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Effects of Age on Face Perception: Reduced Eye Region Discrimination Ability but Intact Holistic Processing

Regan Fry[1, 2], James W. Tanaka[3], Sarah Cohan[4, 5], Jeremy B. Wilmer[6],
Laura T. Germine[2, 7], and Joseph DeGutis[1, 2]
[1] Boston Attention and Learning Laboratory, VA Boston Healthcare System, Boston, Massachusetts, United States
[2] Department of Psychiatry, Harvard Medical School
[3] Department of Psychology, University of Victoria
[4] Vision Sciences Laboratory, Department of Psychology, Harvard University
[5] Department of Population Medicine, Harvard Medical School and Harvard Pilgrim Health Care Institute
[6] Department of Psychology, Wellesley College
[7] Institute for Technology in Psychiatry, McLean Hospital, Belmont, Massachusetts, United States

While age-related decline in face recognition memory is well-established, the degree of decline in face perceptual abilities across the lifespan and the underlying mechanisms are incompletely characterized. In the present study, we used the part-whole task to examine lifespan changes in holistic and featural processing. After studying an intact face, participants are tested for memory of a face part (eyes, nose, mouth) with the target and foil part presented either in isolation or in the context of the whole face. To the extent that parts are encoded into a holistic face representation, an advantage is expected for part recognition when tested in the whole face condition. The task therefore provides measures of holistic processing (whole-over-isolated-part trial advantage) and featural processing for each part when tested in isolation. Using a large sample of 3,341 online participants aged 18–69 years, we found that while discrimination of the eye region decreased beginning in the 50s, both mouth discrimination accuracy and the holistic advantage of whole versus part trial discrimination were stable with age. In separate analyses by gender, we found that age-related declines in eye region accuracy were more pronounced in males than females. We discuss potential mechanistic explanations for this eye region-specific decline with age, including age-related hearing loss directing attention toward the mouth. Further, we discuss how this could be related to the age-related positivity effect, which is associated with reduced sensitivity to eye-related emotions (e.g., anger) but preserved mouth-related emotion sensitivity (e.g., happiness).

Public Significance Statement

The present study had 3,341 participants aged 18–69 years perform a task measuring the ability to process faces as a "whole" and sensitivity to facial feature changes. The results demonstrated that holistic face processing and sensitivity to the mouth region remained stable across the lifespan while eye region discrimination ability significantly declined, starting in the 50s. These age-related declines in eye region accuracy were more pronounced in males than in females. These results may help explain changes in social cognition with age, including challenges in learning new faces and slightly decreased sensitivity to emotions that involve the eye region, such as anger and sadness.

Keywords: holistic processing, aging, face recognition, eye processing

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The decline in face recognition ability with age has been consistently observed (Ferris et al., 1980; Germine et al., 2011; Lamont et al., 2005; Norton et al., 2009; Obermeyer et al., 2012; Smith & Winograd, 1978), and comparisons between younger (18–35) and older adults (65+) have been associated with large effect sizes (face learning and immediate memory, Cohen's $d = 1.46$; delayed recognition, Cohen's $d = 1.77$, Hildebrandt et al., 2010). These declines in face recognition ability in older adults are independent of general age-related cognitive decline

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Regan Fry https://orcid.org/0000-0001-6002-626X
Jeremy B. Wilmer https://orcid.org/0000-0003-1526-4271
Laura T. Germine https://orcid.org/0000-0001-8690-8412
Joseph DeGutis https://orcid.org/0000-0002-7148-9654

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Correspondence concerning this article should be addressed to Joseph DeGutis, Boston Attention and Learning Laboratory, VA Boston Healthcare System, 150 South Huntington Avenue, 182JP, Boston, MA 02130, United States. Email: degutis@wjh.harvard.edu

(Boutet & Meinhardt-Injac, 2021; Boutet et al., 2015; Hildebrandt et al., 2011) and are more pronounced for upright faces than for other visual recognition tasks including objects (Boutet & Faubert, 2006; Meinhardt-Injac et al., 2014) and inverted faces (Boutet & Faubert, 2006). This suggests that age-related declines in general visual recognition and/or general perceptual abilities are unlikely to be the sole contributing factor(s) to worsening face recognition. In younger adults, poor recognition of both familiar and unfamiliar faces has been associated with greater social anxiety (Davis et al., 2011), and it is possible that older adults, who are already vulnerable to social isolation and loneliness (Cudjoe et al., 2020), may have an increased risk for worse functional outcomes due to worsening face recognition ability (Shankar et al., 2017). Despite research showing impaired face recognition in older adults, the specific mechanisms of age-related changes in face perception, a crucial contributor to declines in face recognition performance (Stantic et al., 2021), are currently under debate. While studies have found age-related decline in face perception abilities, including the ability to accurately detect (Carbon et al., 2013) and match/discriminate unfamiliar faces (Grady et al., 2000; Owsley et al., 1981; Stantic et al., 2021), the exact nature of these impairments is still unclear. The goal of the present study was to use a large web-based sample ($N = 3{,}341$) to better characterize changes in face perception across the lifespan by focusing on holistic face processing and investigating differential feature discrimination of both the eye and mouth regions separately.

Holistic processing and feature discrimination ability are two important aspects of face perception (Cabeza & Kato, 2000; Sergent, 1984; Taubert et al., 2011). The holistic face perception hypothesis proposes that upright faces are automatically processed as an integrated “whole,” rather than simply as a collection of parts (Farah et al., 1998; Richler & Gauthier, 2014; though inverted faces may *eventually* be processed holistically, see Richler, Mack, et al., 2011, also see Gold et al., 2012). Behavioral evidence for holistic face processing comes from the (a) face inversion effect, where an inverted face is less efficiently processed than an upright face (FIE; Yin, 1969), (b) composite face effect, where the alignment of two different face halves makes it more difficult to selectively attend to an individual face half (CFE; Young et al., 1987), and (c) part-whole effect (PWE; Tanaka & Farah, 1993), the phenomenon where, after studying a whole face, recognition of a facial feature improves when the feature is viewed in the context of the whole face rather than when viewed in isolation. Several studies in younger adults have found that greater holistic processing is associated with both better face perception ability (Rezlescu et al., 2017) and better face recognition ability (DeGutis et al., 2013; Richler, Cheung, & Gauthier, 2011; though see Konar et al., 2010) across both familiar and unfamiliar faces (Ramon et al., 2016; Rossion, 2018). One study found that the holistic processing/face recognition association was even more pronounced in older than younger adults (Konar et al., 2013).

