Selective age-related changes in orientation perception

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Orientation perception is a fundamental property of the visual system and an important basic processing stage for visual scene perception. Neurophysiological studies have found broader tuning curves and increased noise in orientation-selective neurons of senescent monkeys and cats, results that suggest an age-related decline in orientation perception. However, behavioral studies in humans have found no evidence for such decline, with performance being comparable for younger and older participants in orientation detection and discrimination tasks. Crucially, previous behavioral studies assessed performance for cardinal orientation only, and it is well known that the human visual system prefers cardinal over oblique orientations, a phenomenon called the *oblique effect*. We hypothesized that age-related changes depend on the orientation tested. In two experiments, we investigated orientation discrimination and reproduction for a large range of cardinal and oblique orientations in younger and older adults. We found substantial age-related decline for oblique but not for cardinal orientations, thus demonstrating that orientation perception selectively declines for oblique orientations. Taken together, our results serve as the missing link between previous neurophysiological and human behavioral studies on orientation perception in healthy aging.

Introduction

As we age, many of our abilities change, and visual perception is one of them (Andersen, 2012; Billino & Pilz, 2019; Owsley, 2011). The mechanisms underlying these changes are so far not very well understood, but it has been suggested that, at least to some extent, they relate to changes on the neurophysiological level. Neurons in visual cortices of senescent cats and monkeys have been found to exhibit broader tuning curves, reduced selectivity, and higher spontaneous noise than those of younger animals. Such age-related changes exist from orientation-selective neurons in V1 and V2 (Hua, Li, He, Zhou, Wang, & Leventhal, 2006; Leventhal, Wang, Pu, Zhou, & Ma, 2003; Schmolesky, Wang, Pu, & Leventhal, 2000) up to motion-selective neurons in area MT/V5 (Liang, Yang, Li, Zhang, Wang, Zhou, & Leventhal, 2010; Yang, Liang, Li, Wang, Ma, Zhou, & Leventhal, 2009; Yang, Zhang, Liang, Li, Wang, Ma, Zhou, & Leventhal, 2009). On the basis of this literature, it is then reasonable to expect that such neurophysiological changes relate to humans and become manifest in behavior. Indeed, age-related changes in global motion perception have been reported and discussed in many human behavioral studies (Billino & Pilz, 2019). Surprisingly, however, studies on orientation perception in humans have not found strong indicators of age-related decline (Delahunt, Hardy, & Werner, 2008; Govenlock, Taylor, Sekuler, & Bennett, et al., 2009). It has been suggested that neural networks involved in orientation selective mechanisms reorganize with age to allow efficient orientation perception despite changes in neural sensitivity (Delahunt et al., 2008). It is further possible that only a subset of neurons in early visual areas contributes to psychophysical orientation judgements (Govenlock et al., 2009), an idea that is supported by neurophysiological studies that found small numbers of neurons that remained selective for orientations in older cats and monkeys (Hua et al., 2006; Schmolesky et al., 2000).

Importantly, previous behavioral studies have so far mainly investigated orientation perception for cardinal orientations, that is, horizontal and vertical or did not differentiate between tested orientations (Casco, Barollo, Contemori, & Battaglini , 2017; Delahunt et al., 2008; Govenlock et al., 2009; Peven, Chen, Guo, Zhan, Boots, Dion, Libon, Heilman, & Lamar, 2019; Reynaud, Tang, Zhou, & Hess, 2018). However, it is well known that the human visual system is better at processing cardinal compared to oblique orientations,

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a phenomenon called the *oblique effect* (Appelle, 1972; Furmanski & Engel, 2000; Li, Peterson, & Freeman, 2003; Orban, Vandenbussche, & Vogels, 1984; Storrs & Arnold, 2015). This phenomenon has been related to the prominence of cardinal contours in our visual environment (Annis & Frost, 1973; Coppola, Purves, McCoy, & Purves, 1998; Girshick, Landy, & Simoncelli, 2011; Hansen & Essock, 2004). Here, we investigated the effect of aging on orientation discrimination and reproduction for a large range of orientations. As expected, our results replicated the oblique effect such that performance was worse for oblique compared to cardinal orientations across all age groups. More importantly, we found that performance declined with age only for oblique orientations (Experiments 1 and 2), and, in particular, for those near vertical (Experiment 2). Our study bridges the gap between neurophysiological studies in senescent cats and monkeys and human behavioral studies.

