

Processing own-age vs. other-age faces: Neuro-behavioral correlates and effects of emotion

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ABSTRACT

Age constitutes a salient feature of a face and signals group membership. There is evidence of greater attention to and better memory for own-age than other-age faces. However, little is known about the neural and behavioral mechanisms underlying processing differences for own-age vs. other-age faces. Even less is known about the impact of emotion expressed in faces on such own-age effects. Using fMRI, the present study examined brain activity while young and older adult participants identified expressions of neutral, happy, and angry young and older faces. Across facial expressions, medial prefrontal cortex, insula, and (for older participants) amygdala showed greater activity to own-age than other-age faces. These own-age effects in ventral medial prefrontal cortex and insula held for neutral and happy faces, but not for angry faces. This novel and intriguing finding suggests that processing of negative facial emotions under some conditions overrides age-of-face effects.

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1. Processing own-age vs. other-age faces: Neuro-behavioral correlates and effects of emotion

People have an extraordinary interest in human faces, likely due to the high emotional and social relevance of faces in everyday lives. Facial features such as age, race, and sex are important cues about biological and/or social group membership that have an impact on cognition and behavior. For example, there is growing evidence that faces of one's own age group receive greater attention (Ebner et al., 2011a; Ebner and Johnson, 2010; He et al., 2011) and are better remembered (see Rhodes and Anastasi (2012) for a review) than faces of another age group. There are similar effects for faces of one's own race (Malpass and Kravitz, 1969; see Meissner and Brigham (2001) for a review) and sex (Lewin and Herlitz, 2002; Wright and Sladden, 2003).

Investigators have suggested various factors that may underlie differences in processing in-group vs. out-group faces, such as greater familiarity of, more elaborated schemas for, greater personal interest

in, and/or social motivation for own-group than other-group individuals (Anastasi and Rhodes, 2005; Ebner and Johnson, 2009; Harrison and Hole, 2009; He et al., 2011; Slone et al., 2000; see Hugenberg et al. (2010); Rhodes and Anastasi (2012) for reviews). A systematic examination of such factors is warranted in order to increase our understanding of processing differences between members of the in-group vs. the out-group.

One step in this direction comes from recent neuroimaging studies that compare neural processing of in-group vs. out-group faces. Most of these studies have focused on group membership based on race or experimental assignment to “minimal” groups. Yet, comparatively little is known about the neural processing of *age-based* in-group vs. out-group. To this date, only two functional magnetic resonance imaging (fMRI) studies have addressed processing differences between own-age and other-age faces (Ebner et al., 2011a; Wright et al., 2008).

Some factors, such as increased familiarity, greater preference and/or affective salience, or more available prototypes for the in-group than the out-group may operate in similar ways for group memberships based on age, race, or sex (see Ebner et al., 2011b, for a discussion). At the same time, there are some fundamental differences between different types of group memberships, which likely result in processing differences. For example, for age-based groups, individuals naturally transition out of one group (i.e., young adults) and into the other group (i.e., older adults) over the course of their

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lifetime. Also, having been young once, older adults have personal experience and autobiographical memory of membership in the now (young adult) out-group. These substantial differences argue for the importance and novelty of examining processes involved in age-based group membership in particular, the first goal of the present study. Below, we review findings from neuroimaging studies that have investigated in-group vs. out-group effects.

1.1. Brain regions involved in processing of in-group vs. out-group faces

Amygdala, fusiform gyrus, prefrontal cortex, and insula show differences in activity levels when processing in-group vs. out-group faces. However, evidence is mixed regarding the specific functions of these brain regions, suggesting at least partly different mechanisms at work when processing in-group vs. out-group faces based on age, race, or minimal group.

1.1.1. Amygdala

Amygdala activation has been associated with positive evaluation of faces and greater attention to and importance of in-group compared to out-group members (Van Bavel et al., 2008; see also Cunningham et al., 2005). Some studies using race or minimal group based definitions show greater amygdala activity for in-group than out-group faces (Van Bavel et al., 2008; Wheeler and Fiske, 2005). Wright et al. (2008), as the only study to date that has examined amygdala involvement in processing age-based in-group vs. out-group faces, further supports this interpretation by showing greater activity in right amygdala (MNI: $x = 27, y = -6, z = -15$) to own-age than other-age faces in a passive viewing paradigm.

However, several studies that define group membership based on race found greater amygdala activity to out-group than in-group faces (Phelps et al., 2000; Wheeler and Fiske, 2005), with these effects at least partly attributed to less exposure to racial out-group faces (Hart et al., 2000; Lieberman et al., 2005). It has been suggested that these effects may also be driven by stereotypes and affective evaluations (Cunningham et al., 2004; Phelps et al., 2000), particularly negative ones toward the out-group (Lieberman et al., 2005).

1.1.2. Fusiform gyrus

Fusiform gyrus is an area selectively activated by faces compared to other stimuli (Kanwisher et al., 1997; Puce et al., 1995) and plays a crucial role in face individuation (Rhodes et al., 2004), which may be particularly elaborated for members of the in-group compared to the out-group (Hugenberg et al., 2010). In support of this interpretation, studies using faces from different races or minimal groups have found greater fusiform gyrus activity to in-group than out-group faces (Golby et al., 2001; Kim et al., 2006; Van Bavel et al., 2008).

