Healthy aging impairs face discrimination ability

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Face images enable individual identities to be discriminated from one another. We aimed to quantify age-related changes in different aspects of face identity discrimination. Face discrimination sensitivity was measured with a memory-free "odd-one-out" task. Five age groups (*N* = 15) of healthy adults with normal vision were tested: 20, 50-59, 60-69, 70-79, and 80-89. Sensitivity was measured for full-face images (all features visible), external features (head-shape, hairline), internal features (nose, mouth, eyes, and eyebrows) and closed-contour shapes (control object). Sensitivity to full-faces continuously declined by approximately 13% per decade, after 50 years of age. When age-related differences in visual acuity were controlled, the effect of age on face discrimination sensitivity remained. Sensitivity to face features also deteriorated with age. Although the effect for external features was similar to full-faces, the rate of decline was considerably steeper (approximately 3.7 times) for internal, relative to external, features. In contrast, there was no effect of age on sensitivity to shapes. All age groups demonstrated the same overall pattern of sensitivity to different types of face information. Healthy aging was associated with a continuous decline in sensitivity to both full-faces and face features, although encoding of internal features was disproportionately impaired. This age-related deficit was independent of differences in low-level vision. That sensitivity to shapes was unaffected by age suggests these results cannot be explained by general cognitive decline or lower-level visual deficits. Instead, healthy aging is associated with a specific decline in the mechanisms that underlie face discrimination.

Introduction

Healthy aging reduces sensitivity to several aspects of visual information. For example, reductions in sensitivity to contrast (Elliott, Whitaker, & MacVeigh, 1990), flicker (Nguyen & McKendrick, 2016; Tyler, 1989) and motion (Snowden & Kavanagh, 2006), as well as shape discrimination (McKendrick, Weymouth, & Battista, 2010), have been identified in older, relative to younger, adults. This age-related decline may be partly explained by deterioration of the eye's optics (e.g., reduced light transmission, increased intra-ocular light scatter) (Guirao, Gonzalez, Redondo, Geraghty, Norrby, & Artal, 1999). A wealth of evidence, however, supports the view that healthy aging is also associated with changes within the neural mechanisms that underlie specific functions of the visual system (Andersen, 2012; Csete, Bognár, Csibri, Kaposvári, & Sáry, 2015).

Faces are complex visual objects and contain a wealth of information. In addition to providing cues to an individual's age, gender, ethnicity and emotional state, faces enable the visual system to rapidly and accurately individuate different people. Previous studies suggest that healthy aging reduces sensitivity to several aspects of face perception. Age-related declines have been reported for tasks such as face detection (Norton, McBain, & Chen, 2009), discrimination of eye gaze direction (Slessor, Phillips, & Bull, 2008) and recognition of facial expressions (Hayes, McLennan, Henry, Phillips, Terrett, Rendell, Pelly, Labuschagne, 2020). The focus of the present study is the effect of healthy aging on *face discrimination*: detecting differences between individual identities.

It has been widely reported that the ability to learn and recognize face identities is significantly poorer

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in older, relative to younger, adults (Bartlett, Leslie, Tubbs, & Fulton, 1989; Bartlett & Fulton, 1991; Cheng, Shyi, & Cheng, 2016; Crook & Larrabee, 1992; Maylor & Valentine, 1992; Memon & Bartlett, 2002; Searcy, Bartlett, & Memon, 1999). In particular, older adults are more likely to incorrectly recognize a face which they have never seen before as familiar (Searcy et al., 1999). It is well established, however, that healthy aging is also associated with a general decline in memory (Craik & Jennings, 1992; Fraundorf, Hourihan, Peters, & Benjamin, 2019). Accordingly, impairments of face recognition in older adults may reflect memory deficits, rather than a specific effect of age on the processing mechanisms that are specialized for faces (Habak, Wilkinson, & Wilson, 2008).

Other studies used paradigms with substantially reduced memory demands. For example, participants could be asked to determine whether the identity of two successively viewed faces was the same or different (Chaby, Narme, & George, 2011; Meinhardt-Injac, Persike, & Meinhardt, 2014; Meinhardt-Injac, Persike, Imhof, & Meinhardt, 2015), or to match a previously-viewed target face to a number of alternatives (Boutet & Faubert, 2006; Habak et al., 2008; Konar, Bennett, & Sekuler, 2013). These experimental designs, however, make demands of working memory, which also declines with age (Park, Lautenschlager, Hedden, Davidson, Smith, & Smith, 2002; Rhodes & Katz, 2017).

On the other hand, there is evidence to support the view that healthy aging is associated with a specific decline within the neural mechanisms that underlie the processing of face identity. Behavioral studies suggest that age-related differences in face discrimination persist when memory demands have been eliminated (Cheng et al., 2016; Megreya & Bindemann, 2015; Slessor, Riby, & Finnerty, 2013). Similarly, older adults score more poorly than younger adults on the Benton face recognition test, a clinical test of face matching that has no memory requirement (Cronin-Golomb, Gilmore, Neargarder, Morrison, & Laudate, 2007; Memon & Bartlett, 2002; Searcy et al., 1999). Another approach is to compare the effect of healthy aging on sensitivity to faces with that for non-face objects. A number of reports have found that healthy aging disproportionately impairs identification of faces, relative to that for chairs, houses, cars, and watches (Boutet & Faubert, 2006; Meinhardt-Injac et al., 2014; Thomas, Moya, Avidan, Humphreys, Jung, Peterson, & Behrmann, 2008).

Behavioral reports of a specific age-related decline in sensitivity to face identity information are supported by neuroimaging studies. In order to process face information, the primate brain has developed an interconnected neural network, which includes the occipital face area (Gauthier, Tarr, Moylan, Skudlarski, Gore, & Anderson, 2000), the superior temporal sulcus (Allison, Puce, & McCarthy, 2000), and the fusiform face area (Kanwisher, McDermott, & Chun, 1997). The latter appears to play an important role in discriminating between different face identities (Axelrod & Yovel, 2015; Kanwisher & Yovel, 2006).

Functional magnetic resonance imaging (fMRI) has revealed that the Fusiform face area (FFA) is less identity selective in older, relative to younger, adults (Goh, Suzuki, & Park, 2010; Lee, Grady, Habak, Wilson, & Moscovitch, 2011). Specifically, Goh, Suzuki, and Park (2010) reported that sequential viewing of different face identities in older adults led to adaptation of the fMRI BOLD signal recorded from the FFA. Minimal BOLD adaptation occurred, however, in younger adults viewing the same stimuli. Because fMRI BOLD adaptation is considered to be indicative of neural selectivity (Grill-Spector & Malach, 2001), this result suggests that the face discrimination ability of the FFA declines with healthy aging. Similarly, evidence from electrophysiological studies indicates that healthy aging alters parameters such as the amplitude, latency and hemispheric lateralization of the ERP components associated with face processing (Chaby, George, Renault, & Fiori, 2003; Daniel & Bentin, 2012; Gao, Xu, Zhang, Zhao, Harel, & Bentin, 2009). In particular, a recent study provided evidence that aging reduces the face-selectivity of the N170 component (Boutet, Shah, Collin, Berti, Persike, & Meinhardt-Injac, 2021).

Healthy aging is also associated with a decline in low-level vision; measurements of visual acuity (VA) (Elliott, Yang, & Whitaker, 1995), and contrast sensitivity (Owsley, Sekuler, & Siemsen, 1983) are significantly poorer in older, relative to younger, adults. Because of the hierarchical nature of the visual system, deficiencies of low-level vision are expected to feed-forward and impact on higher-level visual functions. Specifically for face perception, VA and contrast sensitivity are highly correlated with face recognition accuracy (Barnes, De l'Aune, & Schuchard, 2011; Lott, Haegerstrom-Portnoy, Schneck, & Brabyn, 2005; Owsley & Sloane, 1987). Similarly, degradation of low-level vision produces a proportional reduction in face discrimination sensitivity (McCulloch, Loffler, Colquhoun, Bruce, Dutton, & Bach, 2011).

As a result, the age-related decline in face perception may be explained by a combination of deficiencies in low-level vision and a specific effect of age on the neural mechanisms that mediate face processing. The present study's approach achieves a degree of independence from optical factors through the application of a band-pass filter to the face stimuli. This filter removes visual information contained within high spatial frequencies that has been shown to contribute little to face identification (Fiorentini, Maffei, & Sandini, 1983; Näsänen, 1999). In terms of low-level vision, application of the filter creates a level playing field; face discrimination sensitivity measured with the synthetic face stimuli utilized within the presented study is largely unaffected by optical factors. In support of this proposal, discrimination thresholds for synthetic faces are invariant across large changes in viewing distance (up to a factor of four) (Lee, Matsumiya, & Wilson, 2006).

A number of previous investigations have been unable to quantify the range of difference in sensitivity to face information in younger and older adults. In some cases, the face discrimination ability of some participants exceeded the difficulty of the tests used (Barnes et al., 2011; Boutet & Faubert, 2006; Grady, Randy McIntosh, Horwitz, & Rapoport, 2000; Lott et al., 2005). At the other extreme, older adults performed at chance level when asked to discriminate between faces with subtle differences (Chaby et al., 2011; Lott et al., 2005). These ceiling and floor effects may obscure age-related differences in sensitivity to face information (Ruffman, Henry, Livingstone, & Phillips, 2008). We have designed a new test of face discrimination (Logan, Wilkinson, Wilson, Gordon, & Loffler, 2016) which provides a rapid (average test time is approximately four minutes) quantification of face discrimination sensitivity. The range of the Caledonian face test is essentially unlimited, which precludes floor and ceiling effects.

Age-related changes in face learning and recognition have been measured across the lifespan (Crook & Larrabee, 1992; Germine, Duchaine, & Nakayama, 2011). As outlined above, however, it is difficult to dissociate any specific effect of healthy aging on face *recognition* from general, age-related differences in cognitive functioning (e.g., memory, familiarity determination). Previous studies on face *discrimination* ability have focused on making comparisons between younger and older adults (Chaby et al., 2011; Habak et al., 2008; Konar et al., 2013; Meinhardt-Injac et al., 2014). The present study, on the other hand, aims to quantify the profile of age-related changes in face discrimination ability by testing several age groups of older adults (i.e., 50-59, 60-69, 70-79, 80-89).

The aim of this study is to provide a quantitative account of the effect of healthy aging on different aspects of face discrimination sensitivity. Discrimination thresholds were measured for full-faces, face features, and matching closed-contour shapes (as a control object) in adults from a range of age groups. These data will provide insight into the profile of changes in visual sensitivity to face information with healthy aging. Our paradigm is free of memory requirements and uses stimuli that achieve a degree of independence from deficits in sensitivity to high spatial frequency information. These aspects, together with inclusion of a control object (shapes), will help to determine whether healthy aging is associated with a specific reduction in sensitivity to face information or whether age-related differences can be explained by a general decline of cognitive or low-level visual functioning.

