M. R. (2004). Aging reduces neural specialization in ventral visual cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *101*, 13091–13095.
- Park, D. C., & Reuter-Lorenz, P. (2009). The adaptive brain: Aging and neurocognitive scaffolding. *Annual Review of Psychology*, *60*, 173–196.
- Pourtois, G., Schwartz, S., Seghier, M. L., Lazeyras, F., & Vuilleumier, P. (2005). Portraits or people? Distinct representations of face identity in the human visual cortex. *Journal of Cognitive Neuroscience*, *17*, 1043–1057.
- Rajah, M. N., & D'Esposito, M. (2005). Region-specific changes in prefrontal function with age: A review of PET and fMRI studies on working and episodic memory. *Brain*, *128*, 1964–1983.
- Reuter-Lorenz, P., & Cappell, K. A. (2008). Neurocognitive aging and the compensation hypothesis. *Current Directions in Psychological Science*, *17*, 177–182.
- Reuter-Lorenz, P. A., & Lustig, C. (2005). Brain aging: Reorganizing discoveries about the aging mind. *Current Opinion in Neurobiology*, *2005*, 245–251.
- Rossion, B., Caldara, R., Seghier, M., Schuller, A. M., Lazeyras, F., & Mayer, E. (2003). A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain*, *126*, 2381–2395.
- Rotshtein, P., Geng, J. J., Driver, J., & Dolan, R. J. (2007). Role of features and second-order spatial relations in face discrimination, face recognition, and individual face skills: Behavioral and functional magnetic resonance imaging data. *Journal of Cognitive Neuroscience*, *19*, 1435–1452.
- Rotshtein, P., Henson, R. N. A., Treves, A., Driver, J., & Dolan, R. J. (2005). Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nature Neuroscience*, *8*, 107–113.
- Rousselet, G. A., Husk, J. S., Pernet, C. R., Gaspar, C. M., Bennett, P. J., & Sekuler, A. B. (2009). Age-related delay in information accrual for faces: Evidence from a parametric, single-trial EEG approach. *BMC Neuroscience*, *10*, doi:10.1186/1471-2202-10-114.
- Sampson, P. D., Streissguth, A. P., Barr, H. M., & Bookstein, F. L. (1989). Neurobehavioral effects of prenatal alcohol: II. Partial least squares analysis. *Neurotoxicology and Teratology*, *11*, 477–491.
- Schiavetto, A., Kohler, S., Grady, C. L., Winocur, G., & Moscovitch, M. (2002). Neural correlates of memory for object identity and object location: Effects of aging. *Neuropsychologia*, *40*, 1428–1442.
- Schiltz, C., & Rossion, B. (2006). Faces are represented holistically in the human occipito-temporal cortex. *Neuroimage*, *32*, 1385–1394.
- Searcy, J. H., Bartlett, J. C., & Menon, A. (1999). Age differences in accuracy and choosing in eyewitness identification and face recognition. *Memory and Cognition*, *27*, 538–552.
- Steeves, J. K. E., Culham, J. C., Duchaine, B. C., Pratesi, C. C., Valyear, K. F., Schindler, I., et al. (2006). The fusiform face area is not sufficient for face recognition: Evidence from a patient with dense prosopagnosia and no occipital face area. *Neuropsychologia*, *44*, 594–609.
- Taylor, K. S., Seminowicz, D. A., & Davis, K. D. (2009). Two systems of resting state connectivity between the insula and cingulate cortex. *Human Brain Mapping*, *30*, 2731–2745.
- Weale, R. (1982). Senile ocular changes, cell death, and vision. In R. Sekuler, D. Kline, & K. Dismukes (Eds.), *Aging and visual function* (pp. 161–171). New York: Liss.
- Wilkinson, F., Wilson, H. R., & Habak, C. (1998). Detection and recognition of radial frequency patterns. *Vision Research*, *38*, 3555–3568.
- Wilson, H. R., Loffler, G., & Wilkinson, F. (2002). Synthetic faces, face cubes, and the geometry of face space. *Vision Research*, *42*, 2909–2923.
- Wilson, H. R., Mei, M., Habak, C., & Wilkinson, F. (2011). Visual bandwidths for face orientation increase during healthy aging. *Vision Research*, *51*, 160–164.
- Yotsumoto, Y., Kahana, M. J., Wilson, H. R., & Sekuler, R. (2007). Recognition memory for realistic synthetic faces. *Memory and Cognition*, *35*, 1233–1244.
- Zarahn, E., Rakitin, B., Abela, D., Flynn, J., & Stern, Y. (2007). Age-related changes in brain activation during a delayed item recognition task. *Neurobiology of Aging*, *28*, 784–798.