Studies have consistently shown that holistic processing, as measured by part-whole and inversion tasks, develops as early as preschool age (Pellicano et al., 2006; Pellicano & Rhodes, 2003; Tanaka et al., 1998). However, the pattern of holistic processing in adulthood through older age is less clear, perhaps due to studies using a variety of tasks measuring different aspects of holistic processing (and having low between-task correlations, e.g., part-whole vs. composite, $r = .05$, Rezlescu et al., 2017, though see DeGutis et al., 2013). Many studies have found a similar magnitude of the CFE (Boutet & Meinhardt-Injac, 2019; Konar et al., 2013; Meinhardt-Injac et al., 2017) and FIE (Boutet & Faubert, 2006; Bowles et al., 2009) in younger and older adults, while others have failed to find either an FIE (Chaby et al., 2011) or CFE (Boutet & Faubert, 2006) in older adults, despite demonstrating robust effects in younger adults. In terms of the PWE, a 2006 study found that while general face recognition was reduced in older adults, older and younger adults had a similar holistic whole-over-part trial advantage (Boutet & Faubert, 2006). One potential explanation for these inconsistent holistic processing results in older adults could be the way holistic processing is measured. Measures of holistic processing often have little to no correlation with one another (Boutet et al., 2021; Rezlescu et al., 2017; for an exception, see DeGutis et al., 2013), indicating that they may reflect distinct mechanisms. The CFE, which operationalizes holistic processing as a failure of selective attention, has more often failed to show significant associations with overall face matching ability (e.g., Rezlescu et al., 2017; Verhallen et al., 2017). In contrast, the PWE, which operationalizes holistic processing as the degree to which “the whole is greater than the sum of its parts,” and the FIE, which quantifies the degree of specialized face processing that is recruited for upright versus inverted faces, have consistently found significant holistic/face matching individual differences associations (e.g., Rezlescu et al., 2017). A benefit of the part-whole task is its ability to more specifically measure holistic processing, whereas the face inversion effect may also reflect other mechanisms (e.g., feature processing, see McKone & Yovel, 2009). Additionally, the part-whole task can be used to separately quantify feature discrimination ability (e.g., using part trials) and holistic processing of separate features (e.g., by examining the holistic advantage for each feature, DeGutis et al., 2012).

Featural processing is another important and dissociable aspect of face processing (Berger et al., 2022; Cabeza & Kato, 2000) and it is currently debated whether aging is associated with a general decline in featural processing, no decline, or a facial feature-specific decline. The importance of the eye region for face recognition has been well-documented (Peterson & Eckstein, 2012; Royer et al., 2018; Tardif et al., 2019), and Slessor et al. (2013) found that, compared to younger adults, older adults were significantly less sensitive to spacing changes within the eye region (e.g., change in distance between the eyes) but did not differ from younger adults in their sensitivity to mouth region changes (e.g., change in distance between the nose and mouth). Consistent with this, using classification images during a simultaneous face matching task, Creighton et al. (2019) found that their older adult group used the eye/eyebrow region less consistently than younger adults. Older adults have also demonstrated decreased viewing of the eye region compared to younger adults, with more time spent viewing the nose and mouth regions (Firestone et al., 2007). Sullivan et al. (2007) also found that older adults were significantly worse at recognizing eye-dependent emotions (anger, sadness, fear) and that older males showed additionally reduced time looking at the eye region compared to older females. In contrast to these studies showing eye-specific deficits with age, Murray et al. (2010) found that older adults performed similarly to younger adults at perception of featurally distorted faces regardless of whether the eye or mouth region was distorted. However, the distortions they included were quite pronounced, suggesting that the task may have lacked sensitivity. Finally, regarding facial features, spatial frequency information has shown to range from low (broad, spacing information among features) to high (fine-grained feature details; Rotshtein et al., 2007). Boutet and Meinhardt-Injac (2019) found that, compared to younger adults, middle-aged, and older adults had particularly impaired face discrimination ability when shown only high-spatial frequency (HSF) information. This suggests that age-related reductions in face perception could be specific to HSF information and may therefore affect the perception of fine-grained changes to all facial features. A goal of the present study was to better understand the feature specificity versus generality of potential face perception declines with age through separately examining eye and mouth performance across the lifespan.

Gender differences in face processing are widely reported and may further illuminate the mechanisms underlying age-related changes in face perception. Females have been shown to generally outperform males on tasks of face perception (Bowles et al., 2009), face recognition (Herlitz & Lovén, 2013; Mishra et al., 2019), and face emotion recognition (J. A. Hall, 1978; J. K. Hall et al., 2010). A recent study by Knudsen et al. (2021) suggests this advantage is not likely to be due to differences in holistic processing, as both male and female participants showed similar-sized face inversion effects during face perception and recognition. Notably, females have been shown to attend to and use the eye region more compared to males during emotion recognition (J. K. Hall et al., 2010), and this female eye advantage may be greater in older than younger adults (Sullivan et al., 2007). Despite these effects observed during emotion recognition, gender differences in featural and holistic processing and their relation to age-related changes have yet to be investigated during a nonemotional face perception task and this was an exploratory aim of the present study.

The goal of the present study was to compare the relationship between age, eye, and mouth feature sensitivity, and holistic processing across the lifespan using the part-whole task (Tanaka et al., 2004) in a large online sample ($N = 3{,}341$) from the https://TestMyBrain.org website. TestMyBrain.org has previously been used to investigate age-related differences in cognition, and its samples have replicated several findings from more traditional in-lab studies (e.g., Hartshorne & Germine, 2015). TestMyBrain.org has also previously been used to effectively examine age-related changes in face processing, specifically face recognition (Germine et al., 2011; Susilo et al., 2013) and facial emotion recognition (Hartshorne & Germine, 2015; Rutter et al., 2019). By using a much larger sample size than previous studies and including ages ranging from 18 to 69 years, we could more thoroughly investigate the patterns of holistic processing and eye and mouth feature sensitivity across the lifespan and determine whether an interaction exists between aging and gender in terms of holistic and featural processing. Based on the previous finding that the part-whole holistic advantage was similar in younger and older adults (Boutet & Faubert, 2006), we predicted a similar pattern in our larger sample. Though the stimuli used to examine age-related differences in the present study included variations of younger male and female Caucasian and Asian faces, notably, studies have suggested that middle-aged and older adults perform similarly with own-age and younger faces (e.g., Wolff et al., 2012, though see Wiese et al., 2012), suggesting that any age-related processing differences we observed are not likely due to the own-age bias. We hypothesized that there would be differential effects in the eye versus the mouth region with age, based on the theory that older adults attend less to and have less sensitivity to the eye region across both emotional and nonemotional face tasks. Finally, in terms of potential gender differences, based on the theory that older females attend to and use the eye region more than males (J. K. Hall et al., 2010; Sullivan et al., 2007), we predicted that older females would outperform males in featural processing of the eye region.

Method

Transparency and Openness

The study design, analytic plan, and hypotheses were not preregistered. The stimuli/paradigm, deidentified data, and analysis code are all available in an Open Science Framework repository (see author note).

Participants

Participants were 3,341 online visitors to https://TestMyBrain.org, a cognitive testing website, and data were collected during the summer of 2013 (2,428 females—72.7%, $M_{\text{age}} = 33.9$, $SD = 12.9$). The ages of participants ranged from 18 to 69 years (for a distribution, see Supplemental Figure S1) and were located in the United States. Three participants declined to state their gender (only male or female options were provided) and were excluded from the gender analyses. Before participating, all subjects provided informed consent according to the guidelines set by the Committee on the Use of Human Subjects at Harvard University and the Wellesley College Institutional Review Board (Protocol No. 15795, web-based behavioral experiments to understand human variation).