1.1.3. Prefrontal cortex

Medial prefrontal cortex is involved in self-referential processing (see Amodio and Frith, 2006; Murray et al., 2012; Van Overwalle, 2009, for reviews). Self-referential processing is likely more prevalent for own-age than other-age faces, due to increased similarity and identification with the own-age group. In line with this interpretation, Ebner et al. (2011a) found greater activity in a region of ventral medial prefrontal cortex (MNI: $x = -6, y = 30, z = -6$) when participants evaluated personality traits in own-age than other-age individuals. In addition, greater perceived similarity to the own-age vs. the other-age person was related to greater BOLD response to the own-age vs. other-age person in this region of medial prefrontal cortex, suggesting that perceived similarity contributes to processing differences for faces of different ages.

Another prefrontal cortex area, orbitofrontal cortex, is involved in representing subjective affective value (Kringelbach, 2005; Van Bavel et al., 2008). Greater orbitofrontal cortex activity to own-age than other-age faces could thus reflect greater liking of the own-age group.

In support of this interpretation, Van Bavel et al. (2008) found greater activity in a lateral region of orbitofrontal cortex to experimentally assigned in-group compared to out-group faces, with this activity positively related to liking of in-group members.

1.1.4. Insula

Insula activity is associated with processing emotional and social information (Craig, 2009), and thus may play a crucial role in in-group vs. other-group face processing. In line with this suggestion, Lieberman et al. (2005) found greater insula activation for other-race than own-race faces.

Taken together, the existing literature converges on a set of brain regions involved in differentiating in-groups from out-groups. However, the specific function of each of these regions in processing own-age relative to other-age faces (as compared to own-race vs. other-race faces or group membership based on experimental assignment) and the underlying mechanisms are largely unknown. Thus, the first aim of the present study was to investigate neural processing differences between young and older faces in these selected regions of interest (ROIs) in samples of young and older adults.

1.2. Influence of facial expression on processing own-age vs. other-age faces

Our second aim was to investigate whether own-age effects varied as a function of emotional facial expressions. Previous studies of neural processing differences for own-age vs. other-age faces (Ebner et al., 2011a; Wright et al., 2008) used only neutral faces, and thus did not vary the emotional expression of the presented faces. However, both young and older adults find it easier to read positive than negative expressions (Ruffman et al., 2008; Svård et al., 2012). Also, positive vs. negative facial expressions seem to be, at least to some extent, processed in different brain regions (Keightley et al., 2007; see also Ruffman et al., 2008), with some indication that this may be related to processing difficulty between these two types of facial expressions (Ebner et al., 2012). Thus, variations of age-of-face effects as a function of positive vs. negative emotional expression could arise from such differences in processing difficulty for both young and older adults. If the cognitive processes required for expression identification in angry compared to happy, and possibly also neutral, faces are more effortful, less attention may be directed at processing age information in angry than happy and neutral faces. This would then result in less pronounced own-age effects in angry than happy and neutral faces, in young and older adults alike.

1.3. The present study

In sum, the present study conducted the following analyses in the interest of two primary goals: (1) *Age of Face by Participant Age across Facial Expression*: This analysis identified processing differences between young and older faces in selected brain areas (medial prefrontal cortex, orbitofrontal cortex, insula, fusiform gyrus, amygdala). We expected activity in these ROIs to be greater for own-age than other-age faces for both young and older adults (*Hypothesis 1*). (2) *Age of Face by Participant Age as a Function of Facial Expression*: We expected variations of age-of-face effects as a function of facial expression. In particular, we expected that in brain regions sensitive to differentiating between own-age and other-age faces, the own-age effect would be more pronounced for happy and neutral than angry faces in both young and older adults (*Hypothesis 2*). This prediction was based on the assumption that angry faces are more difficult to identify and thus less attention may be available for processing age-of-face information in angry faces.

2. Method

2.1. Participants

Participants were healthy young adults ($n = 30$ [16 females], $M = 25.1$ years [$SD = 3.4$; range = 20–31]) and healthy, active, independently living older adults ($n = 32$ [18 females], $M = 68.2$ years [$SD = 2.5$; range = 65–74]). All participants were in good health, with no known history of stroke, heart disease, or primary degenerative neurological disorder, had normal or corrected-to-normal vision, and none were known to take psychotropic medications. Grey and white matter lesions and/or abnormal extents of atrophy in older participants were ruled out by screening of both a T1-weighted and T2-weighted structural image through a radiologist. For a detailed description of the sample in terms of education and cognitive and affective measures see Ebner et al. (2012).

2.2. Stimuli

Face images were taken from the FACES database (Ebner et al., 2010). Forty-eight pictures of young (18–31 years) and 48 pictures of older (69–80 years) faces (all different face identities) were presented, with equal numbers of neutral, happy, or angry expressions displayed in young and older faces (i.e., 16 per Age of Face by Facial Expression). Stimulus presentation and response collection (accuracy and response time) were controlled using E-Prime (Schneider et al., 2002).

2.3. Procedure, measures, and design

The data reported here were from a larger project. Detailed study procedures are described in Ebner et al. (2012). The ethics committee at the Karolinska Institute approved the protocol, and informed consent was obtained from all participants.

During the fMRI session, participants worked on a *Facial Expression Identification Task* (Fig. 1). This task had a mixed 2 Participant Age (Young, Older) \times 2 Age of Face (Young, Older) \times 3 Facial Expression (Neutral, Happy, Angry) factorial design, with Participant Age as a between-subjects factor and Age of Face and Facial Expression as within-subjects factors. As shown in Fig. 1, participants saw faces, one at a time. Each face was presented for 3500 ms. Participants were asked to indicate whether the displayed face showed a happy, neutral, or angry expression by pressing one of three response buttons on a button box (index finger for “happy”, middle finger for “neutral”, and ring finger for “angry”). Response options appeared in black on a grey background below the faces and were always presented in the same order.