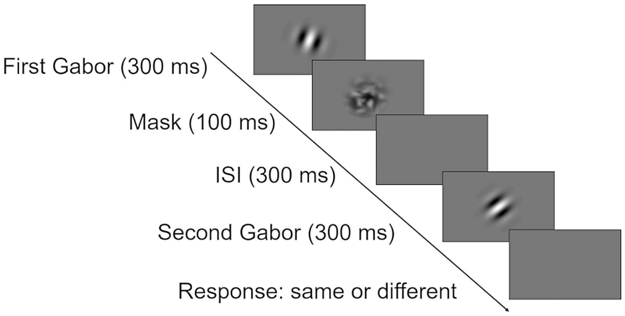

Figure 1. Stimulus sequence of one example trial in Experiment 1. Two Gabor stimuli were sequentially presented for 300 ms. In between the two Gabors, a mask and an interstimulus interval were presented for 100 ms and 300 ms, respectively. Participants had to indicate as to whether the two Gabors were the same or different. Discrimination thresholds for each orientation were determined using Quest (Watson & Pelli, 1983).

Experiment 1

Methods

Participants

Twenty-six younger and 22 older adults participated in this experiment. All participants had corrected-to-normal visual acuity as assessed before the experiment using an Early Treatment Diabetic Retinopathy Study (ETDRS) chart. Older participants were screened for visual deficits. Only adults with no known history of cataract, glaucoma, or macular degeneration were included in the study. In addition, older participants were screened for mild cognitive impairment using the Montreal Cognitive Assessment (MoCa; Nasreddine, Phillips, Bédirian, Charbonneau, Whitehead, Collin, Cummings, & Chertkow, 2005). Three participants (two older and one younger) were excluded because of a visual acuity score below 0.8. One older participant was excluded because of a low score on the MoCa. An additional two older and eight younger participants were excluded because thresholds in at least one of the conditions could not be determined reliably. A total of 17 younger (19–27 years, $M = 22.7$, $SD = 2.3$, 5 male) and 17 older participants (63–82 years, $M = 70.3$, $SD = 7.2$, 3 male) took part in the experiment. The experiment was approved by the local Ethics Committee of the School of Psychology at the University of Aberdeen (UK) and was conducted in accordance with the Declaration of Helsinki. All participants provided written informed consent.

Apparatus and stimuli

Stimuli were generated on an Apple Mac Mini (OS X) computer using the PsychToolbox extension for MATLAB (Brainard, 1997; Kleiner, Brainard, Pelli, Ingling, Murray, & Broussard, 2007) and were presented using a 17-inch Viglen VL950T CRT monitor with a refresh rate of 100 Hz and a resolution of 1024 × 786 pixels. The stimuli were viewed binocularly at a distance of 60 cm from the screen while the participant sat in an adjustable chair in a darkened room. Responses were recorded using a standard QWERTY keyboard. Stimuli were Gabor patches (windowed sine wave gratings) with a peak 25% Michelson contrast, a spatial frequency of 0.5 cycles/degree, and a .90° *SD* Gaussian contrast envelope. Smoothed white noise was added to the stimuli with a mean of zero and a standard deviation of 0.5°. The average luminance of the display was 38 cd/m^2 throughout the experiment.

Procedure

On each trial, two Gabors were presented sequentially in the middle of the screen for 300 ms each, separated by an inter-stimulus-interval (ISI) of 300 ms and a mask of 100 ms (Figure 1A). One of the two Gabors was oriented according to the baseline orientation of that particular block (horizontal [90°], vertical [0°], 22.5°, and 45°). The orientation of the other Gabor was clockwise away from the baseline orientation and was determined using QUEST, a Bayesian adaptive psychometric procedure (Watson & Pelli, 1983). The order of the two Gabors was randomized on each trial. Participants were asked to indicate whether the two Gabors had same or different orientation by pressing “x” for same and “m” for different. We determined performance thresholds at 75% correct. Based on pilot experiments, the orientation difference between the two Gabors on the first trial within each block was set to 12°, and the maximum possible difference between tested orientations was set to 45°.