Previous studies suggest that healthy aging does not reduce sensitivity to face information equally. For example, it has been reported that older adults demonstrate a specific impairment of processing the relative positions of the internal face features (eyes, nose and mouth) (Chard, Cook, & Press, 2021; Murray, Halberstadt, & Ruffman, 2010). Others have reported that sensitivity to the position of the eyes is significantly poorer in older, relative to younger, adults (Chaby et al., 2011; Meinhardt-Injac et al., 2015; Slessor et al., 2013). Consistent with this finding, younger and older adults demonstrate different gaze scanning patterns when viewing the internal face features (Firestone, Turk-Browne, & Ryan, 2007). Finally, Meinhardt-Injac et al. (2014) found that older adults demonstrated particular difficulty when making face matching judgements based on internal, relative to external (hair and face outline), feature information.

In previous work, we provided evidence that the external and internal features of unfamiliar faces are processed independently (Logan, Gordon, & Loffler, 2019). This, together with the reports outlined above, raises the possibility that there are differences in the effects of healthy aging on sensitivity to the internal and external face features. The present study further aimed to investigate this possibility by making a quantitative comparison between sensitivity to external and internal face features in older adults from a range of age groups.

Methods

Synthetic faces

The majority of previous investigations of the effect of healthy aging on face perception have used face photographs as stimuli (Cheng et al., 2016; Meinhardt-Injac et al., 2014; Slessor et al., 2013). These complex images include a wealth of information (e.g., color, wide range of spatial frequencies), which can make it difficult to attribute age-related changes in performance to specific aspects of the stimulus and underlying face processing. In contrast, our approach is based on synthetic faces—simplified face stimuli that can be manipulated within a mathematical framework to precisely control the differences between individual faces.

Synthetic faces have been described in detail elsewhere (Wilson, Loffler, & Wilkinson, 2002) and some details from this brief description are reproduced from earlier work (Logan, Gordon, & Loffler, 2017; Logan et al., 2019; Logan, Gordon, & Loffler, 2020; Swystun & Logan, 2019). Synthetic faces are based on the major geometrical face information from grayscale face photographs of 80 individuals (40 male)

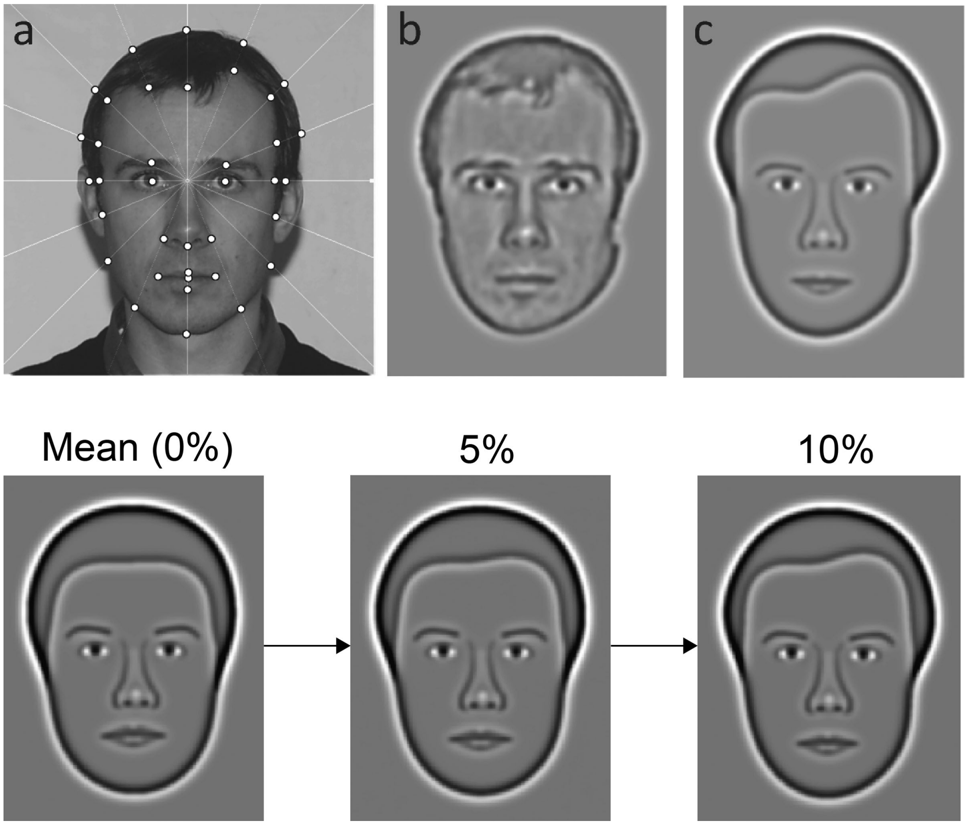

Figure 1. Synthetic faces. Top: (a) Grayscale photograph with superimposed polar coordinate grid centered on the bridge of the nose. The head-shape was measured at 16 locations (*white dots*) around the external contour, angularly positioned at equal intervals of 22.5°. The polar co-ordinates of 14 of the measured points were used to define seven radial frequencies to describe the subject's head-shape. An additional nine points were used to define four radial frequencies that captured the shape of the subject's hairline. All radial frequencies were defined relative to the mean head radius of all synthetic faces of the subject's gender. The location and shape of the internal face features were also digitized. In sum, the face is described by 37 measurements. (b) Photograph filtered with a 2.0 octave bandwidth DOG filter with peak spatial frequency of 10 cycles/face width. (c) Corresponding synthetic face. Bottom: synthetic faces were adjusted by manipulating their distinctiveness (i.e., by how much they differed from the mean face) (left). Increasing face distinctiveness results in individual faces becoming progressively more dissimilar (from middle to right) to the mean face. Distinctiveness is expressed as a percentage of mean head radius and quantifies the total geometric variation between the specified face and the mean face. Typical observers can discriminate a face from the mean at about 5% distinctiveness.

with neutral expressions. To extract this information, a polar coordinate grid was superimposed on the face photograph, centered on the bridge of the subject's nose (Figure 1a). The external head shape was sampled at 16 equally-spaced locations. These points were used to define seven radial frequencies that described the head-shape. Radial frequency patterns are closed contours which can be combined to define complex shapes, including human heads (Wilson & Wilkinson, 2002). Similarly, nine additional locations were used to define the shape of the subject's inner hairline.

The internal features (eyes, nose, mouth, and eyebrows) of the face photograph were defined by a further 14 measurements. These measurements included positional information for all features (defined relative to the center of the face), and shape information for the nose and mouth. Specifically, the nose and mouth shapes were derived from generic forms that were altered in terms of length and width based on individual face measurements (e.g., lip thickness). The shapes of the eyes and eyebrows were generic. Individuating information was contained within variations in horizontal and vertical eye position, in addition to the height of the eyebrows, defined relative to the center of the eyes. In sum, each synthetic face is defined by 37 parameters and represented by a 37-dimensional vector.

Synthetic faces were subsequently band-pass filtered (circular DOG filter with a bandwidth of 2.0 octaves) at the spatial frequency that has been reported to be optimal for face identification (10 cycles/face-width; Figure 1b) (Näsänen, 1999). The resulting faces accentuate geometric information

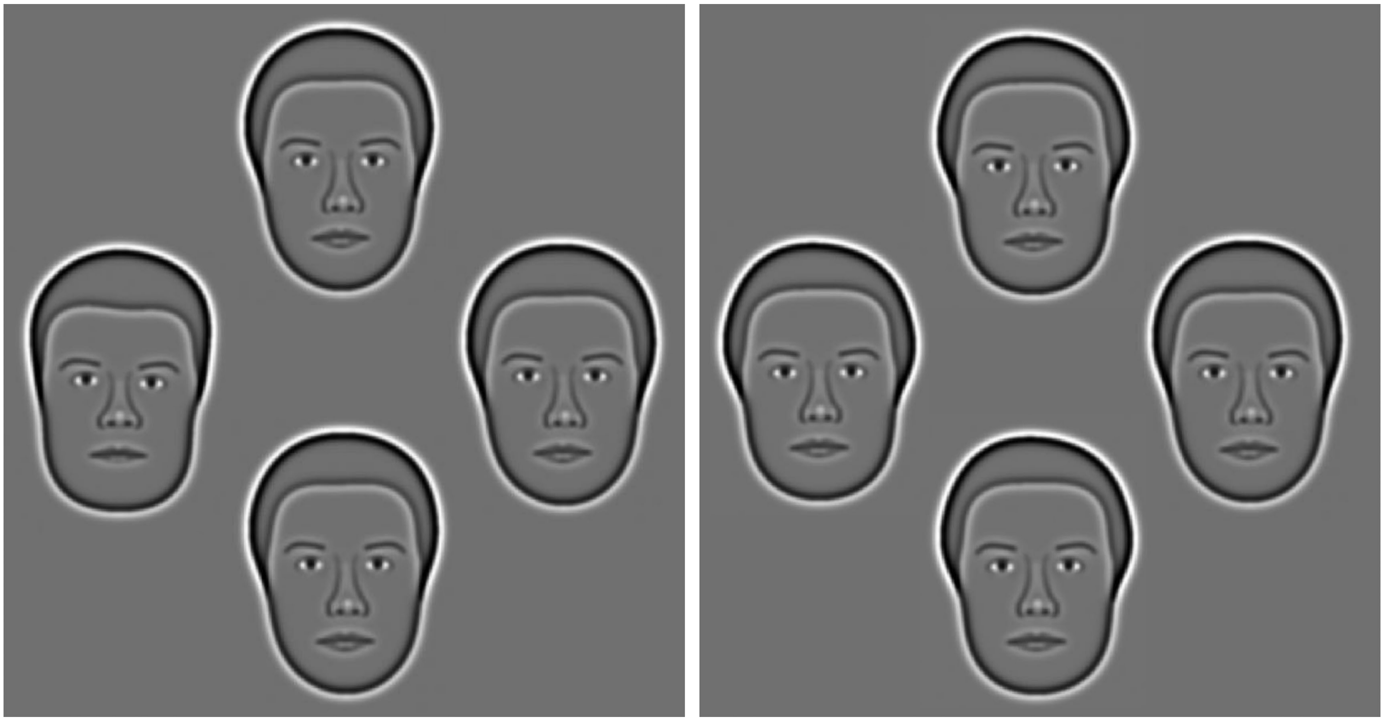

Figure 2. The Caledonian face test. Four faces were presented in a diamond configuration and participants were asked to indicate the "odd" face that differed from the others. Left: supra-threshold trial for most participants (target face differs from mean face by 10%). The target (odd one) is to the left. Right: difficult trial, approximately at threshold for a typical participant (5%). Target is to the right.

in the most important frequency band while omitting cues such as hair texture, skin wrinkles and color.

The rationale for using synthetic faces for the present study is that their simplified nature enabled precise control of differences in face information. Whilst synthetic faces do not contain all of the information available within real faces (e.g., skin texture, surface reflectance), face identification can be performed at 5 m, a distance at which this type of visual information is limited or unavailable (Logan et al., 2016). One further advantage of filtering for the present study is that application of a spatial frequency filter enables synthetic faces to achieve a degree of independence from age-related changes in low-level vision. Specifically, face discrimination thresholds measured with these images are unaffected by modest differences in visual acuity (Logan et al., 2016).

A mean face was produced by averaging each of the 37 dimensions of all synthetic faces of the same gender. All faces were expressed relative to the same gender-appropriate mean face, which served as the origin of a multidimensional face space. Within this framework, synthetic faces can be morphed to have any defined geometric difference from the mean face (Figure 1, bottom). This value, expressed as a percentage of the mean head size, quantifies the difference between the mean face and an individual face (i.e., the distinctiveness of the individual face). Previous studies have shown that this correlates closely with discrimination sensitivity (Wilson et al., 2002). All synthetic faces were scaled to the same size. At the test distance of 1 m, faces subtended 5.5° of visual angle in height.