In between faces, a black fixation cross appeared on a grey background on the screen. The interstimulus interval (ISI) pseudo-randomly varied between 3000 and 4000 ms in 250-ms increments (mean ISI = 3500 ms). In one-third of the trials (48 out of 144 total trials), “low-level baseline events” consisting of three black Xs on a grey background were presented. Participants pressed one of the three buttons that they also used for indicating the facial expressions to indicate appearance of a low-level baseline trial. Low-level baseline trials were not further considered in the present analyses.

The presentation order of face identities was identical for each participant, with facial expressions counterbalanced across participants (each participant only saw each face with one expression). Lists were pseudo-randomized with the constraints that no more than three faces and no more than two null events were presented in a row, and no more than two faces of the same category (i.e., age, sex, facial expression) were repeated in a row. The task started with four practice trials. It was split into two runs, each lasting for 8.4 min.

At the end of the session, participants were debriefed and financially compensated for participation.

2.4. Imaging details

Images were acquired using a 3T Siemens Magnetom Tim Trio scanner at Huddinge Hospital, Stockholm, Sweden. After localizer scans, two runs of 160 functional images each were acquired with a T2*-weighted echo-planar sequence (ep2d_bold; TR = 2500 ms, TE = 40 ms, flip angle = 90°, FOV = 230 mm, voxel size = 3 \times 3 \times 3 mm). Thirty-nine oblique axial slices were positioned parallel to the AC–PC line, and acquired interleaved. A 1 \times 1 \times 1 mm T1-weighted image was used for co-registration with functional images (MP-RAGE; TR = 1900 ms, TE = 2.52 ms, FoV = 256 mm).

2.5. fMRI analyses

Data from this event-related fMRI study were analyzed using Statistical Parametric Mapping (SPM5; Wellcome Department of Imaging Neuroscience). Pre-processing included slice timing correction, motion correction, co-registration of functional images to the participant’s anatomical scan, spatial normalization, and smoothing (9-mm full-width half maximum [FWHM] Gaussian kernel). Spatial normalization used a study-specific template brain composed of the average of the young and older participants’ T1 structural images (detailed procedure for creating the template is available from the authors). After normalization to standard space, functional images had dimensions of 53 \times 63 \times 46 with 3 mm isotropic voxels.

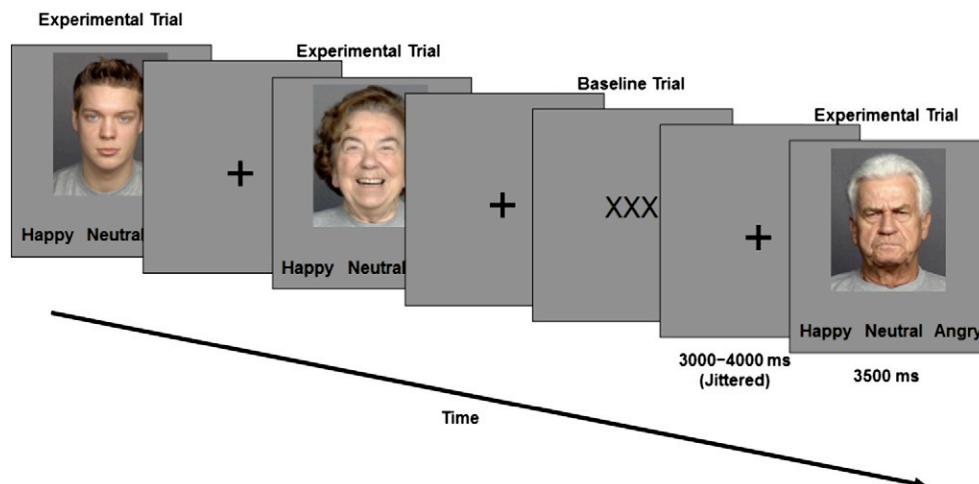


Fig. 1. Facial expression identification task. Trial event timing and sample faces used in the task.

Standard general linear model (GLM) analyses were conducted on ROIs defined by the WFU PickAtlas v2.4 (Maldjian et al., 2003, 2004; http://www.nitrc.org/projects/wfu_pickatlas/; based on the Talairach Daemon). First-level, single-subject statistics were modeled by convolving each trial with the SPM canonical hemodynamic response function to create a regressor for each condition (Young Neutral, Young Happy, Young Angry, Older Neutral, Older Happy, Older Angry). Parameter estimates (beta images) of activity for each condition and each participant were then entered into a second-level random-effects analysis using a mixed 2 Participant Age (Young, Older) \times 2 Age of Face (Young, Older) \times 3 Facial Expression (Neutral, Happy, Angry) analysis of variance (ANOVA), with Participant Age as a between-subjects factor and Age of Face and Facial Expression as within-subjects factors. From within this model, an F -contrast was specified to examine the effects of Age of Face (Young, Older) \times Participant Age (Young, Older), collapsed across all facial expressions. We refer to this F -contrast as *Age of Face \times Participant Age* throughout the text.