Participants performed three blocks of trials for the four baseline orientations. The first block of trials consisted of 10 trials and was discounted for further analysis. The second and third block consisted of 20 trials each. Thresholds from these two blocks were averaged for further analysis. The order in which orientations were presented was randomized for each participant.

Before starting the main experiment as described above, participants performed a training block with trial-based visual and auditory feedback to get accustomed with the stimuli and experimental procedure. There were 10 trials for each orientation, in half of which the two Gabors had the same orientation. In the other half of trials, the Gabor orientation differed by 40°. The order in which the orientations were presented was randomized for each participant. During training, mask, stimuli, and ISI had a duration of 500 ms each. The whole experiment including training took approximately 30 minutes to complete.

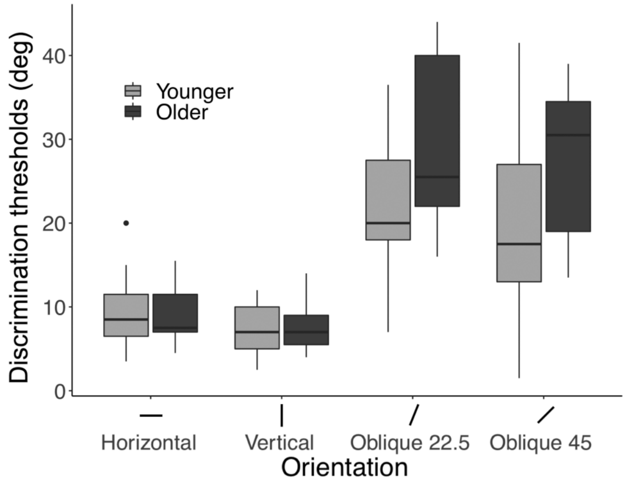

Figure 2. Boxplot of averaged discrimination thresholds from younger and older adults for all four tested orientations. Overall, participants performed better for cardinal compared to oblique orientations, which is in line with the oblique effect. Significant age differences were only present for oblique but not for cardinal orientations.

Results

Figure 2 shows orientation discrimination thresholds for cardinal (vertical [0°], horizontal [90°]) and two intermediate oblique orientations (22.5°, 45°) for younger and older adults. Data were analyzed with a mixed-design 2 (age group) × 4 (orientations) analysis of variance (ANOVA). Mauchly's test of sphericity indicated that the assumption of sphericity had been violated for the main effect of orientation and the age group x orientation interaction, and degrees freedom were corrected using the Greenhouse-Geisser correction ($\varepsilon = 0.74$). The ANOVA revealed main effects of orientation ($F(3,96) = 90.7$, $p < 0.001$), age ($\mathrm{F}(1,32) = 90.698$, $p < 0.001$), and an age group by orientation interaction, ($F(3,96) = 5.5$, $p < 0.01$). Overall, participants performed better for cardinal ($M = 8.2$, $SD = 2.6$) compared to oblique orientations ($M = 24.9$, $SD = 9.2$; $t(33) = 11.6$, $p < 0.001$), confirming the oblique effect.

To further assess the age group × orientation interaction, we conducted one-tailed independent samples *t*-tests and found significant age-differences for oblique orientations but not for cardinal ones (Table 1). Effect sizes were computed for all comparisons using Cliff's delta (Cliff, 2014; Wilcox, 2006), a nonparametric method of calculating effect sizes related to the Wilcoxon-Mann-Whitney U statistics. Cliff's delta estimates the probability that a randomly selected sample from one group is larger than a randomly