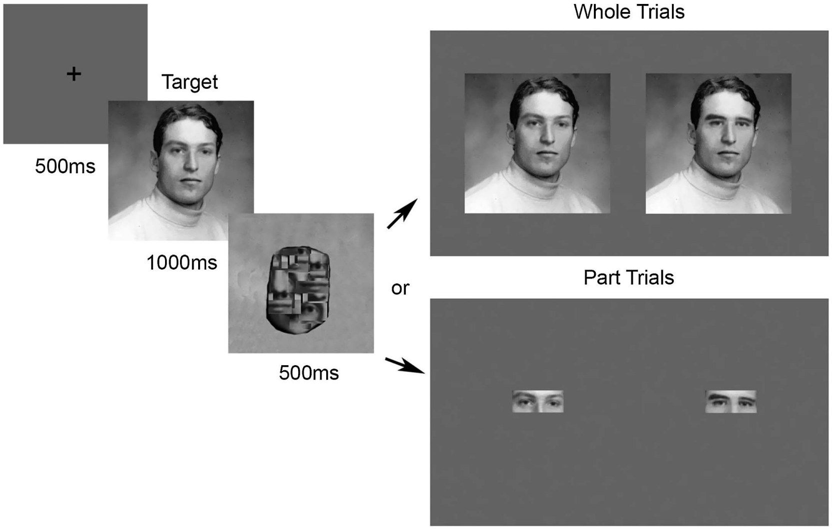
Our sample size was guided by the previous studies characterizing age-related face processing differences (Rutter et al., 2019; Susilo et al., 2013) as well as individual differences studies in face recognition (Wilmer et al., 2012). Given that Susilo et al. (2013) found significant face recognition changes from the ages of 18–33 using sample sizes of 2,032 ($r = .075$) and 1,055 ($r = .086$), Rutter et al. (2019) found a relationship between age and facial emotion sensitivity (R^2 ranging from .03 to .06), and Wilmer et al. (2012) found dissociations between face recognition and more general visual and verbal abilities using a sample size of 1,471, we used a similar-sized sample of 3,341 to examine changes in face perception across the lifespan.

Using our sample size of 3,341, we performed age-related sensitivity analyses for our continuous regression as well as analysis of variance (ANOVA) approaches using five and 13 bins. We found that for the regression approach assuming three predictors (stimulus version, age, and age^2) and using $\alpha = .05$, we would have .80 power to detect an age effect size of Cohen's $f^2 = .0029$ (where small Cohen's $f^2 \geq .02$, medium $\geq .15$, large ≥ 35). For the ANOVAs with five age bins, using $\alpha = .05$ we would have .80 power to detect an effect size of Cohen's $f = .060$ (where small Cohen's $f \geq .10$, medium $\geq .25$, large $\geq .40$). For the ANOVAs with 13 age bins, using $\alpha = .05$, we would have .80 power to detect an effect size of Cohen's $f = .072$. Thus, the current sample should be adequate to allow us to detect very small to small effects.

Part-Whole Task

Participants were randomly assigned to one of four versions of the part-whole task from Tanaka et al. (2004): Asian female, Asian male, Caucasian female, or Caucasian male. For each part-whole version, different target faces were created by modifying a grayscale face template, generated from digitally scanned college yearbook photographs, by changing the eyes, nose, and mouth features to create six unique target faces for each stimulus version. For "whole" face trials, foils for the target were created by switching one of the

Figure 1
Part-Whole Task Procedure



Note. On each trial a target face was presented for 1,000 ms, then a brief 500 ms mask, then either a part or whole trial (in this case eye trials), where participants indicated which face or feature was from the target face. Note that the faces shown are composites of features from multiple individuals.

target face's features (eyes, nose, or mouth) with the corresponding feature from a different face. For "part" trials, a feature from a different target face was shown as a foil to the target feature (see Figure 1). Target faces were presented in the center of the screen for 1,000 ms followed by a scrambled face mask displayed for 500 ms. Participants were then presented with either two whole faces (whole trials) or two isolated features (part trials) and selected the image that matched the target. Participants selected either "1" to indicate that the left image is the target or "2" to indicate that the right image is the target and stimuli remained on the screen until a selection was made. The task included 72 randomized trials (36 parts trials and 36 whole trials), with 24 trials for each feature category.

Statistical Analysis

Age Groups

We ran all key analyses on three different levels of age grouping. First, we examined the individual level where age was a continuous measure. Second, since previous aging studies in this literature typically focus on older (65+) versus younger (18–30) groups, to connect to this literature, we binned our data by decade (five bins; see Table 1). This also provided additional power to examine gender differences. Finally, since the decade age bins had unequal *n*'s, to examine bins of roughly equal sample size, we also used an intermediate approach taking all participants at each consecutive age until we reached over 200 participants in a bin (13 bins; see Table 2). Performing key analyses using these three approaches also provided a robustness check of the effects observed.

Measuring Holistic Processing and Eye/Mouth Discrimination Ability

Using the part-whole task, we calculated the holistic advantage by regressing the part trial "control condition" from the whole trial "condition of interest." Because there has been mixed evidence regarding the presence of intact holistic processing in older adults (Boutet & Faubert, 2006; Boutet & Meinhardt-Injac, 2019; Chaby et al., 2011; Konar et al., 2013; Meinhardt-Injac et al., 2017), we used the regression equation from the current sample of 18–29-year olds[1] to ensure that the part-whole residuals reflected a typical sample, and then applied this equation to calculate the residuals for each participant (see DeGutis et al., 2012). To assess the reliability of the part-whole residuals, we used the equation described in Malgady and Colon-Malgady (1991).[2] This resulted in reliability of the holistic processing residuals of 0.23 using Guttman's $\lambda 2$ and 0.21 using Cronbach's α. The reliability of the individual "part" and "whole" measures were $\lambda 2 = .40$ and $\lambda 2 = .59$, respectively. "Part" trials had lower reliability than "whole" trials, similar to other studies using this identical task (DeGutis et al., 2012, 2013; Rezlescu et al., 2017). This is likely because greater attention to particular parts of the face at encoding could lead to more variable "part" trial performance whereas "whole" trial performance may be less dependent on where participants attend at encoding. To improve reliability within the measures, we averaged the "whole" and "part" trials for the eye and mouth conditions (eyes: $\lambda 2 = .58$, $\alpha = .57$; mouth: $\lambda 2 = .45$, $\alpha = .43$). "Whole" and "part" trials significantly correlated with one another in the entire sample ($r = .378$, $p < .001$), as did "whole" and "part" eye trials ($r = .361$, $p < .001$) and "whole" and "part" mouth trials ($r = .261$, $p < .001$). These correlations were stronger than the correlations between either "whole" eyes and "part" mouth trials ($r = .136$, $p < .001$) or

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[1] We focused on the residual regression equation from younger adults, but the results replicate when using the residual regression equation from the entire sample (see Supplemental Materials).

[2] Reliability of residuals = $(rxx + rxy^2 \times ryy - 2rxy^2)/(1 - rxy^2)$, where rxx = reliability of control condition x; ryy = reliability of condition of interest y; rxy = correlation between x and y.

Table 1

Demographics of Participants Grouped by Decade

Age group	N	M_{age} (SD)	Female:Male
18–29	1,591	23.0 (3.4)	1,062:528
30–39	705	33.8 (2.8)	501:202
40–49	516	44.4 (2.9)	418:98
50–59	391	54.2 (2.8)	328:63
60–69	138	63.0 (2.7)	119:19

Note. Three participants declined to state their gender.