For this F -contrast, two sets of ROI analyses were conducted: (1) We applied a mask to all cortical ROIs, comprising bilateral medial frontal gyrus, anterior cingulate gyrus, Brodmann areas 12 and 47 (orbitofrontal cortex; Chiavaras et al., 2001), insula, and fusiform gyrus as specified in the WFU PickAtlas. For this set of analyses we used a statistical threshold of $p < .005$ (uncorrected) and a cluster size of 22 contiguous voxels, which was determined by the AlphaSim tool from AFNI (Analysis for Functional NeuroImaging; Cox, 1996) to yield a cluster-level corrected threshold of $p < .05$ for the search region in our ROI mask. (2) We conducted a separate analysis on amygdala, as a subcortical, small, and well-circumscribed ROI, using the small volume correction implemented in SPM5. For this analysis we used a bilateral amygdala mask as specified in the WFU PickAtlas.

Within each region of activation identified by the F -contrast, beta values were extracted (in a 6-mm sphere around the peak voxel) to produce a single value for each condition of interest, for each participant. These values are depicted in the bar graphs of Fig. 2. In the fashion of F - and t -tests in ANOVA, subsequent planned statistical comparisons of these values ($p < .05$) were conducted using IBM SPSS Statistics Version 20 to aid interpretation of the activations.

Montreal Neurological Institute (MNI) coordinates are reported. Anatomical localization was verified using the *Talairach Daemon* (Lancaster et al., 1997, 2000) on coordinates transformed using *icbm2tal* (<http://www.brainmap.org/icbm2tal/>), and labels were confirmed visually using the *Talairach and Tournoux* (1988) atlas.

3. Results

3.1. Behavioral data: Facial expression identification: Accuracy and response time

Due to technical problems with the response pad, behavioral data were lost for one older woman and one older man. For the remaining $n = 30$ young and $n = 30$ older participants, accuracy and response time (for accurate responses) data from the expression identification task, collapsed across facial expressions, were submitted to mixed 2 Participant Age (Young, Older) \times 2 Age of Face (Young, Older) repeated-measures ANOVAs (see Table 1). For accuracy, the only significant effect was the main effect for Age of Face ($F(1,58) = 23.10$, $p < .001$, $\eta_p^2 = .29$). Follow-up paired-sample t -tests showed that both young ($t(29) = 4.31$, $p < .001$) and older ($t(29) = -2.90$, $p = .007$) participants were more accurate in identifying expressions in young than older faces. There were comparable results for response time: The main effect for Age of Face ($F(1,58) = 103.66$, $p < .001$, $\eta_p^2 = .64$) and the main effect for Participant Age ($F(1,58) = 5.12$, $p = .027$, $\eta_p^2 = .08$) were significant, but there was no significant Participant Age \times Age of Face interaction. As shown in Table 1, young participants responded faster than older participants and follow-up paired

sample t -tests showed that both young ($t(29) = -7.20$, $p < .001$) and older ($t(29) = 7.20$, $p < .001$) participants were faster in identifying expressions in young than older faces (these accuracy and response time data were reported previously, see Ebner et al., 2012).

3.2. fMRI data

3.2.1. Hypothesis 1: Age of Face by Participant Age across Facial Expression

We expected greater activity to own-age than other-age faces for both young and older adults in medial prefrontal cortex, orbitofrontal cortex, insula, fusiform gyrus, and amygdala across facial expressions (*Hypothesis 1*). Such a result would be supported by a significant Age of Face \times Participant Age interaction.

There was significant activity for *Age of Face \times Participant Age* (F -contrast, across Facial Expression) in clusters of right ventral and dorsal regions of medial prefrontal cortex (see Table 2). In particular, Fig. 2A shows that brain activity in an area of right ventral medial prefrontal cortex, right anterior cingulate, right superior frontal gyrus (BA 9, 32, 10; MNI: $x = 21$, $y = 45$, $z = 9$) was greater for own-age than other-age faces. To explore the significant interaction further, we extracted beta values at the peak voxel of activation of this region ($F(1,60) = 13.47$, $p = .001$, $\eta_p^2 = .18$; see Fig. 2B). Separate paired-sample t -tests in young and older participants on the extracted beta values showed that ventral medial prefrontal cortex activity for young ($p = .001$) and older ($p = .05$) participants was also significantly greater to own-age than other-age faces when considering each group individually, with this own-age effect more pronounced in young than older participants.

A region of superior frontal gyrus, medial prefrontal cortex (BA 8; MNI: $x = 9$, $y = 39$, $z = 42$) showed similar results ($F(1,60) = 9.25$, $p = .003$, $\eta_p^2 = .13$). Follow-up t -tests suggested that the main effect of greater dorsal medial prefrontal cortex activity to own-age than other-age faces in this region was driven by older ($p = .001$) but not young ($p = .626$) participants (see Ebner et al., 2012).

Also in line with our expectations, brain activity in left insula, left claustrum (MNI: $x = -36$, $y = 6$, $z = -3$) was greater for own-age than other-age faces (see Fig. 2C). To explore the significant interaction further, we extracted beta values at the peak voxel of activation of this region ($F(1,60) = 16.20$, $p < .001$, $\eta_p^2 = .21$; see Fig. 2D). Paired-sample t -tests on the extracted beta values showed that insula activity for both young ($p = .003$) and older ($p = .024$) participants was greater to own-age than other-age faces.

Contrary to expectations, there was no significant difference in BOLD response to own-age than other-age faces in any area of orbitofrontal cortex or fusiform gyrus at our cluster-level corrected threshold. Post-hoc, we conducted an exploratory whole-brain analysis using a threshold of $p < .001$, uncorrected, with no minimum cluster threshold, on the F -contrast *Age of Face \times Participant Age* (across Facial Expression). As shown in Table 3 (Supplementary material 1), among those regions identified by this contrast were small clusters of orbitofrontal cortex and fusiform gyrus. Thus, although these areas do not meet strict criteria for significance under a multiple-comparisons-corrected threshold, they may still warrant further investigation in future studies with greater statistical power.

