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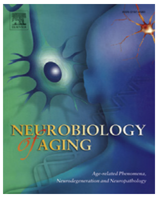

Age-related dedifferentiation and compensatory changes in the functional network underlying face processing

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ABSTRACT

Recent evidence has shown that older adults fail to show adaptation in the right fusiform gyrus (FG) to the same face presented repeatedly, despite accurate detection of the previously presented face. We used functional magnetic resonance imaging to investigate whether this phenomenon is associated with age-related reductions in face specificity in brain activity and whether older adults compensate for these face-processing deficiencies by increasing activity in other areas within the face-processing network, or outside this network. A comparison of brain activity across multiple stimulus categories showed that, unlike young adults who engaged a number of brain regions specific to face processing, older adults generalized these patterns of activity to objects and houses. Also, young adults showed functional connectivity between the right FG and its homologous region during face processing, whereas older adults did not engage the left FG but showed a functional connection between the right FG and left orbitofrontal cortex. Finally, this frontotemporal functional connection was activated more strongly in older adults who performed better on a face-matching task (done outside of the scanner), suggesting increased involvement of this functional link for successful face recognition with increasing age. These findings suggest that 2 neural mechanisms, dedifferentiation and compensatory neural recruitment, underlie age differences in face processing.

1. Introduction

Recent neuroimaging studies have yielded evidence for 2 distinct phenomena in the aging brain: (1) neural representations of different cognitive processes become less selective and their neural signature less distinct (Li et al., 2001); and (2) older adults often have greater brain activity than young adults during cognitive tasks, particularly in the frontal cortex, that might compensate for age-related processing deficiencies (Cabeza et al., 2002; Duverne et al., 2009; Grady, 2012; Reuter-Lorenz et al., 2000). The first finding is consistent with the idea of dedifferentiation, which in terms of brain activity refers to reduced distinctiveness of neural representations in domain-specific areas. For instance, ventral occipital visual areas show reduced category selectivity to faces, places, and words in older relative to younger adults (Park et al., 2004). Dedifferentiation has also been reported in domain-general cognitive areas, including the parietal and prefrontal cortices, during memory encoding and retrieval (Carp et al., 2010a, 2010b), and in areas active specifically for retrieval of autobiographical and episodic memories (St-Laurent et al., 2011). Although such results might indicate reductions in the integrity of the aging brain, other neuroimaging studies have reported an increased engagement of prefrontal and other brain areas, which is interpreted as a compensatory mechanism when associated with maintained performance in older adults (Davis et al., 2008; Grady, 2002; Grady et al., 2002, 1994; Madden et al., 2004; Schiavetto et al., 2002), or when activity in these "over-recruited" areas is correlated with behavior in older adults (Davis et al., 2008; Grady et al., 2005). Indeed, some have suggested that the strongest evidence for compensation is this latter finding, in which a link can be made between more brain activity and better performance in older adults who show the most overrecruitment (Cabeza and Dennis, 2012; Grady, 2008). Albeit 2 distinct phenomena, the dedifferentiation and compensation processes are unlikely to be mutually exclusive. Rather, it is possible that the brain might show reduced neural selectivity in some domain-specific regions and, at the same time or as a consequence, use other task-specific regions, or even a different

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network of areas, to compensate for this deficiency in neural distinctiveness, evincing remarkable brain plasticity or reserve in old age. The purpose of the current study was to investigate this question by exploring age-related neural changes during face processing, using functional magnetic resonance imaging (fMRI).

Many behavioral studies have reported that older adults show reduced recognition and perception of familiar and unfamiliar faces relative to younger adults (Bartlett et al., 1991; Boutet and Faubert, 2006; Habak et al., 2008; Lott et al., 2005; Searcy et al., 1999). On the neural level, age-related deficits in face processing are likely to be observed in multiple areas (Carp et al., 2010a; Goh et al., 2010; Lee et al., 2011), because face processing is distributed widely over many functionally interacting areas that show serial and parallel processing (Barbeau et al., 2008; Gobbini and Haxby, 2007; Haxby et al., 2000). Importantly, deficiencies at early stages of face processing might cascade downstream and yield changes in the entire functional brain network (Davis et al., 2008; Grady, 2000, 2008). Thus, we aimed to examine (1) whole-brain activations during processing of faces and objects, to assess neural selectivity to different categories of objects; and (2) functional connectivity of the distributed face processing network, using multivariate partial least squares (PLS) analysis.