“whole” mouth and “part” eye trials ($r = .202, p < .001$), suggesting that it was valid to create eye and mouth composites. Performance on trials with changes to the nose region were excluded from analyses due to poor or near-chance performance even in the younger participants (similar to DeGutis et al., 2012; $\lambda2 = .35$, $\alpha = .34$).

Because face processing ability has shown to be nonlinear and may improve until the early-to-mid 30s (e.g., Germine et al., 2011), we included regression models with stimulus version and linear and quadratic effects of age predicting either holistic or feature processing ability. Adding a cubic term failed to explain additional variance in any of the models. We also analyzed discrete groups by comparing the magnitude of the holistic advantage/feature discrimination abilities using an ANOVA approach and performed follow-up tests when significant interactions were observed. The ANOVAs were conducted using both the decade age bins and the consecutive 200+-person age bins. Because we included four stimulus versions in the part-whole task (Asian female, Asian male, Caucasian female, and Caucasian male), stimulus version was included as a factor, and we assessed potential Age × Version interactions.

It has previously been demonstrated that the ability to integrate the eyes into the context of the face is reduced in developmental prosopagnosics, those with severe lifelong face recognition difficulties (DeGutis et al., 2012). Given this, we also performed ANOVAs investigating age-related differences between “part” and “whole” performance for the eyes and mouth separately (see Supplemental Materials). This allowed us to determine whether potential holistic processing deficits found in older adults show a similar pattern to individuals with developmental prosopagnosia.

Table 2

Demographics of Participants Grouped by Consecutive Ages Into Minimum Bin Sizes of 200 People

Bin	N	M_{age} (SD)	Female:Male
1	301	18.47 (.50)	215:85
2	344	20.49 (.50)	235:109
3	252	22.49 (.50)	161:91
4	238	24.47 (.50)	144:94
5	244	26.50 (.50)	155:89
6	212	28.50 (.50)	152:60
7	275	30.97 (.83)	193:81
8	222	33.89 (.82)	155:67
9	263	37.95 (1.46)	199:63
10	263	42.90 (1.43)	208:55
11	241	48.00 (1.38)	195:46
12	212	53.02 (1.40)	183:30
13	274	60.23 (3.49)	234:40

Note. Three participants declined to state their gender.

Reaction Time Analyses

The instructions for the part-whole task did not emphasize responding as quickly as possible. Still, we analyzed changes in reaction time across the lifespan to determine whether potential age-related changes in holistic processing or feature discrimination ability could be due to speed–accuracy tradeoffs. Reaction time analyses were conducted using correctly answered trials only, following the procedure used by Tanaka et al. (2004). We reran both the regression models and the ANOVAs using the reaction time data from all correct eye and mouth trials to investigate any potential differences in reaction time between features.

Exploratory Participant Gender Analyses

Finally, to investigate whether there was an interaction between gender and age on holistic processing and eye sensitivity, we divided each of the age groups by gender and ran ANOVAs to determine whether an interaction between participant gender, stimuli gender, age, and holistic processing or feature sensitivity could be found. Because of the small number of male participants in the older age groups, to achieve adequate statistical power, we combined the 50–59 and 60–69-year-old age groups into one group of 50+ year olds for the decade bin analyses. Because the group of 50+-year-old males was comparatively smaller ($n = 82$) than the other age groups, we also ran post hoc robust regressions looking at the effects of gender and age (both young/old and continuous) on eye sensitivity to further check the robustness of the interaction effects using SPSS Version 25 (IBM Corp., 2017).

Results

Participants

The 3,341 participants were analyzed at the individual level, binned by age decade (five groups, see Table 1), and binned by taking participants at each consecutive age until we reached over 200 participants in a bin (13 groups, see Table 2). All groups had a significantly higher proportion of females than males. Chi-square tests revealed that the decade, $\chi^2(8, N = 3{,}338) = 88.17$, $p < .001$, $w = .16$, and the minimum 200-person bins, $\chi^2(24, N = 3{,}338) = 108.17$, $p < .001$, $w = .18$, differed in their female:male ratios, with the female:male ratio increasing with age. Because there were fewer males in the older age bins, for the exploratory participant gender analyses, we collapsed across 50s and 60s age bins (see below).

In terms of the four different part-whole stimulus versions, 802 participants completed the Asian female version, 831 completed the Asian male version, 816 completed the Caucasian female version, and 892 completed the Caucasian male version. There were no significant age or gender differences between participants taking each version (Asian female version: $M_{\text{age}} = 33.40$, $SD = 12.77$, 72.06% female; Asian male version: $M_{\text{age}} = 34.52$, $SD = 13.13$, 74.12% female; Caucasian female version: $M_{\text{age}} = 33.76$, $SD = 12.80$, 74.50% female; Caucasian male version: $M_{\text{age}} = 33.87$, $SD = 12.91$, 70.17% female, all p’s $> .10$). While the versions did not interact with participant age or gender, we did find a main effect of reduced holistic processing of the Asian face versions compared to Caucasian face versions, holistic advantage residuals: $t(3339) = 13.94$, $p < .001$, mean difference = .048, Cohen's $d = .49$. Given the sample was from the United States, and presumably predominantly Caucasian, this is consistent with previous studies showing reduced holistic processing of other-compared to own-race faces when using this paradigm (e.g., Tanaka et al., 2004) as well as others (Michel et al., 2006). Participants also performed better on male face stimuli compared to female for the eye trials, $t(3339) = 5.59$, $p < .001$, and the mouth trials, $t(3339) = 5.37$, $p < .001$, but there was no difference in holistic advantage for male versus female stimuli, $t(3339) = .63$, $p = .526$.

Age-Related Changes in Holistic Processing

We first examined the holistic processing advantage residuals (whole trial accuracy after regressing out part accuracy) across the lifespan at the individual level, including stimulus version and linear/quadratic effects of age as predictors, with holistic advantage being the dependent variable. Neither the overall model (adjusted $R^2 = .017$), nor the linear or quadratic terms were significant for age (linear: $\beta = .177$, $p = .102$; quadratic: $\beta = -.202$, $p = .062$; see Table 3); however, there was a significant effect of stimulus version ($\beta = -.129$, $p < .001$), with overall reduced holistic processing on Asian male faces compared to the other versions (see Supplemental Figures S2 and S3).

When investigating group differences in holistic processing residuals, the binned data demonstrated a very similar pattern. We first ran a 5 decade bin × 4 version between-subjects ANOVA and found neither a main effect of decade bin, $F(4, 3321) = 1.49$, $p = .204$; $\eta^2 = .002$, nor a Decade Bin × Version interaction, $F(12, 3321) = 0.73$, $p = .723$. However, there was a significant main effect of stimulus version, $F(33, 321) = 33.45$, $p < .001$; $\eta^2 = .029$. This was again driven by reduced holistic processing of the Asian face versions, particularly the Asian male eye trials, compared to Caucasian face versions, $t(3339) = 13.94$, $p < .001$, mean difference = .048, Cohen's $d = .49$, see Supplemental Figures S2 and S3. This is consistent with previous studies showing reduced holistic processing of other-race compared to own-race faces when using this paradigm (e.g., Tanaka et al., 2004) as well as others (Michel et al., 2006) and the fact that the current sample was from the United States, which is predominantly Caucasian. We found a very similar pattern of results when examining the 13-bin groups, with the 13 (bin) × 4 (version) between-subjects ANOVA. There was no main effect of bin, $F(12, 3289) = 1.42$, $p = .149$; $\eta^2 = .005$, or Bin × Version interaction, $F(36, 3289) = 0.92$, $p = .607$, but again there was a significant main effect of stimulus version, $F(3, 3289) = 61.88$, $p < .001$; $\eta^2 = .053$.