The Caledonian face test

Our primary outcome measure was the face discrimination threshold: the minimum difference required between an individual face and the mean face for reliable discrimination. Measurements were made with the Caledonian face test: an odd-one-out task that uses an adaptive design to provide an accurate and efficient measurement of the face discrimination threshold (Logan et al., 2016; Logan et al., 2020).

The test presented participants with four faces in a diamond configuration (Figure 2). Three of the faces were identical (distracters) whereas one face (target) was morphed to differ from the distracters by a specified amount. Participants were asked to respond by indicating the odd-one-out via computer mouse click and guess when uncertain. Viewing time was unlimited. The mean face featured on every trial and was randomly assigned as the target face on 50% of trials. The identity of the other face was randomly selected from a large database (40 male, 40 female). Face

Age group	*N*	*N* male	Mean age (range)	Mean VA LogMAR (range)	Mean CS log units (range)	Mean MoCA score (range)
'20'	15	8	19.9 (19–21)	−0.15 (−0.2 to −0.1)	1.89 (1.80 to 1.95)	29.1 (28–30)
50–59	15	6	54.3 (50–59)	−0.10 (−0.02 to −0.2)	1.88 (1.80 to 1.95)	29.5 (28 to 30)
60–69	15	8	64.7 (60–69)	−0.05 (−0.18 to 0.06)	1.81 (1.65 to 1.95)	29.2 (28 to 30)
70–79	15	9	75.8 (70–79)	−0.02 (−0.1 to 0.1)	1.74 (1.65 to 1.80)	29.3 (27 to 30)
80–89	15	7	84.5 (80–89)	0.01 (−0.08 to 0.08)	1.69 (1.65 to 1.80)	28.8 (27 to 30)

Table 1. Participant information MoCA, Montreal Cognitive Assessment (Nasreddine et al., 2005).

gender was randomly selected for each trial; the gender of the mean face was matched to that of the non-mean face.

The magnitude of the difference between the faces (i.e., task difficulty) on each trial was controlled by a QUEST adaptive procedure (Watson & Pelli, 1983). This highly efficient algorithm adjusts task difficulty to concentrate testing around the face discrimination threshold. QUEST utilizes a maximum likelihood procedure to produce a threshold estimate after each trial based on all responses made from the beginning of the test run.

To maintain participant engagement, dummy trials (face difference set to 3 times current threshold estimate) were included after every seventh trial. After earlier validation work (Logan et al., 2016), the face discrimination threshold was defined as the best estimate of threshold at the conclusion of a 30-trial-run.

Apparatus

The study was carried out with binocular viewing under an ambient illumination of 75 cd m^{-2}. Participants were seated at 1 m from an HP P1230 monitor (1024 × 768 at 85 Hz; HP, Palo Alto, CA, USA) of 64 cd m^{-2} mean luminance that was controlled by an Apple Mac Pro computer (Apple, Cupertino, CA, USA). The color look-up table was defined to maximize contrast linearity of the monitor. The Caledonian face test was written in Matlab (www.mathworks.com) and includes routines from the Psychtoolbox extension (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997).

Participants

In total, 75 naïve adults took part in the study (Table 1). Young adults were recruited from the undergraduate student population of the University of Bradford. Older adults were recruited from among the staff of the University of Bradford and patients of the university's eye clinic. All participants were in good health. Record cards from recent eye examinations were screened to ensure that participants with a history of ocular disease (e.g., age-related macular degeneration, glaucoma), visual field loss, raised intra-ocular pressure (>21 mm Hg), amblyopia (greater than one line difference in VA between the eyes) or strabismus were excluded. Participants with a refractive error of greater than ±6.00 DS or 2.50 DC were also excluded. Participants gave informed consent in accordance with the Declaration of Helsinki, as approved by the Committee for Ethics in Research of the University of Bradford.

All participants had normal, or corrected-to-normal, vision. Participants were required to have a best-achievable binocular VA of at least +0.10 LogMAR and no significant deficit in contrast sensitivity (relative to their age group) (Elliot, Sanderson, & Conkey, 1990; Mäntyjärvi & Laitinen, 2001). Optimal refractive correction was determined for each participant through refraction by an Optometrist and, where required, provided by trial lenses mounted in a trial frame. This correction was adjusted for the test viewing distance of 1m. Distance visual acuity (VA) was measured with an Early Treatment Diabetic Retinopathy Study (ETDRS) chart at 3m (Ferris, Kassoff, Bresnick, & Bailey, 1982). Contrast sensitivity (CS) was assessed with a Pelli-Robson test chart (Pelli & Robson, 1988). Both charts were displayed at the luminance recommended by the manufacturers.

The Montreal Cognitive Assessment (MoCA) (Nasreddine, Phillips, Bédirian, Charbonneau, Whitehead, Collin, Cummings, Chertkow, 2005) was used to screen for cognitive impairment. All participants passed this test (i.e., scores exceeded 26 points out of a possible 30).

Procedure

The Caledonian face test was utilized to quantify discrimination thresholds for several aspects of face information. Separate threshold measurements were made for full-faces (in which all of the features changed by equivalent proportions), presented both upright (Figure 3a) and inverted (Figure 3b), as well as combinations of face features.

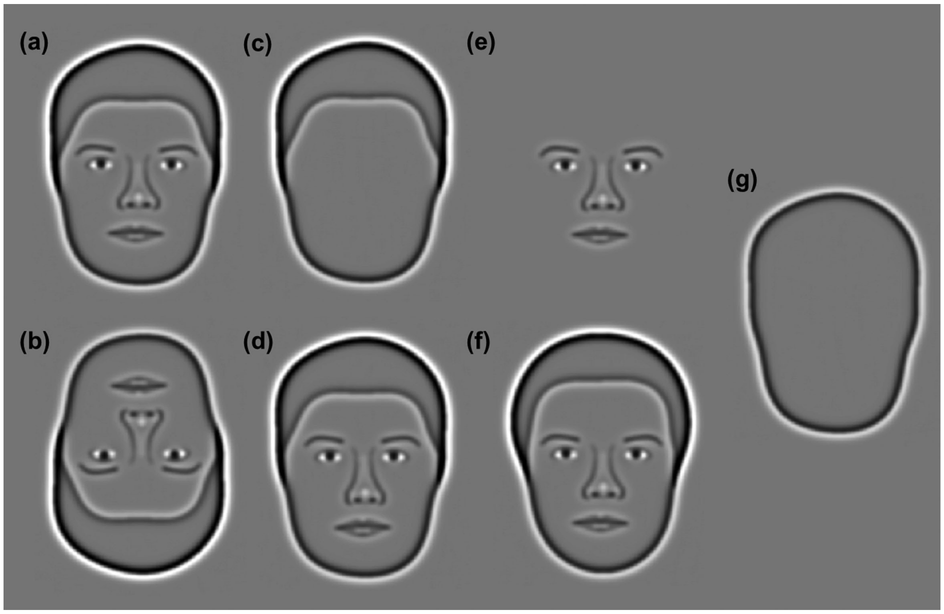

Figure 3. Face features. The Caledonian face test was administered under the following conditions: (a) full-faces: all features varied by equivalent proportions, (b) inverted full-faces: as for (a), but presented upside-down, (c) isolated external features: only the head-shape and hairline were visible, (d) embedded external features: the same stimulus as (b), where only external features varied within an otherwise fixed face context, (e) isolated internal features: only the eyes, nose, mouth and eyebrows are visible, (f) embedded internal features: the same stimulus as (e), embedded within an otherwise fixed face context, and (g) closed-contour shapes.

Combinations of face features were the external (head-shape and hairline) and internal (nose, mouth, eyes and eyebrows) features. Thresholds were measured for these feature combinations presented both in isolation and embedded within a fixed face context. The isolated condition presented the relevant features extracted from the corresponding full-face (Figures 3c, 3e). For example, the isolated internal feature condition presented only the nose, mouth, eyes, and eyebrows obtained from the corresponding full-face.

Embedded conditions enabled measurement of discrimination thresholds for internal and external features while participants viewed whole faces, rather than face parts. Only the features of interest (i.e., either internal or external) varied between the target and distracters; the other features were identical (Figures 3d, 3f). For example, in the embedded external feature condition, the target and distracter faces only differed in terms of the head shape and hairline; the internal features were identical. Because the task-irrelevant features were identical across all options, faces in the embedded feature condition contained no more discrimination cues than the associated isolated feature condition but presented them within complete faces.

Comparing thresholds for the isolated and external feature conditions will provide insight into the effect of healthy aging on face processing strategies. We have previously reported that young adults demonstrate similar thresholds for isolated and embedded features of unfamiliar faces (Logan et al., 2019). We argued that this indicates independent processing of external and internal face feature information. The present study will investigate if older adults demonstrate the same overall pattern of sensitivity to face features. Differences in thresholds for isolated and embedded features in older adults would suggest that healthy aging leads to a qualitative change in face processing strategy. Previous reports suggest that, compared to younger controls, older adults are less sensitive to internal feature information (Chaby et al., 2011; Meinhardt-Injac et al., 2014; Murray et al., 2010). Accordingly, one possible outcome is that healthy aging may encourage reliance on the external features for face discrimination. The present study will investigate this possibility by comparing thresholds for isolated and embedded feature conditions across age groups.

To investigate the specificity of any age-related decline in visual sensitivity that is related to faces, rather than objects more widely, we adapted the test to measure discrimination thresholds for closed-contour shapes, a non-face control object (Figure 3g). Shapes were selected because they represent a category of objects distinct from faces and can be described by a mathematical framework which enables direct comparison with our metric for quantifying face discrimination sensitivity. We reasoned that, if our data suggest that healthy aging is associated with a comparable increase in thresholds for faces and shapes, this would be suggestive of a general reduction in visual sensitivity in older adults. On the other hand, our data may suggest that healthy aging disproportionately impairs a particular aspect of visual function (such as face discrimination) relative to another (e.g., shape discrimination).

The order of testing was randomized. Participants were not informed of the condition being tested and were always instructed to identify the odd-one-out. Each participant completed a single practice run of the full-face condition of the Caledonian face test to allow familiarization with the test design before data collection. Feedback was only provided during the practice run.

Statistical analysis

All statistical analyses used a one-factor, repeated measures analysis of variance (ANOVA), unless otherwise specified. Where Mauchly's test indicated a violation of the sphericity assumption, the Greenhouse-Geisser correction was used. An alpha value of 0.05 was used as the criterion for statistical significance.

Results

Mean discrimination thresholds for each age group are presented in Figure 4. The young adults (20-year-olds) were used as a baseline to which thresholds from the other age groups were compared.