Using small volume correction, we observed significant clusters in bilateral amygdala (see Table 2). Fig. 2E depicts brain activity in left amygdala, left parahippocampus (BA 28; MNI: $x = -21$, $y = -9$, $z = -15$) for the F -contrast *Age of Face \times Participant Age* (across Facial Expression). To explore the significant interaction further, we extracted beta values at the peak voxel of activation of this region ($F(1,60) = 5.23$, $p = .026$, $\eta_p^2 = .08$; see Fig. 2F). Paired-sample t -tests on the extracted beta values showed that amygdala activity for older ($p = .047$), but not young ($p = .290$), participants was significantly greater to own-age than other-age faces.

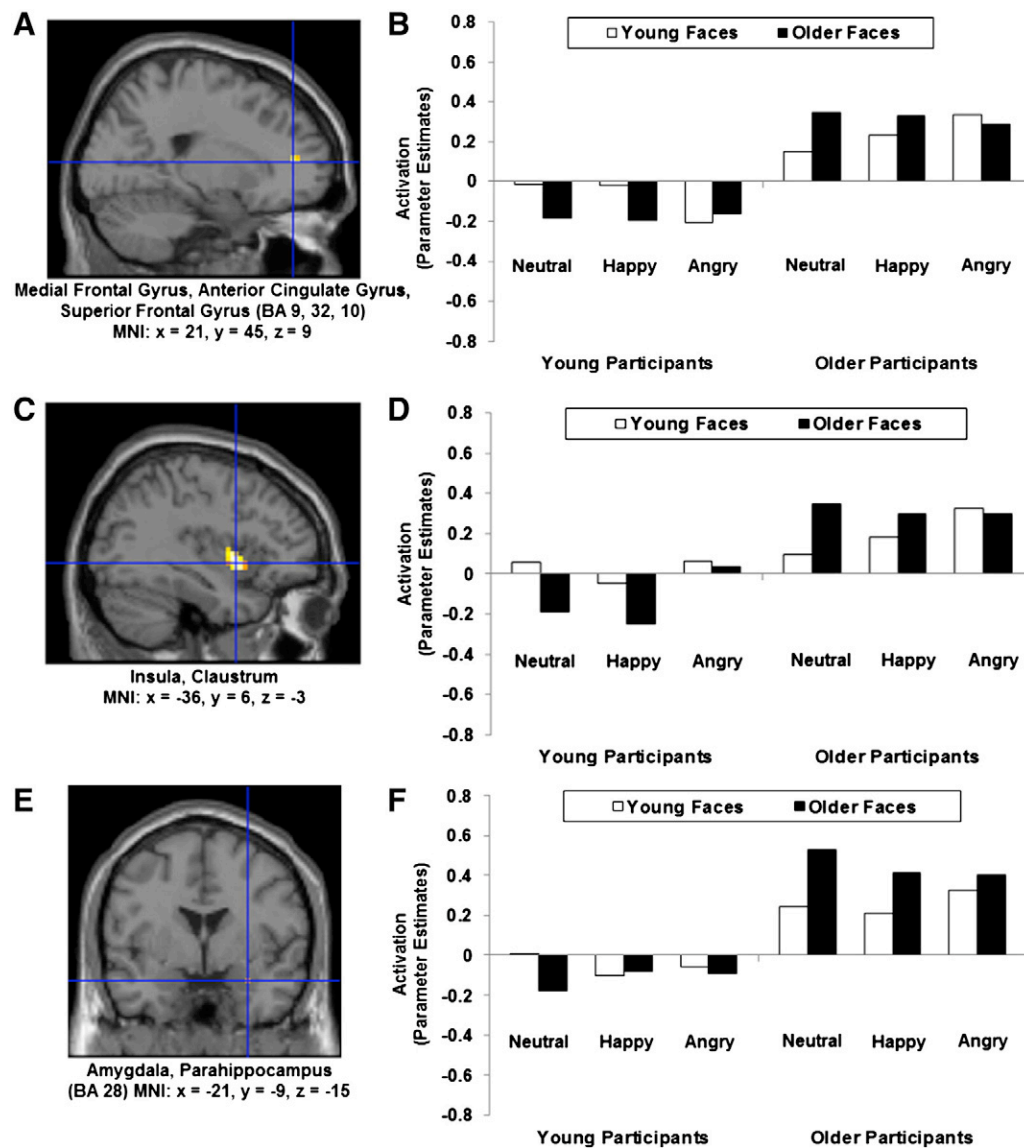


Fig. 2. Age of Face \times Participant Age: (A) MNI: x = 21, y = 45, z = 9: right medial prefrontal cortex, right anterior cingulate, right superior frontal gyrus (BA 9, 32, 10); (C) MNI: x = -36, y = 6, z = -3: left insula, left claustrum, left putamen; and (E) MNI: x = -21, y = -9, z = -15: left amygdala, left parahippocampus (BA 28); all showing own-age faces > other-age faces. The region of activation represents the F -map of the contrast; it is displayed on the standard reference brain in SPM. The crosshair indicates the peak voxel (local maximum) within the region of activation. Bar graphs show the mean (B) right medial prefrontal cortex and (D) left insula, both showing own-age faces > other-age faces for young and older participants for neutral and happy but not angry faces; and (F) left amygdala, showing own-age faces > other-age faces for older but not young participants. Parameter estimates (beta values) separately for Age of Face, Participant Age, and Facial Expression; betas for this region of activation identified by the F -contrast Age of Face \times Participant Age extracted for each individual from a 6-mm sphere around the local maximum within the region of activation and averaged to produce a single value for each condition of interest respectively.