To complement these holistic advantage residual analyses, we also examined holistic processing across the life span by performing Part/Whole Trial Type × Version × Age bin repeated-measure ANOVAs for overall performance as well as split up by eyes and mouth trials (see Supplemental Materials). Consistent with the analyses of the residuals, we found a whole-over part trial main effect that did not interact with age bin (either decade bin or 200+ bin) and there were no Part/Whole Trial × Age × Version interactions. Very similar patterns of results were found when separately examining the eyes and mouth trials.

Age-Related Changes in Feature Discrimination Ability

We next sought to examine eye and mouth region accuracy across the lifespan. We first performed regressions predicting accuracy for each feature using stimulus version and linear/quadratic effects of age as predictors. When predicting eye region accuracy, both the linear and quadratic effects of age were significant (adjusted $R^2 = .013$, linear: $\beta = .232$, $p = .032$; quadratic: $\beta = -.341$, $p = .002$), and there was not a significant effect of stimulus version (adjusted $R^2 = .001$, $\beta = .006$, $p = .716$). In contrast, when predicting mouth region accuracy, neither linear nor quadratic effects of age were significant predictors (adjusted $R^2 = .025$, linear: $\beta = .066$, $p = .541$; quadratic: $\beta = -.034$, $p = .749$; see Table 3). However, stimulus version was a significant predictor ($\beta = .156$, $p < .001$), with worse overall performance on Asian female mouth trials.

Complementing this regression-based approach, we next examined the relative eye versus mouth accuracy across the lifespan averaged across part and whole trials. We first performed a 2 (eye/mouth) × 5 (decade bin) × 4 (version) repeated-measures ANOVA and found a main effect of participants performing better overall on eye than mouth trials, $F(1, 3321) = 46.83$, $p < .001$; $\eta^2 = .014$, and importantly, a significant eye/mouth by decade bin interaction, $F(4, 3321) = 12.71$, $p < .001$, with eye performance decreasing with age and mouth performance remaining more stable with age (see Figure 2). Notably, though the relative eye and mouth accuracy varied across versions, Eye/Mouth × Version interaction, $F(3, 3321) = 11.48$, $p < .001$, driven by higher performance on Caucasian versus Asian stimuli for both eyes and mouth, Eyes: $t(3339) = 8.67$, $p < .001$; Mouth: $t(3339) = 3.26$, $p = .001$, see Supplemental Figure S4, we did not find a significant Eye/Mouth × Decade Bin × Version interaction, $F(12, 3321) = 0.98$, $p = .469$, and each version showed either a significant or a trend toward significant Age Bin × Eye/Mouth interaction (see Supplemental Materials). These effects were similar when examining the 13 age bins. When performing a 2 (eye/mouth) × 13 (bin) × 4 (version) repeated-measures ANOVA, we found a significant eye/mouth difference, $F(1, 3289) = 213.20$, $p < .001$; $\eta^2 = .061$, and an Eye/Mouth × Version interaction, $F(3, 3289) = 16.38$, $p < .001$. Critically, we found an Eye/Mouth × Age Bin interaction, $F(12, 3289) = 4.98$,

Table 3

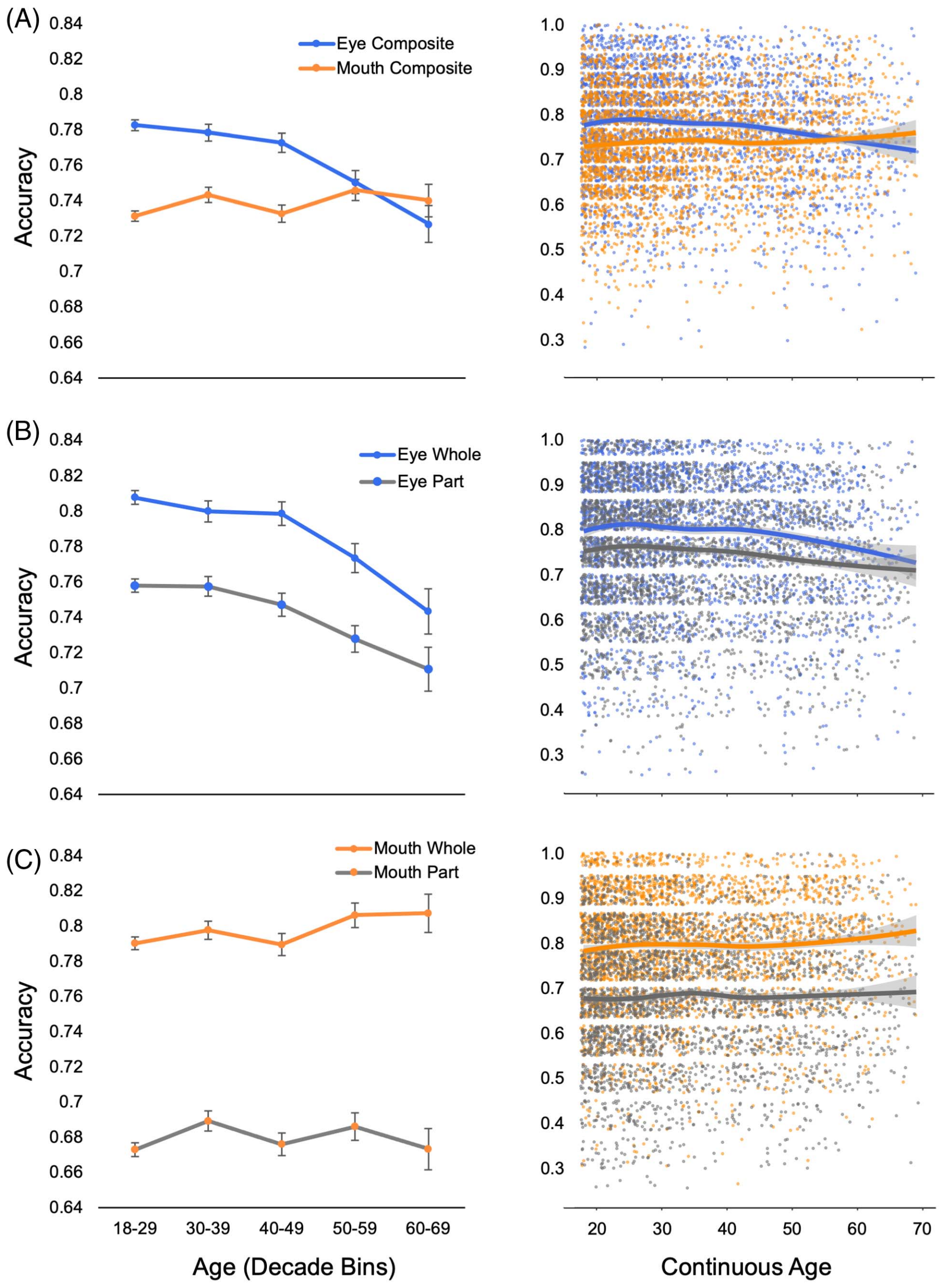
Regression Analysis Summary for Age Predicting Eye Accuracy, Mouth, Accuracy, or the Part-Whole Residuals

			Age		Age^2		Stimulus version	
Dependent variables	R	R^2	Standardized β	p	Standardized β	p	Standardized β	p
Model 1: Eye average***	.118	.014	.232	.032*	−.341	.002**	.008	.631
Model 2: Mouth average	.159	.025	.066	.541	−.034	.749	.156	<.001***
Model 3: Part/whole effect residual	.135	.018	.177	.102	−.202	.062	−.129	<.001***

* $p < .05$. ** $p < .01$. *** $p < .001$.