A two-factor (face feature [full-face, isolated external features, embedded external features, isolated internal features, embedded internal features and shape] and age group [20, 50-59, 60-69, 70-79, and 80-80]) mixed ANOVA identified a significant main effect of face feature on discrimination thresholds ($F_{5,350} = 945.43$; $p < 0.001$; $\eta_p^2 = 0.93$). There was also a significant main effect of age group on discrimination thresholds ($F_{4,70} = 53.63$; $p < 0.001$; $\eta_p^2 = 0.75$). The interaction

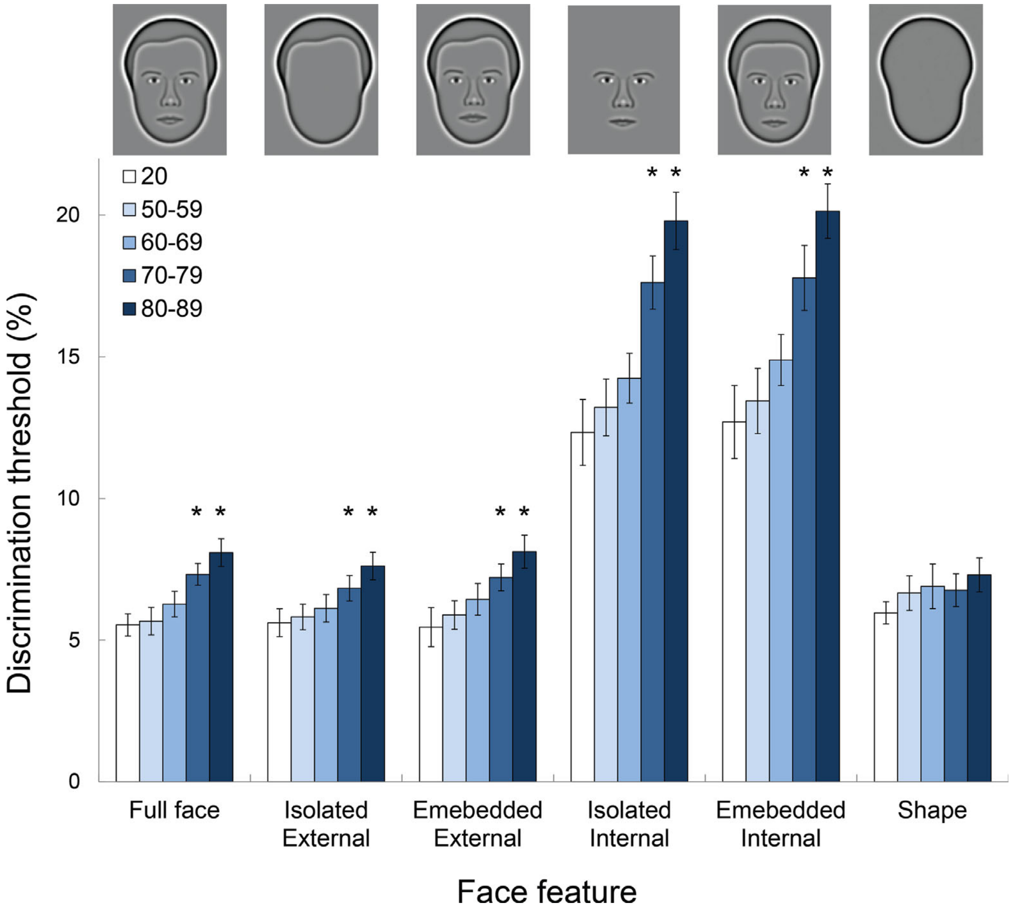

Figure 4. Discrimination thresholds for different face features. Icons illustrate the feature being tested. Here, and elsewhere, *error bars* represent 95% confidence intervals. *Asterisks* indicate significant difference in discrimination thresholds from the young adult baseline (20-year-olds) (pairwise comparisons; $p < 0.05$).

between face features and age group was significant ($F_{20,350} = 12.84$; $p < 0.001$; $\eta_p{}^2 = 0.42$). Accordingly, the effect of healthy aging was analyzed separately for each face feature.

Healthy aging

Discrimination thresholds for full-faces (in which all of the features changed by equivalent proportions) increased monotonically as a function of age ($F_{4,70} = 23.73$; $p < 0.001$; $\eta_p{}^2 = 0.58$). This age-related decline, relative to the young adult baseline, reached significance at age 70 (pairwise comparisons with Bonferroni correction $p < 0.001$; Figure 4). For example, full-face discrimination thresholds were approximately 1.33 times greater for 70- to 79-year-old participants (mean ± 95% confidence interval = 7.3% ± 0.4%), compared to those for younger adults (5.5% ± 0.4%; $p < 0.001$). These results suggest that healthy aging reduces full-face discrimination sensitivity (i.e., higher thresholds in older adults).

We next sought to determine whether this effect of healthy aging on face discrimination thresholds could be explained by poorer VA in older, relative to younger, adults. A one-way analysis of covariance investigated the effect of aging on face discrimination thresholds, while controlling for differences in VA across age groups. This analysis provided evidence of a significant effect of healthy aging on full-face discrimination thresholds ($F_{4,69} = 12.24$; $p < 0.001$; $\eta_p{}^2 = 0.42$). As before, this age-related decline reached significance at age 70, relative to the young adult baseline (pairwise comparisons with Bonferroni correction $p < 0.001$). These results indicate that healthy aging impairs face discrimination sensitivity, and that this effect can be dissociated from age-related changes in low-level vision (i.e., VA).

There was a similar age-related decline in sensitivity to the external features, presented either in isolation ($F_{4,70} = 11.56$; $p < 0.001$; $\eta_p{}^2 = 0.40$) or embedded within a fixed-face context ($F_{4,70} = 13.57$; $p < 0.001$; $\eta_p{}^2 = 0.44$). In the same way, sensitivity to the internal features declined with healthy aging (isolated: $F_{4,70} = 37.93$; $p < 0.001$; $\eta_p{}^2 = 0.68$; embedded $F_{4,70} = 30.78$; $p < 0.001$; $\eta_p{}^2 = 0.64$). As for full-faces, the age-related decline in sensitivity to external and internal features reached significance at age 70, under both isolated and embedded conditions (pairwise comparisons with Bonferroni correction $p < 0.05$; Figure 4).

Figure 4 suggests that healthy aging is associated with a more rapid increase in discrimination thresholds for the internal, relative to external, features. For example, thresholds for isolated internal features in 70- to 79-year-old participants were 1.43 times higher than those measured in 20-year-olds ($p < 0.001$). On the other hand, thresholds for isolated *external* features were 1.22 times higher in 70- to 79-year-old participants, compared to the young adults ($p = 0.007$). This is suggestive of a disproportionate effect of healthy aging on sensitivity to the internal face features, which will be further investigated in Section 3.3. There was, however, no significant effect of aging on discrimination thresholds for shapes ($F_{4,70} = 1.48$; $p = 0.22$; $\eta_p{}^2 = 0.08$).

Face features

Across all age groups, discrimination thresholds depended strongly on the face features (full-face, isolated external features, embedded external features, isolated internal features, embedded internal features) that differed between the target and distracters (two-factor mixed ANOVA $F_{4,280} = 1017.79$; $p < 0.001$; $\eta_p{}^2 = 0.94$). This can be seen by comparing columns across conditions in Figure 4. Specifically, in all groups, discrimination thresholds for internal features (both isolated and embedded) were significantly higher than those for full-faces ($p < 0.001$; pairwise comparisons with Bonferroni correction). Thresholds for the external features (both isolated and embedded), on the other hand, were comparable to those for full-faces ($p > 0.99$). These results are consistent with the premise of an external feature advantage for unfamiliar face discrimination (Logan et al., 2017). That all age groups demonstrated this same qualitative pattern (Figure 4) suggests that healthy aging does not lead to changes in this processing strategy.

Moreover, there was no effect on discrimination thresholds of embedding either external or internal features within a fixed face context. Specifically, there was no significant difference between discrimination thresholds for external features presented in isolation and embedded within a fixed face context ($p > 0.99$). Similarly, discrimination thresholds for internal features shown in isolation were not significantly different from those for internal features embedded within a fixed face context ($p > 0.99$). For young adults, we have argued previously that this supports the view that the external and internal features of unfamiliar faces are processed independently (Logan et al., 2019). Figure 4 demonstrates that the same qualitative pattern was demonstrated by all age groups. This indicates that, like younger adults, older adults demonstrate independent processing of external and internal features within this type of face discrimination task.

Overall, our data indicate that, like their younger counterparts, older adults demonstrate both an external feature advantage and independent processing of external and internal features of unfamiliar faces. The results suggest that healthy aging does not lead to a qualitative change in face processing strategy.

Comparing the effect of healthy aging on sensitivity to different features

The effect of healthy aging was analyzed separately for each face feature that was tested (Figure 5). The age-related increase in discrimination thresholds for full-faces between 50 and 90 years of age was well captured by a linear fit (Figure 5a). Specifically, there was a positive correlation ($r = 0.70$, $N = 60$, $p < 0.001$) between age and full-face discrimination thresholds. Age accounted for 49% of the variance in full-face discrimination thresholds for older adults ($r^2 = 0.49$; $F_{1,58} = 56.43$; $p < 0.001$).

One attractive feature of the specific face stimuli used in this study lies in the ability to relate performance