3.2.2. Hypothesis 2: Age of Face by Participant Age as a function of Facial Expression

In line with our hypotheses, we expected the own-age vs. other-age effect that was identified under *Hypothesis 1* to be magnified for happy and neutral compared with angry faces (*Hypothesis 2*). First, the Participant Age (Young, Older) \times Age of Face (Young, Older) \times Facial Expression (Neutral, Happy, Angry) interaction was examined in F -tests on extracted beta values at the peak voxel of activation for all four areas separately. The 3-way interaction was significant for ventral medial prefrontal cortex (MNI: x = 21, y = 45, z = 9; $F(2,59) = 4.08$, $p = .022$, $\eta_p^2 = .12$) and insula (MNI: x = -36, y = 6, z = -3; $F(2,59) = 3.60$, $p = .034$, $\eta_p^2 = .11$) but not dorsal medial prefrontal cortex (MNI: x = 9, y = 39, z = 42; $F(2,59) = 2.28$, $p = .111$, $\eta_p^2 = .07$) or amygdala (MNI: x = -21, y = -9, z = -15; $F(2,59) = .96$, $p = .388$, $\eta_p^2 = .03$).

Follow-up Age of Face \times Participant Age F -tests separately for each of the three facial expressions showed that in ventral medial prefrontal

cortex, the Age of Face \times Participant Age interaction was significant for neutral ($F(1,60) = 10.66$, $p = .002$, $\eta_p^2 = .15$) and happy ($F(1,60) = 9.05$, $p = .004$, $\eta_p^2 = .13$) but not angry ($F(1,60) = 1.18$, $p = .281$, $\eta_p^2 = .02$; see Fig. 2B) faces. Similarly, in insula, the Age of Face \times Participant Age interaction was significant for neutral ($F(1,60) = 11.05$, $p = .002$, $\eta_p^2 = .16$) and happy ($F(1,60) = 7.85$, $p = .007$, $\eta_p^2 = .12$) but not angry ($F(1,60) = .00$, $p = .998$, $\eta_p^2 = .00$; see Fig. 2D) faces.

4. Discussion

The present study examined neural and behavioral correlates of differences in processing of young and older neutral, happy, and angry faces during facial expression identification in a relatively large sample of young ($n = 30$) and older ($n = 32$) adults. As discussed below, there were two primary and novel contributions of this study: Evidence of (1) own-age effects in medial prefrontal cortex and insula in both young

Table 1

Means (M) and standard deviations (SD) for accuracy (%) and response time (ms) in facial expression identification for young and older participants.

	Accuracy M (SD)		Response time M (SD)	
	Young participants	Older participants	Young participants	Older participants
Across facial expressions				
Young faces	94.2 (9.6)	96.4 (5.9)	1236 (194)	1360 (215)
Older faces	91.1 (9.8)	93.3 (5.1)	1359 (248)	1485 (211)
Neutral expressions				
Young faces	92.1 (11.9)	96.0 (6.0)	1292 (241)	1318 (228)
Older faces	90.2 (10.7)	91.3 (9.9)	1469 (295)	1567 (267)
Happy expressions				
Young faces	95.8 (9.5)	98.5 (3.6)	1077 (145)	1234 (241)
Older faces	94.6 (10.6)	96.7 (5.9)	1159 (216)	1250 (212)
Angry expressions				
Young faces	94.8 (9.6)	94.6 (10.2)	1340 (251)	1527 (288)
Older faces	88.5 (12.9)	91.9 (9.9)	1451 (295)	1638 (293)

and older adults, and amygdala in older adults; (2) variations of the own-age effect as a function of the facial expression in ventral medial prefrontal cortex and insula.

4.1. Greater activity in medial prefrontal cortex, insula, and amygdala to own-age than other-age faces

We provide evidence for a role of medial prefrontal cortex, insula, and amygdala in processing own-age vs. other-age faces: Activity was greater for own-age than other-age faces in medial prefrontal cortex and insula for both young and older participants, and there was greater amygdala activity for own-age than other-age faces for older (but not young) participants.

In line with evidence from Ebner et al. (2011a), our finding of greater activity in medial prefrontal cortex for own-age than other-age faces may reflect greater similarity and identification with and/or greater preference and personal interest in own-age than other-age individuals. This interpretation is further supported by evidence that medial prefrontal cortex is associated with self-referential processing (Gutchess et al., 2007; Mitchell et al., 2009; see Murray et al., 2012; Van Overwalle, 2009, for reviews), impression formation (Schiller et al., 2009), third-person perspective taking (Ames et al., 2008; D'Argembeau et al., 2007; Ruby and Decety, 2004), and evaluative processing (Bush et al., 2000; Cunningham et al., 2004; see also Amodio and Frith, 2006).