Figure 2

Part-Whole Task Eye and Mouth Trials Across the Life Span



Note. (A) Part-whole average eye and average mouth performance across decade bins and with age as a continuous variable (with locally estimated scatterplot smoothing). Average eye performance declines with age while mouth performance is stable. Part and whole eye trials (B) and mouth trials (C) across decade bins and with age as a continuous variable. Holistic processing of the eyes and mouth are maintained throughout the lifespan. Error bars in decade bins and shaded areas in the continuous plots indicate the standard error of the mean. See the online article for the color version of this figure.

$p < .001$, but no Eye/Mouth × Age Bin × stimulus version interaction, $F(36, 3289) = 0.85$, $p = .723$.

Finally, focusing on just the eye trials, we sought to determine whether the age-related decreases in eye region accuracy interacted with stimulus version. Using the decade bins, we first ran a 5 (decade bin) × 4 (version) between-subjects ANOVA and found a main effect of decade bin, $F(4, 3321) = 11.04$, $p < .001$; $\eta^2 = .013$, with eye region accuracy decreasing across the lifespan. We also found a main effect of version, $F(3, 3321) = 25.73$, $p < .001$; $\eta^2 = .023$, with participants performing particularly worse on the Asian female eye trials (see Supplemental Figure S4). We did not find a significant Decade Bin × Version interaction, $F(123, 321) = 0.85$, $p = .598$, and three out of four versions showed a significant effect of age bin on eye accuracy except for the Caucasian male version, $p = .195$ (see Supplemental Materials). The pattern of results was very similar when examining the 13 age bins. When performing a 13 (bin) × 4 (version) ANOVA, there was a main effect of age bin, $F(12, 3289) = 5.32$, $p < .001$; $\eta^2 = .019$, and stimulus version, $F(3, 3289) = 44.85$, $p < .001$; $\eta^2 = .039$, but no significant Age Bin × Version interaction, $F(36, 3289) = 1.19$, $p = .199$.

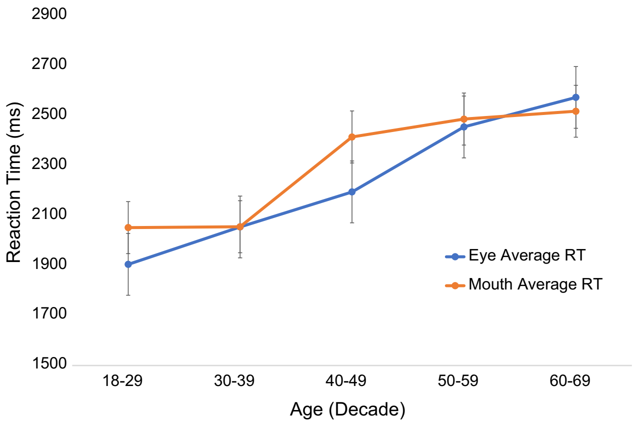
Together, these analyses converge to demonstrate that eye region accuracy significantly declined with age, whereas mouth region accuracy was relatively stable with age or showed a slight increase.

Reaction Time

We next examined reaction time (RT) to determine if the age-related declines in eye region accuracy might be due to a speed–accuracy tradeoff. We first ran regression models predicting eye and mouth RT using stimulus version and linear and quadratic effects of age as predictors. Although age and age^2 were not independent predictors, combined they predicted significant variance in eye RT (7.10%) and to a lesser extent variance in mouth RT (.70%). Stimulus version did not explain additional variance beyond age/age^2. We next performed a repeated-measures ANOVA on the decade bins, testing for an age by feature (eye/mouth RT) interaction with stimulus version as a factor. We found a main effect of age group, $F(4, 3321) = 18.05$, $p < .001$, $\eta^2 = .021$; see Figure 3, but did not find a significant Age Group × Feature interaction, $F(4, 3321) = .97$, $p = .420$, nor an Age Group × Feature × Stimulus Version interaction, $F(12, 3321) = .67$, $p = .782$. Using the consecutive 200+-person bins resulted in similar findings, with a main effect of age, $F(12, 3289) = 6.68$, $p < .001$, $\eta^2 = .024$, and neither a significant Age Group × Feature interaction, $F(12, 3289) = .73$, $p = .725$, nor an Age Group × Feature × Version Type interaction, $F(36, 3289) = .82$, $p = .769$. This consistent age-related slowing for both the eye and mouth trials suggests that the age-related eye region accuracy decline is not due to a shift in participants' speed versus accuracy tradeoff.

Figure 3

Part-Whole Task Eye and Mouth Trial Reaction Time Across Decade Bins



Note. The error bars show the standard error of the mean in each decade bin. RT = reaction time. See the online article for the color version of this figure.

Exploratory Participant Gender Analyses

Finally, we examined potential gender differences in age-related changes in face perception. Because there were so few males in the older age groups, to increase power to discover effects, we collapsed the 50–59 and 60–69-year-old age groups into one group of 50+ year olds. Using a decade-binned approach with 50s/60s collapsed and including stimulus gender as a factor, there was a significant Age Bin × Participant Gender interaction, $F(4, 3322) = 2.65$, $p = .031$, but we failed to find either a significant Age Bin × Feature (eye/mouth) × Participant Gender interaction, $F(4, 3322) = .70$, $p = .592$, or a significant Age Bin × Feature × Participant Gender × Stimulus Gender interaction, $F(3, 3322) = .44$, $p = .727$. No significant interaction between either age bin and participant gender, $F(33, 322) = .79$, $p = .532$) or Stimulus Gender × Age Bin × Participant Gender, $F(33, 322) = .17$, $p = .919$, was evident when holistic processing residuals were the dependent variable, although there was a main effect of gender, $F(33, 322) = 7.02$, $p = .001$, driven by a greater whole-over-part advantage in females.

Because females have shown greater eye sensitivity and attention to the eyes than males (Hall et al., 2010; Sullivan et al., 2007), we also specifically examined whether male versus female participants had a larger decrease in eye accuracy with age and whether this interacted with the part-whole stimulus version. We ran a 2 (male/female participants) × 4 (age bin: 18–29, 30–39, 40–49, 50–69) × 4 (stimulus version) between-subjects ANOVA. We found significant main effects of participant gender, $F(13, 322) = 9.19$, $p < .001$, $\eta^2 = .006$, females outperforming males, and age bin, $F(3, 3322) = 14.59$, $p < .001$, $\eta^2 = .013$, performance declining with age. Importantly, we found a significant Age Bin × Participant Gender interaction, $F(43, 322) = 2.99$, $p = .018$, with males having a more pronounced decline in eye accuracy with age than females (see Figure 4). Notably, we did not find a significant Age Bin × Participant Gender × Version interaction, $F(33, 322) = 0.47$, $p = .70$, see Supplemental Figure S5.