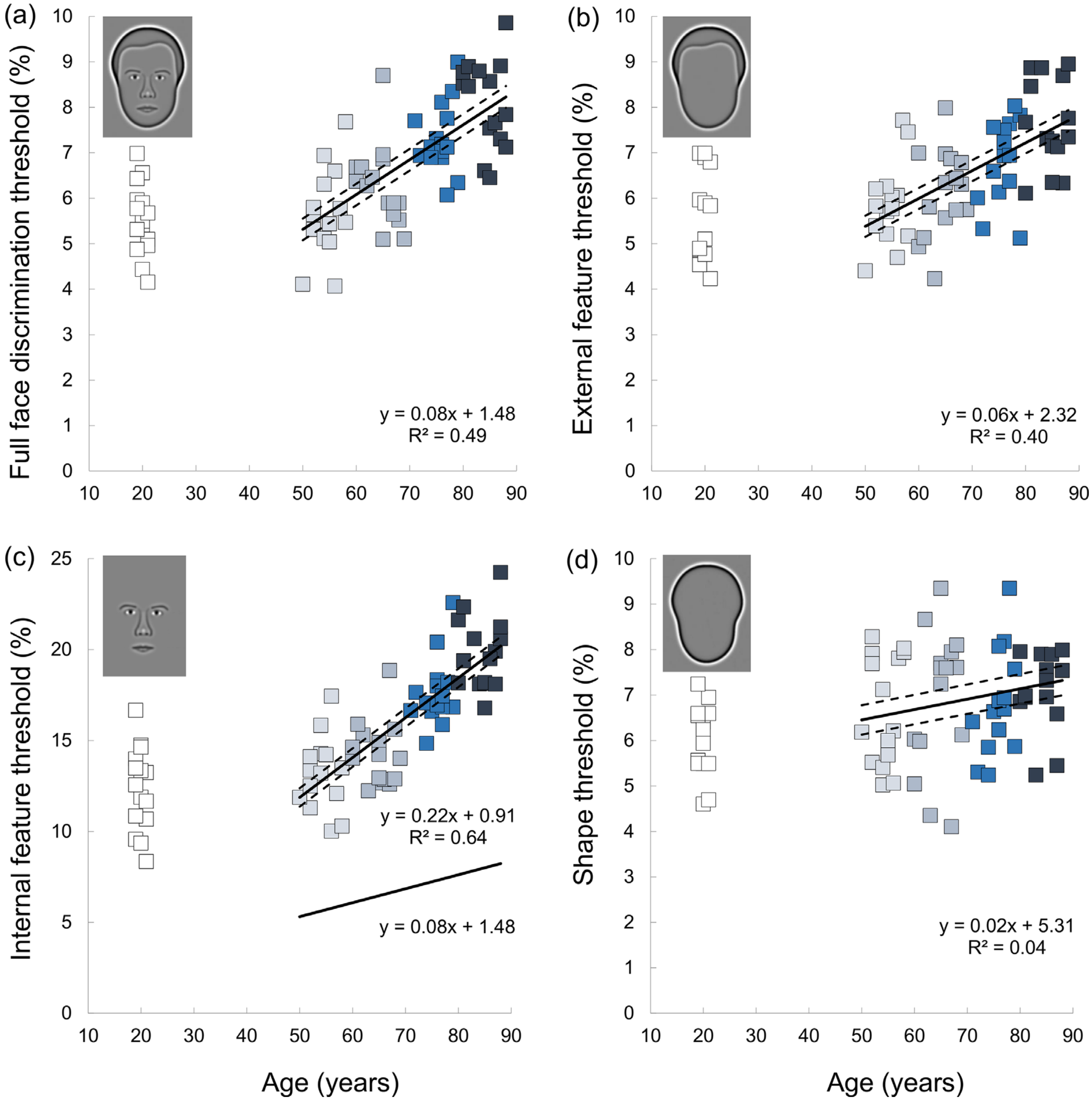

Figure 5. Discrimination thresholds as a function of age for (a) full-faces (b) external features (c) internal features and (d) shapes. *Solid line* indicates the line of best fit; *dashed lines* represent 95% confidence intervals. Note that the data for external (b) and internal (c) features here are for the cases where they were presented in isolation. Thresholds for these features embedded within a fixed face context were not significantly different from those presented in isolation (see Section 3.2). Because of significant differences in sensitivity across all age groups, data for the internal features (c) are presented on a different y-axis scale. The line of best fit for full-faces (a) has been replicated within (c) (i.e., the *lower line*) to illustrate the difference in slope between these two conditions.

across conditions. Because the external and internal feature conditions (Figures 5b, 5c) used features that were extracted from the same faces used within the full-face condition (Figure 5a), the effect of healthy aging on sensitivity to different face features can be directly compared.

As for full-faces, between the ages of 50 and 90, there was a positive correlation ($r = 0.63$, $N = 60$, $p < 0.001$) between age and external feature discrimination thresholds ($r^2 = 0.40$; Figure 5b), as well as between age and internal feature discrimination thresholds ($r = 0.80$, $N = 60$, $p < 0.001$; $r^2 = 0.64$; Figure 5c). Both regressions were significant (external: $F_{1,58} = 38.22$; $p < 0.001$; internal; $F_{1,58} = 101.49$; $p < 0.001$).

The rate of sensitivity decline depended on the face feature that was tested. Specifically, the regression line for full-faces had a slope of 0.08 ($t_{58} = 7.51$; $p < 0.001$). Accordingly, we calculated that sensitivity to full-faces declined by a factor of approximately 1.13 per decade after 50 years of age. A comparable age-related decline was identified for the external features (slope = 0.06 [$t_{58} = 6.18$; $p < 0.001$]; factor = 1.10).

The slope of the best-fitting line for the internal feature data, on the other hand, was considerably steeper than that for full-faces (slope = 0.22 [$t_{58} = 10.01$; $p < 0.001$]). The age-related decline in sensitivity to internal features was approximately 3.7 times steeper than that for external features. These results indicate that healthy aging disproportionately reduces sensitivity to the internal face features.

In contrast, there was no significant correlation ($r = 0.21$, $N = 60$, $p = 0.11$) between age and shape discrimination thresholds (Figure 5d). The regression ($r^2 = 0.04$) was not significant ($F_{1,58} = 2.70$; $p = 0.11$).

Overall, healthy aging significantly impairs face discrimination sensitivity. This cannot be explained by an age-related decline in low-level vision (i.e., VA), which compromises input to higher-level aspects of visual function. That no equivalent effect of aging was identified for a shape discrimination task is also inconsistent with the premise that aging is associated with a general reduction in visual sensitivity, other low-level visual effects, or because of a cognitive influence. Rather, our results suggest that face discrimination per se is vulnerable to the effects of aging. Moreover, healthy aging does not reduce sensitivity to all aspects of face information equally. For each decade of aging (between 50-90 years), the reduction in sensitivity to the internal features is considerably greater (approximately three times) than that for full-faces or the external features.

Healthy aging, holistic processing and the face inversion effect

We found evidence of a significant effect of healthy aging on sensitivity to all types of face information that were tested (full-faces, external features and internal features), but not non-face objects (shapes). Although our data are limited to only one type of non-face object, these results are in line with the premise that face perception may be particularly vulnerable to the effects of healthy aging (Boutet & Faubert, 2006; Meinhardt-Injac et al., 2014).

We next sought to investigate whether the differential effects of aging on discrimination of faces and shapes could be explained by differences in the strategies used to process faces and non-face objects.

Faces are processed holistically—the component face features (e.g., eyes, nose, mouth) are integrated into an interdependent representation, rather than processed as individual parts (Maurer, Le Grand, & Mondloch, 2002; Richler, Cheung, & Gauthier, 2011; Rossion, 2013). This holistic processing is illustrated by the composite face effect: aligning the top half of one identity with the bottom half of another gives rise to the perception of a third, novel identity (Richler & Gauthier, 2014; Young, Hellawell, & Hay, 1987). Similarly, the part-whole effect describes the finding that individual features are recognized more accurately when embedded within a face context, relative to when presented in isolation (Tanaka & Farah, 1993).

Holistic processing is also generally considered to underlie the face inversion effect: compared to that for other objects, sensitivity to face information is disproportionately reduced when faces are presented upside-down (Robbins & McKone, 2007; Rossion, 2008; Rossion, 2009; Valentine & Bruce, 1986; Yin, 1969). Given this relationship between face inversion and holistic processing, we reasoned that differences in the magnitude of the face inversion effect in younger and older adults would indicate that holistic face processing strategies change with healthy aging.

Accordingly, we quantitatively compared the face inversion effect across the different age groups. The data in Figure 6 are presented as threshold elevations, relative to thresholds for the upright full-faces (threshold elevation of 1.00), which served as a baseline.

There was a significant effect of orientation on full-face discrimination thresholds (two-factor (orientation [upright and inverted] and age group [20, 50–59, 60–69, 70–79 and 80–80]) mixed ANOVA $F_{1,70} = 474.61$; $p < 0.001$; $\eta_p{}^2 = 0.87$). All age groups demonstrated a significant face inversion effect ($p < 0.001$) (Figure 6).

Importantly, the extent of the inversion effect did not change with age. There was no significant effect of age group on the magnitude of the face inversion effect ($F_{4,70} = 0.56$; $p = 0.69$; $\eta_p{}^2 = 0.08$). This result is inconsistent with the view that healthy aging is associated with a qualitative change in face processing strategy. It seems that younger and older adults process faces in the same way, albeit with significant differences in processing efficiency.

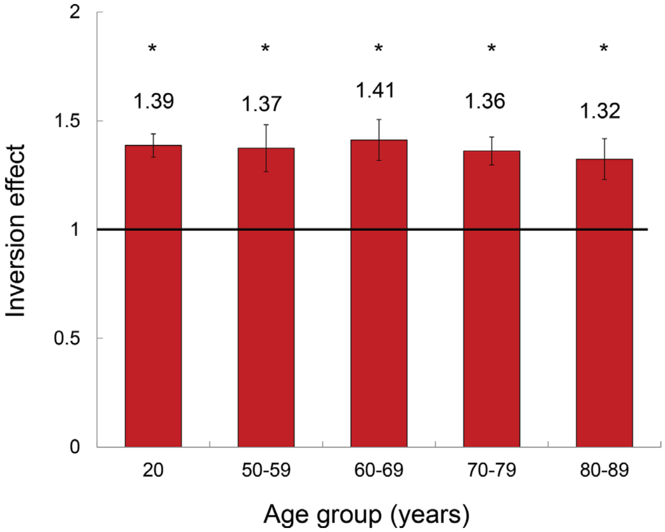

Figure 6. Healthy aging and the face inversion effect. Data are presented as threshold elevations: inverted, relative to upright, face discrimination thresholds. *Solid horizontal line* indicates line of no effect. *Asterisks* indicate significant face inversion effect ($p < 0.001$).

Discussion

In line with previous reports, the results presented here provide clear evidence that healthy aging impairs the ability to discriminate between different face identities (Boutet & Faubert, 2006; Cheng et al., 2016; Habak et al., 2008; Konar et al., 2013; Meinhardt-Injac et al., 2014). The present study, however, has provided a quantitative account of how face discrimination ability declines with age. Our data indicate that sensitivity to face identity demonstrates a continuous, age-related decline, at least after the sixth decade. Sensitivity to full-faces deteriorated by a factor of approximately 1.13 per decade after 50 years of age. The present study also revealed that healthy aging does not affect discrimination of all face features equally; sensitivity to the internal features declined approximately 3.7 times more rapidly than that for the external features.

General and specific effects of healthy aging

We aimed to separate any specific effect of healthy aging on the neural mechanisms that underlie face discrimination from general, age-related declines in cognitive functioning (e.g., memory, processing speed) (Craik & Jennings, 1992; Fraundorf et al., 2019; Salthouse, 1996) and low-level vision (Elliott, Sanderson, & Conkey, 1995). Accordingly, the task was self-paced and made no memory demands. During testing, participants were provided with their optimal, rather than habitual, refractive correction, and this correction was modified for the test distance. This is particularly important because, unlike young adults, older adults are unable to exert accommodation (i.e., adjust the refractive power of their eyes to compensate for changes in viewing distance) (Fricke, Tahhan, Resnikoff, Papas, Burnett, Ho, Naduvilath, Naidoo , 2018). Furthermore, as outlined in the introduction, spatial frequency filtering of the face stimuli was used to create a level playing field in terms of low-level vision (Wilson et al., 2002). This represents an advantage over previous studies that have used unfiltered face photographs (Boutet & Faubert, 2006; Cheng et al., 2016; Konar et al., 2013; Meinhardt-Injac et al., 2014). Using such broadband stimuli limits interpretation of an age-related decline in performance: reduced accuracy in older adults could be explained by impaired spatial resolution, specific deficiencies in the neural encoding of faces or a combination of the two (Logan et al., 2016).

Our analysis showed that, while controlling for differences in VA between age groups, a significant decline in face discrimination ability with healthy aging remained evident. That we found no age-related deficit for shape discrimination with the same paradigm indicates that differences in face discrimination sensitivity between age groups cannot be explained by general cognitive decline. Overall, we interpret the results of the present study as evidence that healthy aging specifically impairs the mechanisms which underlie the processing of face discrimination. Our finding of no effect of healthy aging on shape discrimination sensitivity is consistent with previous reports which found that discrimination thresholds for deformed circular shapes are comparable in younger and older adults (Habak, Wilkinson, & Wilson, 2009; Wang, 2001). Combined with our data for faces, this result indicates that healthy aging impacts upon certain aspects of visual function to a considerably greater extent than others.