Similarly, insula has been shown to play a role in self-awareness (Allman et al., 2011; Modinos et al., 2009), and, in particular, left insula has been shown to be involved in positive and affiliative feelings (Craig,

2009), which may be the kind of feelings one typically experiences more for the own-age than the other-age group. It should be noted that, in contrast to the present study, Wright et al. (2008) did not find significant differences in insula activity to own-age compared to other-age faces in their exploratory whole-brain analysis. Also, Lieberman et al. (2005) observed a reversed effect, with greater insula activity for the other-race than the own-race group. A recent finding by Castle et al. (2012) furthermore showed greater insula activity to untrustworthy-looking compared to trustworthy-looking faces. These findings seem to suggest that increased insula activation may be associated with heightened negative visceral feelings, perhaps in the service of an “early warning system” (cf. Castle et al., 2012). However, in both Lieberman et al. (MNI: $y = 14$ and 21 , respectively for left and right insula) and Castle et al. (MNI: $y > 15$), anterior insula was activated, whereas in the present study more posterior insula was involved (MNI: $y = 6$). This pattern of findings across studies may suggest an interesting functional dissociation in insula (cf. Chang et al., 2013). In particular, anterior insula may be associated with heightened negative feelings and gut reactions (Castle et al.; Lieberman et al.). In contrast, posterior insula may be recruited during increased self-referential processing such as involved when processing own-age compared to other-age faces, when taking a first-person relative to a third-person perspective (David et al., 2006; Ruby and Decety, 2001), or during self-experienced pain relative to perceived pain in others (Singer et al., 2004; see also Lamm et al., 2007).

The greater amygdala activity we saw for own-age than other-age faces was driven by older participants and was not significant in young participants (see also Wright et al., 2008). It is possible that age represents a more salient and relevant feature for older than young adults. This may be due to age-associated declines in various domains of functioning (e.g., cognition, health); thus, older compared to young adults might be reminded of their age more frequently throughout their daily routines. This in-group effect in amygdala is consistent with several studies of face processing based on race and minimal groups (Van Bavel et al., 2008). It may suggest an association of amygdala with more affective evaluation, and increased importance, of members of the own than the other age group. At the same time, our finding contrasts with results of some studies that used race as the definition for group membership and found greater amygdala activity for other-race than own-race faces (Hart et al., 2000; Phelps et al., 2000). Thus, it could well be that amygdala response to the in-group vs. the out-group varies as a function of personal motivation or situational/task-related demands (see Cunningham et al., 2005).

As detailed in the Supplementary material 2, secondary analyses provided preliminary evidence of a positive correlation between self-reported frequency of contact to own-age relative to other-age individuals, as a proxy for familiarity, and amygdala activity to own-age relative to other-age faces in young but not older adults. Future studies will have to determine whether frequency of contact indeed constitutes one of the potential underlying factors for differences in processing in-group vs. out-group faces in amygdala (cf. Wright et al., 2008).

Evidence for reversed patterns in insula and amygdala response to age-based and race-based faces suggest that, at least in part, different processes underlie these types of group memberships (Ebner et al., 2011b). As suggested above, age-based in-group vs. out-group processing is unique compared to other types of group processing because individuals naturally transition from one age group to another. That is, young adults anticipate maturing into older adults, and older adults retain memories of being a young adult. This makes age-based in-groups vs. out-groups less exclusive categories and may imply relatively higher self-relevance of both the age-based, compared to race-based, in-group and out-group. However, in addition to age- or race-specific processes, there may be general mechanisms deployed for differentiating between salient stimulus categories (e.g., in-group vs.

Table 2

ROI analysis: areas showing an Age of Face \times Participant Age interaction (F -contrast; all in the direction Own-Age Faces $>$ Other-Age Faces).

Hemi	BA	Anatomical area	Activation peak			F-value	# vox
			x	y	z		
(1) ROI (mPFC, OFC, INS, FFG): $p < .005$, 22 contiguous voxels							
R	8	Superior Frontal Gyrus, Medial Frontal Gyrus	9	39	42	12.86	43
R	9, 32, 10	Medial frontal gyrus, anterior cingulate gyrus, superior frontal gyrus	21	45	9	15.45	44
L		Insula, claustrum	-36	6	-3	17.27	33
(2) ROI (AMY): small volume correction							
L	28	Amygdala, parahippocampal gyrus	-21	-9	-15	8.04	6

Notes. Areas sorted from dorsal to ventral. Bolded areas discussed in text and presented in Fig. 2. MNI coordinates (x, y, z) and maximum F -value are given for the peak voxel (local maximum) within each region of activation. Hemi: hemisphere; L: left, R: right; BA: Brodmann Area; # vox: number of voxels in cluster. Full activation maps for all areas shown in the table are available from the authors; mPFC = medial prefrontal cortex, OFC = orbitofrontal cortex, INS = insula, FFG = fusiform gyrus, AMY = amygdala.

out-group) which may operate in similar ways for different types of group memberships and may rely on factors such as familiarity, greater preference and/or affective salience, or more available prototypes for the in-group than the out-group. For example, Ebner et al. (2011b) showed striking similarity between the electrophysiological correlates of processing young and older faces and those that differentiated between Black and White faces in the context of a sex categorization task. It will be particularly important to determine in future research the specific lower-level perceptual mechanisms (e.g., compositional detail) and/or higher-level cognitive mechanisms (e.g., differential representations based on prototypicality, familiarity, or expertise, and/or differences related to attention, arousal, or social motivation) involved in different types of in-group vs. out-group processing.

There were no significant effects for orbitofrontal cortex or fusiform gyrus at our cluster-level corrected threshold. This is in line with findings by Wright et al. (2008) but differs from our expectation and other studies on in-group vs. out-group processing based on race and/or minimal groups (Golby et al., 2001; Kim et al., 2006; Van Bavel et al., 2008).