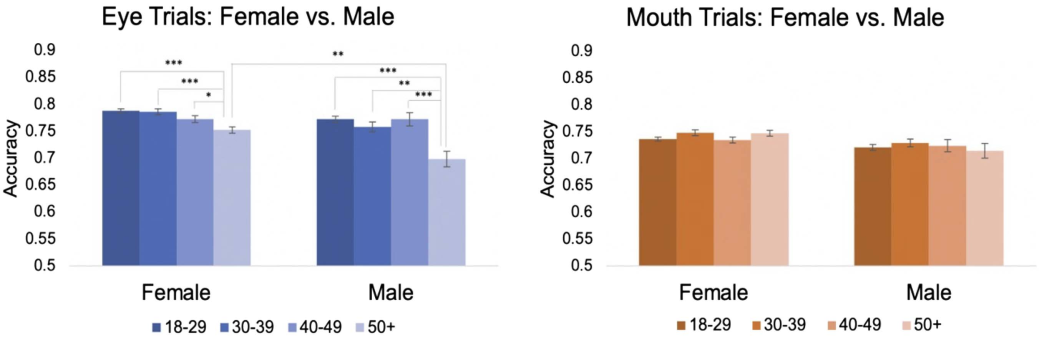
One potential issue is that the group of 50+ males was still significantly smaller ($N = 82$) than the other age groups. To further check the robustness of the interaction effects observed, we additionally ran analyses looking at the effects of gender and age (both young/old and continuous) on eye sensitivity. When participants were dichotomized by age (under 50/over 50), there was a significant Age Group × Gender interaction when eye processing was the dependent variable ($p = .008$, though we did not find significant interactions when examining each stimulus version separately, all p's $> .130$, see Supplemental Materials). Also, when age was included as a continuous variable, there was only a trend toward an Age × Gender interaction when predicting eye accuracy ($p = .090$).

Discussion

Prior studies have shown that older adults experience declines in face perception ability, but the mechanisms underlying these deficits remain incompletely characterized. Administering the part-whole task to a large, age-diverse adult sample, we found that overall holistic face processing abilities remained consistent across the

Figure 4

Eye and Mouth Average Accuracy of Age Groups Split by Participant Gender



Note. Error bars indicate the standard error of the mean of each age bin. See the online article for the color version of this figure.
* $p < .05$. ** $p < .01$. *** $p < .001$.

lifespan. Notably, compared to younger adults (18–40s), older adults (50s/60s) showed decreased eye region accuracy but had similar mouth region accuracy. Exploratory gender analyses also revealed that males showed a significantly greater age-related decline in eye region accuracy compared to females, but we found no evidence for age-related gender differences in holistic processing or mouth accuracy. Together, our results suggest that age-related decreases in face perception are not due to changes in the ability to process faces holistically, but rather that older adults have a specific decreased ability to discriminate the eye region. Notably, the effects observed were very similar across stimuli that differed both in ethnicity and gender. These results have important implications for understanding age-related changes in face perception and recognition and may have implications for socioemotional models of lifespan development such as the age-related positivity effect.

The current results demonstrate that holistic processing ability, as measured by the part-whole effect, is maintained throughout the lifespan. We also found that although eye region accuracy decreased with age (see below), the magnitude of the holistic advantage for the eye region remained stable with age. These findings differ from impairments on the identical task found in developmental prosopagnosics (DPs), those with lifelong face recognition deficits, who showed reduced holistic processing specifically on eye trials (DeGutis et al., 2012). This suggests that, in contrast to perceptual deficits found in DPs, older adults do not experience holistic processing deficits and are able to holistically process the eye region. The current finding of a robust and stable holistic advantage across the lifespan is consistent with several studies showing similar holistic processing abilities in younger and older adults using the composite face effect (Boutet & Meinhardt-Injac, 2019; Konar et al., 2013; Meinhardt-Injac et al., 2017), face inversion effect (Boutet & Faubert, 2006; Bowles et al., 2009), and part-whole effect (Boutet & Faubert, 2006). The current results extend these findings by using a substantially larger sample with more fine-grained age bins and showing these holistic effects are maintained with age across both the eye and mouth regions.

Regarding feature processing with age, our results demonstrate a clear association between aging and reduced eye region discrimination ability, with a pronounced decline beginning in the 50s and continuing into the 60s. This could not be explained by a general featural processing decline as we found that mouth accuracy was maintained or in some analyses showed small effects of improvement with age. The finding of declining eye region performance with age is consistent with previous studies showing that (a) compared to younger adults, older adults are less sensitive to configural changes in the eyes but perform similarly with mouth configural changes (Slessor et al., 2013), (b) older adults less consistently use the eye/eyebrow region during face matching compared to younger adults (Creighton et al., 2019), and (c) older adults both spend *less* time viewing the eye region and *more* time viewing the nose and mouth regions compared to younger adults (Firestone et al., 2007). This suggests that older adults may be less able to detect both configural/spacing and feature differences in the eye region, which could be a cause or consequence of reduced eye region viewing time in older adults. Interestingly, older adults' preserved whole-over-part advantage for the eye region suggests that they have an intact ability to integrate the eye region with the rest of the face into a holistic representation. Our finding of an age-related decrement in eye accuracy is consistent with face emotion recognition findings in older adults showing worse recognition of eye-mediated emotions (anger, sadness, fear) and longer and more frequent lower face fixations (e.g., Chaby et al., 2017; Firestone et al., 2007; Sullivan et al., 2007, 2017). The current results extend these studies by showing that an eye processing decrement occurs during a nonemotional face perception task and together, suggests that there may be a general age-related attentional shift downward on the face resulting in poorer eye region accuracy (see more on this below). Since the eye region has been shown to be critical for face recognition (Royer et al., 2018; Tardif et al., 2019), one important potential implication of decreased eye discrimination in older adults is its potential contribution to age-related decreases in face recognition ability. This would be an important association to characterize in future studies.

The current results also revealed an interesting gender difference in age-related declines for the eye region but not the mouth region or holistic processing. We found that females performed better than males at all aspects of the part-whole task, including more accurate eye and mouth region performance and a greater holistic advantage. Better overall performance in females compared to males is consistent with previous face perception tasks (e.g., Bowles et al., 2009) but contrasts a recent study showing similar holistic processing between males and females (using the face inversion effect, Knudsen et al., 2021). Notably, our results demonstrated that females had a smaller age-related decline in eye region accuracy compared to males, who showed a more precipitous decline in the 50s and 60s. This pronounced eye accuracy advantage in older females versus older males aligns with previous findings that females attend to the eye region more than males during a facial emotion recognition task (J. K. Hall et al., 2010) and that during an emotion recognition task older females spent over 70% of their time looking at the eyes versus 56.9% for males, although this gender effect was absent in younger adults (Sullivan et al., 2017). Importantly, the current results extend these findings by showing that the older females-over-older males advantage for the eye region extends to a nonemotional face perception task.