Electrophysiological studies provide evidence of a specific effect of healthy aging on the neural substrates of different aspects of visual functioning. Specifically, single cell recording studies point to a reduction in the selectivity of neurons within regions such as V1 (Schmolesky, Wang, Pu, & Leventhal, 2000), V2 (Yu, Wang, Li, Zhou, & Leventhal, 2006) and MT (Liang, Yang, Li, Zhang, Wang, Zhou, & Leventhal, 2010) in older, relative to younger, macaques. An age-related decline in neural selectivity has also been identified within area IT of the macaque brain (Csete et al., 2015), a region that features cells that demonstrate selectivity for face information (Gross, 2008). Mirroring this age-related decline in neural selectivity with non-human primates, fMRI studies have reported that regions of the human brain which are face-selective in younger adults are engaged by both faces and other categories of object (e.g., houses) in older adults (Burianová, Lee, Grady, & Moscovitch, 2013; Park, Polk, Park, Minear, Savage, & Smith, 2004). Moreover, selectivity for face identity within the FFA is significantly reduced in older, relative to younger, adults (Goh et al., 2010; Lee et al., 2011). In line with our behavioral data, these results support the proposal that the neural mechanisms that encode face identity change with age.

Face features

Consistent with previous work (Logan et al., 2017), we identified a significant external feature advantage for unfamiliar face discrimination (Bruce, Henderson, Greenwood, Hancock, Burton, & Miller, 1999; Nachson & Shechory, 2002; Veres-Injac & Persike, 2009). Specifically, younger adults were approximately 2.2 times more sensitive to the external, relative to internal, face features. All age groups demonstrated a comparable external feature advantage: 50-59 = 2.3; 60-69 = 2.3; 70-79 = 2.6; 80-89 = 2.6. These data indicate that, when discriminating between faces, older adults used the same information as younger adults. This suggests that the older adults used the same strategy as that of the younger adults, albeit less efficiently, in extracting salient information from faces.

Furthermore, we found no effect of embedding the external or internal face features within a fixed face context. We have argued previously that this supports the view that external and internal features are processed independently (Logan et al., 2019). That all age groups demonstrated the same lack of an embedding effect for external and internal features is consistent with the premise that younger and older adults use the same face processing strategies.

A key finding of the present study is that healthy aging disproportionately reduces sensitivity to the internal face features. Specifically, sensitivity to the internal face features declined 2.8 and 3.7 times more rapidly with age than that for full-faces and external features, respectively. Internal feature discrimination requires resolution of local differences in the shapes and positions of individual features (e.g., interocular separation, nose width). Specific impairments of processing this configural face information have been identified in older adults (Chaby et al., 2011; Chard et al., 2021; Murray et al., 2010). External feature discrimination, on the other hand, is largely based on global differences in shape (e.g., head contour, hairline) (see Figure 3). In agreement with the present study, Meinhardt-Injac et al. (2014) found that sensitivity to this type of face information is significantly less impaired by healthy aging than that for the internal features.

Extending this result, our data indicate that the ability to discriminate between shapes- which could be considered as components of external features- is unaffected by aging Reduced sensitivity to the internal features may underlie the finding that healthy aging impairs the ability to match face identity across viewing angles (Habak et al., 2008). On a practical note, it is well established that older adults are considerably more likely to incorrectly identify an innocent person from a police lineup as being the perpetrator of a crime (Searcy et al., 1999). The results of the present study suggest that older adults may prove to be particularly unreliable witnesses when external feature information is obscured (e.g., the suspect is wearing a balaclava).

Holistic processing

As outlined in Section 3.4, faces are generally considered to be processed holistically, as a unified whole, rather than a collection of individual parts (Maurer et al., 2002; Richler et al., 2011; Rossion, 2013). Evidence regarding the effect of healthy aging on holistic processing is mixed. Although a number of studies found no evidence of significant differences between age groups (Boutet & Faubert, 2006; Boutet & Meinhardt-Injac, 2019; Meinhardt-Injac et al., 2014), others have reported that older adults engage holistic processing to a greater (Konar et al., 2013) or lesser (Schwarzer, Kretzer, Wimmer, & Jovanovic, 2010) extent than younger adults. These conflicting results may be partly explained by the variety of paradigms used to investigate holistic processing (e.g., the composite face and part-whole effects) and differences in how holistic processing has been defined and measured (Boutet, Taler, & Collin, 2015; J. Richler, Palmeri, & Gauthier, 2012).

The present study applied the synthetic face metric to quantitatively investigate age-related differences in holistic processing. Specifically, we measured the magnitude of the face inversion effect across different age groups. Turning a face upside-down disrupts holistic processing (Rossion, 2009). This is demonstrated by the finding that both the part-whole and composite face effects are significantly reduced for inverted, relative to upright, faces (Tanaka & Farah, 1993; Young et al., 1987). Accordingly, we reasoned that, if older adults use holistic processing to a lesser extent than younger adults, this would be reflected in a decrease in the magnitude of the face inversion effect with healthy aging. Similarly, increased holistic processing in older adults would be expected to increase the cost of face inversion.

The results of the present study indicate that the magnitude of the face inversion effect is equivalent across all of the age groups that were tested. This is in agreement with a previous report which compared the size of the face inversion effect demonstrated by younger and older adults (Boutet & Faubert, 2006).

On the other hand, Chaby et al. (2011) reported that, relative to younger adults, older adults demonstrated a smaller face inversion effect. This difference may be partly explained by differing memory demands: although the task used in the present study was memory-free, that used by Chaby and colleagues required working memory.

Overall, the results presented here for the face inversion effect are in line with the premise that older adults use holistic face processing strategies to the same extent as younger adults (Boutet & Faubert, 2006; Boutet & Meinhardt-Injac, 2019; Meinhardt-Injac et al., 2014; Meinhardt-Injac, Boutet, Persike, Meinhardt, & Imhof, 2017). Combined with our other data, this result indicates that healthy aging is associated with a quantitative, rather than qualitative, change in face processing. In particular, our data indicate that the age-related decline in face discrimination sensitivity is approximately linear in nature after the sixth decade. This suggests that healthy aging reduces the efficiency of encoding and processing face information, rather than initiating a step-change in processing strategy.

Limitations

The present study found that face discrimination ability declined monotonically after 50 years of age. Comparisons were made with data for younger adults (20-year-olds), which served as a baseline. Data were not, however, collected for intermediate age groups (30-49 years), and this could be addressed by future studies to investigate how face discrimination ability changes across the adult lifespan. The present study, though, specifically investigated declines in face discrimination ability with healthy aging. We found that differences in performance between older adults and the young adult baseline (20-year-olds) did not become significant until age 70: there was no significant difference between young adults and 50- to 59- or 60- to 69-year-old adults. Based on these data, we hypothesize that healthy aging is unlikely to significantly impair face discrimination ability between the ages of 30 to 49 years. We cannot, however, exclude the possibility that face discrimination ability continues to improve beyond the age of 20, and peaks sometime between 20 to 9 years.

We aimed to isolate any specific effect of healthy aging on face discrimination ability from the general, age-related decline in low-level vision (Elliott et al., 1995). Accordingly, participants were provided with their optimal refractive correction and spatial frequency filtering was used to accentuate the most important visual information for the face discrimination task. The effects of healthy aging on the mechanisms used for face discrimination and on low-level vision, though, are likely to be additive. As a result, the results of the present study may underestimate the difficulties encountered by older adults with everyday face discrimination. Our data should be considered as a specific quantification of the effects of healthy aging on the mechanisms that underlie face discrimination.

Synthetic faces enabled the present study to quantify the age-related decline in face discrimination ability and directly compare the effect of healthy aging on sensitivity to different face features. These simplified stimuli, however, exclude some aspects of face information, which are included in face photographs (e.g., skin texture, surface reflectance). It is important to note, however, that, despite these simplifications, synthetic faces contain sufficient information to be recognized at the level of individual identities, and across changes in viewpoint (Swystun & Logan, 2019; Wilson et al., 2002). Furthermore, there is considerable evidence that synthetic faces engage the same neural mechanisms as face photographs. For example, synthetic faces and face photographs elicit a comparable fMRI BOLD signal within the FFA (Loffler, Yourganov, Wilkinson, & Wilson, 2005). In addition, patients with developmental prosopagnosia demonstrate impaired discrimination of both synthetic faces and face photographs, but not control objects (e.g., shapes) (Lee, Duchaine, Wilson, & Nakayama, 2010; Logan et al., 2016).

Conclusions

Healthy aging was associated with a continuous, approximately linear decline in sensitivity to full-faces and face features, at least after 50 years of age. This age-related decline cannot be explained by a general decline in either low-level vision or cognitive functioning. Healthy aging did not impair sensitivity to all face features equally; sensitivity to internal features declined about three times more rapidly than that for either full-faces or external features. Older adults did, however, demonstrate the same overall pattern of sensitivity to face information as younger adults. Moreover, there was no effect of healthy aging on the magnitude of the face inversion effect. These results suggest that older adults employ the same processing strategy as younger adults, albeit less efficiently, in extracting salient information from faces. In sum, these results suggest that healthy aging reduces sensitivity within the neural mechanisms that underlie face discrimination and disproportionately impairs encoding of the internal features.

Keywords: face perception, face discrimination, healthy aging, psychophysics, face features, holistic processing

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References

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences, 4*(7), 267–278, https://doi.org/10.1016/s1364-6613(00)01501-1.

Andersen, G. J. (2012). Aging and vision: Changes in function and performance from optics to perception. *Wiley Interdisciplinary Reviews: Cognitive Science, 3*(3), 403–410, https://doi.org/10.1002/wcs.1167.

Axelrod, V., & Yovel, G. (2015). Successful decoding of famous faces in the fusiform face area. *PloS One, 10*(2), e0117126, https://doi.org/10.1371/journal.pone.0117126.

Barnes, C. S., De l'Aune, W., & Schuchard, R. A. (2011). A test of face discrimination ability in aging and vision loss. *Optometry and Vision Science, 88*(2), 188–199, https://doi.org/10.1097/OPX.0b013e318205a17c.

Bartlett, J. C., & Fulton, A. (1991). Familiarity and recognition of faces in old age. *Memory & Cognition, 19*(3), 229–238, https://doi.org/10.3758/bf03211147.

Bartlett, J. C., Leslie, J. E., Tubbs, A., & Fulton, A. (1989). Aging and memory for pictures of faces. *Psychology and Aging, 4*(3), 276–283, https://doi.org/10.1037/0882-7974.4.3.276.

Boutet, I., Shah, D. K., Collin, C. A., Berti, S., Persike, M., & Meinhardt-Injac, B. (2021). Age-related changes in amplitude, latency and specialization of ERP responses to faces and watches. *Aging, Neuropsychology, and Cognition, 28*(1), 37–64, https://doi.org/10.1080/13825585.2019.1708253.

Boutet, I., & Faubert, J. (2006). Recognition of faces and complex objects in younger and older adults. *Memory & Cognition, 34*(4), 854–864, https://doi.org/10.3758/bf03193432.

Boutet, I., & Meinhardt-Injac, B. (2019). Age differences in face processing: The role of perceptual degradation and holistic processing. *The Journals of Gerontology: Series B, 74*(6), 933–942, https://doi.org/10.1093/geronb/gbx172.