In our recent study (Lee et al., 2011), older adults showed no adaptation in the right fusiform gyrus (FG), 1 of the regions considered to be crucial for face recognition (Clarke et al., 1997; Kanwisher et al., 1997; Nestor et al., 2011; Steeves et al., 2006), to repeatedly presented faces, even when facial identity and view were kept constant. Contrary to these deficiencies in neural adaptation, on a behavioral level older adults 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 and Searcy et al., 1999). Additionally, we found that older adults recruited a unique set of brain regions in which activity correlated with their behavioral performance. It has been suggested that older adults compensate for processing deficits because of decreased activity in the occipital lobe by increasing frontal activity (Davis et al., 2008; Grady et al., 2002). If compensation occurs, 1 possible frontal area of compensatory recruitment might be the orbitofrontal cortex (OFC), in which activity has been often observed during processing of faces and nonfacial objects (Bar, 2009; Bar et al., 2006; Fairhall and Ishai, 2007; Ishai, 2007, 2008; Johnson, 2005; Kveraga et al., 2007; Li et al., 2010). The OFC is argued to be a part of the extended cortical network for face processing (Fairhall and Ishai, 2007; Haxby et al., 2000) and is involved in a variety of face tasks, including assessment of facial attractiveness (Ishai, 2007), facial sex categorization (Freeman et al., 2010), facial emotion recognition (Harmer et al., 2001), and detection of blurred faces (Li et al., 2010; Summerfield et al., 2006). More activity or stronger functional connectivity in the OFC in older adults would be consistent with the compensation-related utilization of neural circuits hypothesis (Reuter-Lorenz and Cappell, 2008). The compensation-related utilization of neural circuits hypothesis is based on the idea that as task demands increase, reliance on neural resources increases regardless of age, but that this demand/resource function is shifted to the left in older adults. That is, older adults recruit more resources at lower levels of cognitive load. For basic face recognition, this increased reliance on neural resources could involve task-specific regions, such as the OFC, which younger adults might only recruit when the cognitive demands are greater or more complex processing of faces is required. Additional domain-general resources might also be recruited by older adults. Both of these types of recruitment could be compensatory, especially if this additional engagement of brain activity was associated with improved performance in older adults (Grady, 2012).

To measure functional connectivity between the frontal cortex and the fusiform areas, we identified seed regions in the fusiform gyri and in the left medial OFC. Activity in this latter area has been found during viewing of famous and emotional faces in young adults (Fairhall and Ishai, 2007; Ishai et al., 2005). We expected that age-related deficiencies at early processing stages (i.e., in the FG) would cascade downstream and alter the face-processing network (Davis et al., 2008; Grady, 2002, 2008). We hypothesized that: (1) older adults would exhibit a general decrease in neural specificity across activated face-processing areas; (2) young and older adults would show differences in the functional connectivity of the face-processing network, with older adults showing stronger connectivity with OFC; and (3) activity in the face-processing network specific to older adults would correlate with their behavioral performance (i.e., reaction times [RTs] and accuracy), reflecting the importance of the OFC in face-matching performance with increasing age.

2. Methods

2.1. Participants

Fifteen healthy older adults (mean age, 68 years; SD, 4.2; range, 61–75 years; 6 men) and 14 healthy young adults (mean age, 24 years; SD, 4.9; range, 8–32 years; 7 men) participated in the study. Older adults were screened via a detailed phone interview for general health (e.g., cardiovascular disease or stroke), medications, and normal vision (e.g., cataract or glaucoma, eye exam within a year). They achieved an average score of 29.3 (SD, 1.1) on the Mini-Mental State Examination (Folstein et al., 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 and no history of eye disease or neurological or psychiatric problems. All participants provided written informed consent approved by the Baycrest Centre Research Ethics Board.

2.2. Study design

The study consisted of: (1) an imaging experiment; and (2) a postscan behavioral test. The imaging experiment was block-designed and consisted of 2 runs of the face/object same/different task. The postscan test was conducted outside the scanner on a different day (on average, within a month) and involved sequential matching of unfamiliar faces across identity and/or viewpoints (Lee et al., 2011).

2.3. Experimental procedure

Stimuli for the same/different task consisted of gray-scaled photographs of natural faces (frontal, 20° side views), houses (frontal, 20° side views), and common household objects. For the postscan face-matching task, we used novel, natural faces that were not presented during the fMRI experiment. In each trial, a fixation cross was displayed for 250 ms, followed by a first stimulus displayed for 750 ms, a fixation cross for 250 ms, a second stimulus for 2000 ms, and a blank screen for 750 ms. Participants were asked to indicate whether the 2 stimuli were identical during the same/different task.

2.4. fMRI data acquisition

Anatomical and functional images were acquired at the Rotman Research Institute, Baycrest Centre, Toronto, Ontario, using a 3 Tesla Siemens Magnetom Trio scanner with a matrix 12-channel head