Though the current findings clearly show an age-related decline in eye region accuracy and that males have a more pronounced decline than females, the specific cause of this decline remains to be characterized. One potential contributing factor is that decreased ability to comprehend speech with age (speech-frequency hearing impairment affects 39.3% of adults 60–69, Hoffman et al., 2017) and the use of lipreading as a compensatory strategy could cause a general downward attentional shift toward the mouth. This explanation is supported by studies showing that loss of hearing ability is correlated with increased fixation of the mouth for visual speech cues (e.g., Tye-Murray et al., 2007), and a study of deaf versus hearing participants found that deaf participants spent over 20% more time viewing the mouth when perceiving spoken language than hearing participants (Mastrantuono et al., 2017). Further, hearing sensitivity declines twice as fast in males as it does in females (Agrawal et al., 2008; Pearson et al., 1995) and males are less likely than females to regularly use corrective hearing aids (Staehelin et al., 2011), increasing the chances that they would need to rely on visual cues from the mouth to help with deciphering speech. Our result demonstrating greater age-related decreases in eye region accuracy in males versus females is consistent with this. That being said, Thompson and Malloy (2004) showed that while older adults demonstrated better detection performance of the mouth region during speech compared to younger adults, there was no difference between younger and older adults attending to the mouth when audible speech was removed. This suggests that we may not expect to see hearing-related attentional biases toward the mouth in tasks lacking audible speech, such as in the present study. Thus, though hearing loss may lead some older adults to shift focus away from the eye region during speech, it may not fully explain decreased eye region discrimination ability when viewing non-speaking or static faces such as in the current task.

Age-related decreases in lower level vision or oxytocin levels could also contribute to the age-related decreases in eye region accuracy we observed. Reduced lower level visual abilities, such as contrast sensitivity or sensitivity to high-spatial frequencies (HSF), may differentially affect perception of the eyes versus mouth. For example, impaired HSF processing in older adults with age-related macular degeneration has shown to lead to increased reliance on the mouth region rather than the eyes to identify emotional expressions (Boucart et al., 2008). However, the onset of age-related macular degeneration is significantly later (>70 years old, Friedman et al., 2004) than the effects observed in the present study (50s/60s) and there is mixed evidence regarding the effects of healthy aging on HSF sensitivity (e.g., Govenlock et al., 2010), though Boutet and Meinhardt-Injac (2019) demonstrated that middle-aged and older adults had particularly impaired face discrimination ability when shown HSF information. Further, in contrast to the greater eye region accuracy declines observed in males, females typically show earlier and more severe lower level visual deficits (Bergman & Rosenhall, 2001; Zetterberg, 2016). Besides these lower level vision changes with age, an additional factor that may contribute to age-related eye region accuracy declines is oxytocin, a neuropeptide shown to play an important role in emotion and face recognition. Intranasal oxytocin has been shown to increase attention to the eyes (Guastella et al., 2008; Le et al., 2020; Lopatina et al., 2018) and temporarily improves face perception and recognition in developmental prosopagnosics (Bate et al., 2014). Regarding gender differences, a 2014 study found that older males who received oxytocin improved in their general emotion recognition ability, while no effect was found for older females or younger adults (Campbell et al., 2014). However, evidence for changes in oxytocin levels with age has been mixed (for a review, see Ebner et al., 2013), with some studies finding age-related decreases in oxytocin levels (Arsenijevic et al., 1995) and others finding increases in older female rhesus monkeys but not in males (Parker et al., 2010). Additional studies will be needed to characterize whether lower level vision and oxytocin changes significantly contribute to age-related performance decrements in eye region processing.

The current finding of reduced eye region discrimination ability with age could also be at least partially driven by an age-related positivity effect (Mather & Carstensen, 2005), or conversely, could contribute to this bias. The socioemotional selectivity theory of aging suggests a motivational shift following the perception of limited time that typically accompanies aging (Carstensen, 1991, 1993). According to the theory, younger adults have a greater perceived time horizon and tend to focus on acquisition of knowledge, while perceived limited time leads older adults to focus on nurturing the more emotionally meaningful aspects of their life (Carstensen et al., 1999). This motivational shift is thought to increase attention to and preference for positive information in older adults (age-related positivity effect, Charles et al., 2003). This is relevant in the context of differential feature attention because the eyes are more strongly associated with negative valence expressions including anger, sadness, and fear, whereas the mouth region is associated more with recognizing happiness (Dunlap, 1927; Iwasaki & Noguchi, 2016; Wegrzyn et al., 2017). Thus, a stronger inclination toward positive information with age could explain a movement from a preferential fixation location around the eye region down toward the mouth region, leading to a decrease in eye region accuracy. To our knowledge, no studies have convincingly demonstrated gender differences in the age-related positivity effect, so this phenomenon may not fully explain the significant gender by age interaction we observed for eye region accuracy. If the age-related positivity effect were a driving factor in the decline of eye region accuracy, we would predict that females would show reduced age-related positivity since they are more likely to retain their sensitivity to negative facial emotions such as anger (Abbruzzese et al., 2019) and attend more to the eye region with age than males (Sullivan et al., 2017). In addition to age-related positivity potentially influencing face perception, it also could be that age-related decreases in eye region performance contributes to the age-related positivity effect in the context of processing facial information. Increased attention toward the lower half of the face may lead to decreased memory for negative emotional face stimuli with age (Grady et al., 2007). Previous studies have argued that the age-related positivity effect primarily reflects a change in motivation but have not thoroughly examined whether age-related sensory or perceptual changes contribute to this positivity effect (Carstensen & DeLiema, 2018), which would be an important future direction.

There are several limitations to the present study. First, the current sample is cross-sectional, and the age range only extends to 69 years old. Including a gender-balanced longitudinal sample of adults ages 70 and older in future studies would help to create a more comprehensive characterization of changes to face perception abilities in old age. Second, although stimulus version (Asian/Caucasian male and female faces) did not significantly interact with any key effects of age, patterns of results varied across stimulus versions (see Supplemental Materials). Though this is likely due to the other-race effect, it would be important for future studies to collect detailed information on demographics and frequency of contact with members of other races to characterize perceptual changes in own- and other-race face processing. Additionally, it would be informative to examine how stimulus factors (e.g., faces with higher vs. lower contrast eye regions) interact with the perceptual aging effects we observed. Third, our use of an online sample may have resulted in a higher functioning sample of older adults than the general population, since participation requires both proficiency with a computer and the motivation to seek out cognitive tests online. This may be underestimating potential age-related declines. Additionally, the part-whole task measures face perception abilities but not face recognition memory and including a measure of face memory would help further disentangle the independent contributions of eye sensitivity and holistic processing to age-related declines in face recognition. While this study provides important evidence regarding face perception declines with age, future studies would benefit from measuring objective hearing ability, lower level visual abilities, and incorporating eye-tracking to measure attentional changes (e.g., Peterson et al., 2019). Including tasks measuring biases toward positively versus negatively valenced social information along with measures of face recognition would also help to assess if changes in the age-related positivity effect are related to changes eye region discrimination ability. Finally, it would be important for future studies to investigate if gender differences in eye performance are driven more by biological factors (e.g., oxytocin) or differences in socialization (e.g., greater social engagement).

Overall, this study provides important evidence that while feature sensitivity to the eye region decreases with age, particularly in older males, mouth discrimination ability and holistic processing is similar in older and younger adults. While the exact mechanisms of these age-related eye region-specific declines will require additional research, the current findings provide an important step forward in characterizing the specificity and trajectory of face perception changes across the lifespan.

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