Finally, even though we found neural processing differences for own-age vs. other-age faces in several ROIs, there was no evidence of an own-age effect in facial expression identification. Rather, in line with previous work (Ebner et al., 2011c; Riediger et al., 2011), expressions in young faces were more correctly and quickly identified than expressions in older faces, for both young and older adults. Low-level perceptual differences between young and older faces (see Ebner et al., 2011b, for a discussion) may play a role here as well as increased affect involved in processing young faces and more cognitive control in processing the more complex older faces (see Ebner et al., 2012, for a discussion). In contrast, own-age effects are typically seen in face recognition (Rhodes and Anastasi, 2012). Also, recent eye-tracking studies suggest increased attention to own-age than other-age faces (Ebner et al., 2011c; He et al., 2011). It will be interesting in future research to follow up on the differential impact of the age of the face on attention and memory processes related to face identity, facial emotion, facial age, and facial attractiveness, respectively.

4.2. Own-age effects pronounced in neutral and happy but not angry faces

Importantly, this project is the first to systematically vary the emotional expression of the presented young and older faces, with the goal to examine the impact of facial expression on the own-age effect and thus clearly goes beyond earlier research (Ebner et al., 2011a; Wright et al., 2008). As expected, there was greater activity in ventral medial prefrontal cortex and insula for own-age than other-age faces for neutral and happy but not angry faces in young and older adults. This finding is novel and intriguing in that it suggests that processing of negative facial emotions may override age-of-face effects under certain conditions.

One explanation for this effect could be that facial expression identification in the present study was better for happy than angry faces (see Table 1; see also Ebner et al., 2012; Ruffman et al., 2008). The greater difficulty of identifying angry faces may have resulted in less attention to processing age-of-face information, thus decreasing the own-age effect for angry faces. At the same time, facial emotion of anger constitutes a salient and immediate situational cue of danger and threat that may receive preferential attention (over age-of-face information), as it is crucial for well-being and survival (LeDoux, 1998; Öhman and Mineka, 2001; cf. Ebner and Johnson, 2010). Age cues in faces, even though also an important social signal, in contrast, may just have less likely immediate practical consequences and thus may be processed with lower priority. This interpretation is supported by evidence of a “threat advantage” (Hansen and Hansen, 1988; Öhman et al., 2001; see Palermo and Rhodes (2007) for a review), seen in both young and older adults (Hahn et al., 2006; Mather and

Knight, 2006). Also, a functional intergroup argument could be made in that happy expressions of in-group faces as well as angry expressions of out-group faces may form a congruent category, whereas happy expressions of out-group faces or angry expressions of in-group faces may form an incongruent category, with the latter inducing negative or at least ambivalent emotions (see also Weisbuch and Ambady, 2008).

Interestingly, the present study’s evidence of an “overriding effect” of emotion over facial age differs from results by Ebner and Johnson (2010) that suggested a “potentiating effect” of emotion and facial age. In particular, in young but not older adults, task-unrelated angry own-age faces were more distracting than angry other-age faces, with no comparable effect for happy faces. For older adults, task-unrelated happy compared to angry faces were more distracting, and this effect did not differ for own-age compared to other-age faces. This finding is in line with evidence that older compared to young adults prioritize processing of positive over negative emotions (Carstensen and Mikels, 2005; Mather and Carstensen, 2005), an effect that is further supported by evidence of a shift from subcortical to cortical processing of negative information in older compared to young adults (Fischer et al., 2010; Samanez-Larkin and Carstensen, 2011; St. Jacques et al., 2009).

Ebner and Johnson’s (2010) participants processed number trials while *task-unrelated faces* were shown in the background and behavioral interference effects (slowing of response time) for different types of faces (young vs. older, and neutral vs. happy vs. angry) were measured. In contrast, participants in the present study were asked to *explicitly process the faces*, with a particular focus on the emotion expressed in the faces, while their brain activity and their ability to identify the facial expressions were assessed. The difference in findings across these two studies is interesting and seems to suggest that under some conditions emotion-of-face effects are potentiated by age-of-face effects, whereas under other conditions emotion-of-face effects are primary and override age-of-face effects. Examination of these kinds of interactions of the age of the face and the emotion of the face under varying conditions in future studies would help identify conditions under which either the emotion or the age of a face “trumps” the other.

4.3. Conclusion

The present study extends the literature on processing in-group vs. out-group faces in several ways: By targeting a wider range of regions of interest based on the literature, it provides evidence of insula in addition to the previously shown medial prefrontal cortex (Ebner et al., 2011a) and amygdala (Wright et al., 2008) involvement in differentiating between age-based in-group vs. out-group faces in young and older adults. It furthermore supports evidence of neural processing differences for own-age faces compared to other-age faces in the context of an emotion identification task that drew attention away from the age-of-face information as compared to a passive viewing task (Wright et al.) or a personality rating task (Ebner et al.). Most importantly, however, the present study systematically varied the emotional expression of the presented young and older faces, to determine the impact of facial expression on the own-age effect. Thus, it clearly goes beyond earlier research (e.g., Ebner et al.; Wright et al.) and provides novel evidence that under certain conditions emotional facial expression, particularly anger, can override the own-age effect in specific brain areas sensitive to own-age effects.

The present study does not allow for a direct comparison of effects of race-based vs. age-based group membership. However, it further qualifies the literature on in-group vs. out-group processing and underscores the importance of considering varying definitions of group membership. In addition, methodological and design-related differences among the present study and previous research suggest that orienting tasks (e.g., passive viewing, emotion identification, implicit vs. explicit processing), details of face presentation (i.e., single

vs. repeated), and features of face stimuli (neutral vs. emotional) are important sources of variance that need to be sorted out in future research in order to clarify the mechanisms driving differences in processing members of the in-group vs. the out-group.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2013.04.029>.

Conflict of interest

No conflict of interest exists for any of the authors.

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