Boutet, I., Taler, V., & Collin, C. A. (2015). On the particular vulnerability of face recognition to aging: A review of three hypotheses. *Frontiers in Psychology, 6*, 1139, https://doi.org/10.3389/fpsyg.2015.01139.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*, 433–436. [PubMed]

Bruce, V., Henderson, Z., Greenwood, K., Hancock, P. J., Burton, A. M., & Miller, P. (1999). Verification of face identities from images captured on video. *Journal of Experimental Psychology: Applied, 5*(4), 339–360, https://doi.org/10.1037%2F1076-898X.5.4.339.

Burianová, H., Lee, Y., Grady, C. L., & Moscovitch, M. (2013). Age-related dedifferentiation and compensatory changes in the functional network underlying face processing. *Neurobiology of Aging, 34*(12), 2759–2767, https://doi.org/10.1016/j.neurobiolaging.2013.06.016. [PubMed]

Chaby, L., George, N., Renault, B., & Fiori, N. (2003). Age-related changes in brain responses to personally known faces: An event-related potential (ERP) study in humans. *Neuroscience Letters, 349*(2), 125–129, https://doi.org/10.1016/s0304-3940(03)00800-0.

Chaby, L., Narme, P., & George, N. (2011). Older adults' configural processing of faces: Role of second-order information. *Psychology and Aging, 26*(1), 71–79, https://doi.org/10.1037/a0020873.

Chard, J., Cook, R., & Press, C. (2021). Impaired sensitivity to spatial configurations in healthy aging. *PsyArXiv*, https://doi.org/10.31234/osf.io/h5x6g.

Cheng, Y., Shyi, G. C., & Cheng, P. (2016). Age differences in face memory and face processing between younger and older adults in Taiwan. *Chinese J.Psychol, 58*, 233–262, https://doi.org/10.6129/CJP.20161008.

Craik, F. I. M., & Jennings, J. M. (1992). Human memory. In F. I. M. Craik, & T. A. Salthouse (Eds.), *The handbook of aging and cognition* (pp. 51–110). Mahwah, NJ: Lawrence Erlbaum Associates, Inc.

Cronin-Golomb, A., Gilmore, G. C., Neargarder, S., Morrison, S. R., & Laudate, T. M. (2007). Enhanced stimulus strength improves visual cognition in aging and Alzheimer's disease. *Cortex, 43*(7), 952–966, https://doi.org/10.1016/s0010-9452(08)70693-2.

Crook, T. H., III, & Larrabee, G. J. (1992). Changes in facial recognition memory across the adult life span. *Journal of Gerontology, 47*(3), 138–141, https://doi.org/10.1093/geronj/47.3.p138.

Csete, G., Bognár, A., Csibri, P., Kaposvári, P., & Sáry, G. (2015). Aging alters visual processing of objects and shapes in inferotemporal cortex in monkeys. *Brain Research Bulletin, 110*, 76–83, https://doi.org/10.1016/j.brainresbull.2014.11.005.

Daniel, S., & Bentin, S. (2012). Age-related changes in processing faces from detection to identification: ERP evidence. *Neurobiology of Aging, 33*(1), 206. e1-206. e28, https://doi.org/10.1016/j.neurobiolaging.2010.09.001.

Elliott, D. B., Yang, K. C., & Whitaker, D. (1995). Visual acuity changes throughout adulthood in normal, healthy eyes: Seeing beyond 6/6. *Optometry and Vision Science: Official Publication of the American Academy of Optometry, 72*(3), 186–191, https://doi.org/10.1097/00006324-199503000-00006.

Elliott, D.B., Sanderson, K., & Conkey, A. (1990). The reliability of the Pelli-Robson contrast sensitivity chart. *Ophthalmic and Physiological Optics, 10*(1), 21–24, https://doi.org/10.1111/j.1475-1313.1990.tb01100.x.

Elliott, D.B., Whitaker, D., & MacVeigh, D. (1990). Neural contribution to spatiotemporal contrast sensitivity decline in healthy aging eyes. *Vision Research, 30*(4), 541–547, https://doi.org/10.1016/0042-6989(90)90066-t.

Ferris, F. L., III, Kassoff, A., Bresnick, G. H., & Bailey, I. (1982). New visual acuity charts for clinical research. *American Journal of Ophthalmology, 94*(1), 91–96, https://doi.org/10.1016/0002-9394(82)90197-0.

Fiorentini, A., Maffei, L., & Sandini, G. (1983). The role of high spatial frequencies in face perception. *Perception, 12*(2), 195–201, https://doi.org/10.1068/p120195.

Firestone, A., Turk-Browne, N. B., & Ryan, J. D. (2007). Age-related deficits in face recognition are related to underlying changes in scanning behavior. *Aging, Neuropsychology, and Cognition, 14*(6), 594–607, https://doi.org/10.1080/13825580600899717.

Fraundorf, S. H., Hourihan, K. L., Peters, R. A., & Benjamin, A. S. (2019). Aging and recognition memory: A meta-analysis. *Psychological Bulletin, 145*(4), 339–371, https://doi.org/10.1037/bul0000185.

Fricke, T. R., Tahhan, N., Resnikoff, S., Papas, E., Burnett, A., & Ho, S. M., . . .Naidoo, K. S. (2018). Global prevalence of presbyopia and vision impairment from uncorrected presbyopia: Systematic review, meta-analysis, and modelling. *Ophthalmology, 125*(10), 1492–1499, https://doi.org/10.1016/j.ophtha.2018.04.013.

Gao, L., Xu, J., Zhang, B., Zhao, L., Harel, A., & Bentin, S. (2009). Aging effects on early-stage face perception: An ERP study. *Psychophysiology, 46*(5), 970–983, https://doi.org/10.1111/j.1469-8986.2009.00853.x.

Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). The fusiform "face area" is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience, 12*(3), 495–504, https://doi.org/10.1162/089892900562165.

Germine, L. T., Duchaine, B., & Nakayama, K. (2011). Where cognitive development and aging meet: Face learning ability peaks after age 30. *Cognition, 118*(2), 201–210, https://doi.org/10.1016/j.cognition.2010.11.002.

Goh, J. O., Suzuki, A., & Park, D. C. (2010). Reduced neural selectivity increases fMRI adaptation with age during face discrimination. *NeuroImage, 51*(1), 336–344, https://doi.org/10.1016/j.neuroimage.2010.01.107.

Grady, C. L., Randy McIntosh, A., Horwitz, B., & Rapoport, S. I. (2000). Age-related changes in the neural correlates of degraded and nondegraded face processing. *Cognitive Neuropsychology, 17*(1-3), 165–186, https://doi.org/10.1080/026432900380553.

Grill-Spector, K., & Malach, R. (2001). fMR-adaptation: A tool for studying the functional properties of human cortical neurons. *Acta Psychologica, 107*(1-3), 293–321, https://doi.org/10.1016/s0001-6918(01)00019-1.

Gross, C. G. (2008). Single neuron studies of inferior temporal cortex. *Neuropsychologia, 46*(3), 841–852, https://doi.org/10.1016/j.neuropsychologia.2007.11.009.

Guirao, A., Gonzalez, C., Redondo, M., Geraghty, E., Norrby, S., & Artal, P. (1999). Average optical performance of the human eye as a function of age in a normal population. *Investigative Ophthalmology & Visual Science, 40*(1), 203–213. [PubMed]

Habak, C., Wilkinson, F., & Wilson, H. R. (2008). Aging disrupts the neural transformations that link facial identity across views. *Vision Research, 48*(1), 9–15, https://doi.org/10.1016/j.visres.2007.10.007.

Habak, C., Wilkinson, F., & Wilson, H. R. (2009). Preservation of shape discrimination in aging. *Journal of Vision, 9*(12), 18, https://doi.org/10.1167/9.12.18.

Hayes, G. S., McLennan, S. N., Henry, J. D., Phillips, L. H., Terrett, G., Rendell, P. G., . . . Labuschagne, I. (2020). Task characteristics influence facial emotion recognition age-effects: A meta-analytic review. *Psychology and Aging, 35*(2), 295–315, https://doi.org/10.1037/pag0000441.

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*(11), 4302–4311, https://doi.org/10.1523/JNEUROSCI.17-11-04302.1997.

Kanwisher, N., & Yovel, G. (2006). The fusiform face area: A cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society B: Biological Sciences, 361*(1476), 2109–2128, https://doi.org/10.1098/rstb.2006.1934.

Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in psychtoolbox-3? *Perception, 36*, 14.

Konar, Y., Bennett, P. J., & Sekuler, A. B. (2013). Effects of aging on face identification and holistic face processing. *Vision Research, 88*, 38–46, https://doi.org/10.1016/j.visres.2013.06.003.

Lee, Y., Duchaine, B., Wilson, H. R., & Nakayama, K. (2010). Three cases of developmental prosopagnosia from one family: Detailed neuropsychological and psychophysical investigation of face processing. *Cortex, 46*(8), 949–964, https://doi.org/10.1016/j.cortex.2009.07.012.

Lee, Y., Grady, C. L., Habak, C., Wilson, H. R., & Moscovitch, M. (2011). Face processing changes in normal aging revealed by fMRI adaptation. *Journal of Cognitive Neuroscience, 23*(11), 3433–3447, https://doi.org/10.1162/jocn_a_00026.

Lee, Y., Matsumiya, K., & Wilson, H. R. (2006). Size-invariant but viewpoint-dependent representation of faces. *Vision Research, 46*(12), 1901–1910, https://doi.org/10.1016/j.visres.2005.12.008.

Liang, Z., Yang, Y., Li, G., Zhang, J., Wang, Y., Zhou, Y., . . . Leventhal, A. G. (2010). Aging affects the direction selectivity of MT cells in rhesus monkeys. *Neurobiology of Aging, 31*(5), 863–873, https://doi.org/10.1016/j.neurobiolaging.2008.06.013.

Loffler, G., Yourganov, G., Wilkinson, F., & Wilson, H. R. (2005). fMRI evidence for the neural representation of faces. *Nature Neuroscience, 8*(10), 1386–1391, https://doi.org/10.1038/nn1538.

Logan, A. J., Gordon, G. E., & Loffler, G. (2017). Contributions of individual face features to face discrimination. *Vision Research, 137*, 29–39, https://doi.org/10.1016/j.visres.2017.05.011.

Logan, A. J., Gordon, G. E., & Loffler, G. (2019). From individual features to full faces: Combining aspects of face information. *Journal of Vision, 19*(4), 23, https://doi.org/10.1167/19.4.23.

Logan, A. J., Gordon, G. E., & Loffler, G. (2020). The effect of age-related macular degeneration on components of face perception. *Investigative Ophthalmology & Visual Science, 61*(6), 38, https://doi.org/10.1167/iovs.61.6.38.

Logan, A. J., Wilkinson, F., Wilson, H. R., Gordon, G. E., & Loffler, G. (2016). The Caledonian face test: A new test of face discrimination. *Vision Research, 119*, 29–41, https://doi.org/10.1016/j.visres.2015.11.003.

Lott, L. A., Haegerstrom-Portnoy, G., Schneck, M., & Brabyn, J. A. (2005). Face recognition in the elderly. *Optometry and Vision Science, 82*(10), 874–881, https://doi.org/10.1097/01.opx.0000180764.68737.91.

Mäntyjärvi, M., & Laitinen, T. (2001). Normal values for the Pelli-Robson contrast sensitivity test. *Journal of Cataract & Refractive Surgery, 27*(2), 261–266, https://doi.org/10.1016/S0886-3350(00)00562-9.

Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences, 6*(6), 255–260, https://doi.org/10.1016/s1364-6613(02)01903-4.

Maylor, E. A., & Valentine, T. (1992). Linear and nonlinear effects of aging on categorizing and naming faces. *Psychology and Aging, 7*(2), 317–323, https://doi.org/10.1037//0882-7974.7.2.317.

McCulloch, D. L., Loffler, G., Colquhoun, K., Bruce, N., Dutton, G. N., & Bach, M. (2011). The effects of visual degradation on face discrimination. *Ophthalmic and Physiological Optics, 31*(3), 240–248, https://doi.org/10.1111/j.1475-1313.2011.00828.x.

McKendrick, A. M., Weymouth, A. E., & Battista, J. (2010). The effect of normal aging on closed contour shape discrimination. *Journal of Vision, 10*(2), 1, https://doi.org/10.1167/10.2.1.

Megreya, A. M., & Bindemann, M. (2015). Developmental improvement and age-related decline in unfamiliar face matching. *Perception, 44*(1), 5–22, https://doi.org/10.1068/p7825.

Meinhardt-Injac, B., Boutet, I., Persike, M., Meinhardt, G., & Imhof, M. (2017). From development to aging: Holistic face perception in children, younger and older adults. *Cognition, 158*, 134–146, https://doi.org/10.1016/j.cognition.2016.10.020.

Meinhardt-Injac, B., Persike, M., Imhof, M., & Meinhardt, G. (2015). The sensitivity to replacement and displacement of the eyes region in early adolescence, young and later adulthood. *Frontiers in Psychology, 6*, 1164, https://doi.org/10.3389/fpsyg.2015.01164.

Meinhardt-Injac, B., Persike, M., & Meinhardt, G. (2014). Holistic processing and reliance on global viewing strategies in older adults' face perception. *Acta Psychologica, 151*, 155–163, https://doi.org/10.1016/j.actpsy.2014.06.001.

Memon, A., & Bartlett, J. (2002). The effects of verbalization on face recognition in young and older adults. *Applied Cognitive Psychology: The Official Journal of the Society for Applied Research in Memory and Cognition, 16*(6), 635–650, https://doi.org/10.1002/acp.820.

Murray, J. E., Halberstadt, J., & Ruffman, T. (2010). The face of aging: Sensitivity to facial feature relations changes with age. *Psychology and Aging, 25*(4), 846, https://doi.org/10.1037/a0019864.

Nachson, I., & Shechory, M. (2002). Effect of inversion on the recognition of external and internal facial features. *Acta Psychologica, 109*(3), 227–238, https://doi.org/10.1016/s0001-6918(01)00058-0.

Näsänen, R. (1999). Spatial frequency bandwidth used in the recognition of facial images. *Vision Research, 39*(23), 3824–3833, https://doi.org/10.1016/s0042-6989(99)00096-6.

Nasreddine, Z. S., Phillips, N. A., Bédirian, V., Charbonneau, S., Whitehead, V., & Collin, I., . . .Chertkow, H. (2005). The Montreal cognitive assessment, MoCA: A brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society, 53*(4), 695–699, https://doi.org/10.1111/j.1532-5415.2005.53221.x.

Nguyen, B. N., & McKendrick, A. M. (2016). Visual contextual effects of orientation, contrast, flicker, and luminance: All are affected by normal aging. *Frontiers in Aging Neuroscience, 8*, 79, https://doi.org/10.3389/fnagi.2016.00079.

Norton, D., McBain, R., & Chen, Y. (2009). Reduced ability to detect facial configuration in middle-aged and elderly individuals: Associations with spatiotemporal visual processing. *Journals of Gerontology: Series B, 64*(3), 328–334, https://doi.org/10.1093/geronb/gbp008.

Owsley, C., Sekuler, R., & Siemsen, D. (1983). Contrast sensitivity throughout adulthood. *Vision Research, 23*(7), 689–699, https://doi.org/10.1016/0042-6989(83)90210-9.

Owsley, C., & Sloane, M. E. (1987). Contrast sensitivity, acuity, and the perception of 'real-world 'targets. *British Journal of Ophthalmology, 71*(10), 791–796, https://doi.org/10.1136/bjo.71.10.791.

Park, D. C., Lautenschlager, G., Hedden, T., Davidson, N. S., Smith, A. D., & Smith, P. K. (2002). Models of visuospatial and verbal memory across the adult life span. *Psychology and Aging, 17*(2), 299–320, https://doi.org/10.1037/0882-7974.17.2.299.

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, 101*(35), 13091–13095, https://doi.org/10.1073/pnas.0405148101.

Pelli, D. G., & Robson, J. G. (1988). The design of a new letter chart for measuring contrast sensitivity. *Clinical Vision Sciences, 2*, 187–199

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*, 437–442. [PubMed]

Rhodes, R. E., & Katz, B. (2017). Working memory plasticity and aging. *Psychology and Aging, 32*(1), 51–59, https://doi.org/10.1037/pag0000135.

Richler, J. J., Cheung, O. S., & Gauthier, I. (2011). Holistic processing predicts face recognition. *Psychological Science, 22*(4), 464–471, https://doi.org/10.1177/0956797611401753.

Richler, J. J., & Gauthier, I. (2014). A meta-analysis and review of holistic face processing. *Psychological Bulletin, 140*(5), 1281–1302, https://doi.org/10.1037/a0037004.

Richler, J., Palmeri, T. J., & Gauthier, I. (2012). Meanings, mechanisms, and measures of holistic processing. *Frontiers in Psychology, 3*, 553, https://doi.org/10.3389/fpsyg.2012.00553.

Robbins, R., & McKone, E. (2007). No face-like processing for objects-of-expertise in three behavioural tasks. *Cognition, 103*(1), 34–79, https://doi.org/10.1016/j.cognition.2006.02.008.

Rossion, B. (2008). Picture-plane inversion leads to qualitative changes of face perception. *Acta Psychologica, 128*(2), 274–289, https://doi.org/10.1016/j.actpsy.2008.02.003.

Rossion, B. (2009). Distinguishing the cause and consequence of face inversion: The perceptual field hypothesis. *Acta Psychologica, 132*(3), 300–312, https://doi.org/10.1016/j.actpsy.2009.08.002.

Rossion, B. (2013). The composite face illusion: A whole window into our understanding of holistic face perception. *Visual Cognition, 21*(2), 139–253, https://doi.org/10.1080/13506285.2013.772929.

Ruffman, T., Henry, J. D., Livingstone, V., & Phillips, L. H. (2008). A meta-analytic review of emotion recognition and aging: Implications for neuropsychological models of aging. *Neuroscience & Biobehavioral Reviews, 32*(4), 863–881, https://doi.org/10.1016/j.neubiorev.2008.01.001.

Salthouse, T. A. (1996). The processing-speed theory of adult age differences in cognition. *Psychological Review, 103*(3), 403–428, https://doi.org/10.1037/0033-295x.103.3.403.

Schmolesky, M. T., Wang, Y., Pu, M., & Leventhal, A. G. (2000). Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. *Nature Neuroscience, 3*(4), 384–390, https://doi.org/10.1038/73957.

Schwarzer, G., Kretzer, M., Wimmer, D., & Jovanovic, B. (2010). Holistic face processing among school children, younger and older adults. *European Journal of Developmental Psychology, 7*(4), 511–528, https://doi.org/10.1080/17405620903003697.

Searcy, J. H., Bartlett, J. C., & Memon, A. (1999). Age differences in accuracy and choosing in eyewitness identification and face recognition. *Memory & Cognition, 27*(3), 538–552, https://doi.org/10.3758/bf03211547.

Slessor, G., Phillips, L. H., & Bull, R. (2008). Age-related declines in basic social perception: Evidence from tasks assessing eye-gaze processing. *Psychology and Aging, 23*(4), 812–822, https://doi.org/10.1037/a0014348.

Slessor, G., Riby, D. M., & Finnerty, A. N. (2013). Age-related differences in processing face configuration: The importance of the eye region. *Journals of Gerontology Series B: Psychological Sciences and Social Sciences, 68*(2), 228–231, https://doi.org/10.1093/geronb/gbs059.

Snowden, R. J., & Kavanagh, E. (2006). Motion perception in the aging visual system: Minimum motion, motion coherence, and speed discrimination thresholds. *Perception, 35*(1), 9–24, https://doi.org/10.1068/p5399. [PubMed]

Swystun, A. G., & Logan, A. J. (2019). Quantifying the effect of viewpoint changes on sensitivity to face identity. *Vision Research, 165*, 1–12, https://doi.org/10.1016/j.visres.2019.09.006.

Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *The Quarterly Journal of Experimental Psychology, 46*(2), 225–245, https://doi.org/10.1080/14640749308401045. [PubMed]

Thomas, C., Moya, L., Avidan, G., Humphreys, K., Jung, K. J., Peterson, M. A., … Behrmann, M. (2008). Reduction in white matter connectivity, revealed by diffusion tensor imaging, may account for age-related changes in face perception. *Journal of Cognitive Neuroscience, 20*(2), 268–284, https://doi.org/10.1162/jocn.2008.20025.

Tyler, C. W. (1989). Two processes control variations in flicker sensitivity over the life span. *Josa A, 6*(4), 481–490, https://doi.org/10.1364/josaa.6.000481.

Valentine, T., & Bruce, V. (1986). The effect of race, inversion and encoding activity upon face recognition. *Acta Psychologica, 61*(3), 259–273, https://doi.org/10.1016/0001-6918(86)90085-5.

Veres-Injac, B., & Persike, M. (2009). Recognition of briefly presented familiar and unfamiliar faces. *Psihologija, 42*(1), 47–66, https://doi.org/10.2298/PSI0901047V.

Wang, Y. (2001). Effects of aging on shape discrimination. *Optometry and Vision Science, 78*(6), 447–454, https://doi.org/10.1097/00006324-200106000-00019.

Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics, 33*(2), 113–120, https://doi.org/10.3758/bf03202828.

Wilson, H. R., Loffler, G., & Wilkinson, F. (2002). Synthetic faces, face cubes, and the geometry of face space. *Vision Research, 42*(27), 2909–2923, https://doi.org/10.1016/s0042-6989(02)00362-0.

Wilson, H. R., & Wilkinson, F. (2002). Symmetry perception: A novel approach for biological shapes. *Vision Research, 42*(5), 589–597, https://doi.org/10.1016/s0042-6989(01)00299-1.

Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology, 81*(1), 141, https://doi.org/10.1037/h0027474.

Young, A. W., Hellawell, D., & Hay, D. C. (1987). Configurational information in face perception. *Perception, 16*(747–759), 1166–1178, https://doi.org/10.1068/p160747n [PubMed]

Yu, S., Wang, Y., Li, X., Zhou, Y., & Leventhal, A. G. (2006). Functional degradation of extrastriate visual cortex in senescent rhesus monkeys. *Neuroscience, 140*(3), 1023–1029, https://doi.org/10.1016/j.neuroscience.2006.01.015.