		Threshold					CI	
Angle	Age group	Mean	SD	*t* value	*p* value	Cliff's delta	Low	High
Horizontal (90°)				$t(29.8) = 0.45$	0.65	0.05	−0.34	0.43
	Younger	10.65	6.18					
	Older	8.78	3.02					
Vertical (0°)				$t(30.6) = -0.5$	0.64	0.02	−0.40	0.37
	Younger	7.84	3.7					
	Older	7.72	2.39					
Oblique (22.5°)				$t(30.1) = -2.6$	0.015^{*}	−0.46	−0.73	−0.07
	Younger	25.34	13.5					
	Older	31.58	12.22					
Oblique (45°)				$t(30.1) = -2.4$	0.02^{*}	−0.43	−0.72	−0.02
	Younger	23.26	14.4					
	Older	28.11	8.47					

Table 1. Descriptive statistics, and results for Welch two-sample *t*-tests between age groups for all tested orientations, effect sizes (Cliff's delta) and confidence intervals (CI) for effect sizes. *Note*: $^{*}p < 0.5$.

selected sample from another group minus the reversed probability. Values range from −1 when all values from one group are lower than from the other to 1 when all values from one group are higher than from the other. As shown in Table 1, effect sizes for oblique age differences were of medium size.

Discussion

In Experiment 1, we asked participants to discriminate two subsequently presented Gabors and estimated orientation discrimination thresholds for both cardinal and two oblique orientations. Our results are in line with previous literature on the oblique effect such that discrimination thresholds for oblique orientations were around three times larger than for cardinal ones (Appelle, 1972; Furmanski & Engel, 2000; Orban et al., 1984). Strikingly, however, older participants performed worse for oblique orientations compared to younger participants. There was no age difference in performance for cardinal orientations. These results show that orientation perception changes selectively with age for oblique orientations and suggest that an absence of age-differences in previous experiments is due to the fact that only cardinal orientations were tested (Delahunt et al., 2008; Govenlock et al., 2009). Particularly interesting is also the difference in variability for oblique compared to cardinal orientations: whereas individual thresholds for cardinal orientations were closely clustered around the mean, thresholds in the oblique orientations were spread out dramatically. It has to be noted that thresholds for cardinal gratings were generally low and participants performed close to ceiling in those conditions. Overall, however, the task was rather difficult to perform given the number of participants for which we were unable to determine reliable thresholds in at least one of the tested orientations.

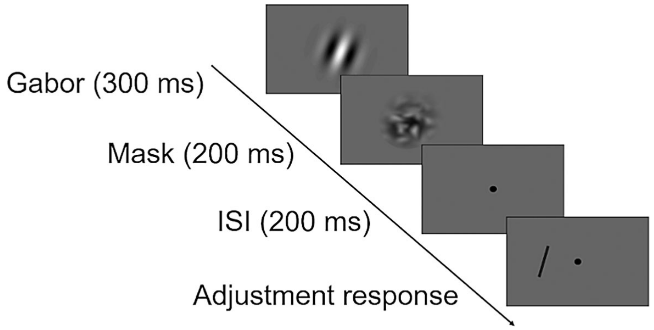

Figure 3. Stimulus sequence of one example trial in Experiment 2. A Gabor was presented in the center of the screen. After a mask and an interstimulus interval of 200 ms each, participants were asked to adjust a bar to match the orientation of the previously presented Gabor.

To further quantify the selective age differences observed in Experiment 1 and to confirm our results with another experimental paradigm, we conducted a second experiment, in which we asked participants to reproduce the orientation of a briefly presented Gabor by adjusting a response bar to match their perceived orientation of the stimulus. By measuring the reproduction error for cardinal and oblique orientations around horizontal and vertical, we were able to assess participants' biases towards or away from certain axes of orientation. In addition, we also computed perceptual uncertainty, that is, participants' response variability for a specific orientation.

Experiment 2

Methods

Participants

A total of 21 older (63–78 years, $M = 68.2$, $SD = 4.4$, 6 male) and 26 younger adults (19–33 years, $M = 22.4$, $SD = 3.0$, 7 male) took part in the experiment. Visual and cognitive screening procedures were the same as in Experiment 1. Three older participants were excluded: one due to a low score on the MoCa, one because of a visual acuity below 0.8, and one because s/he was unable to perform the task as indicated by a completely random answer pattern. Two younger participants were excluded because they were familiar with the experimental hypotheses. Eighteen older and 24 younger participants were included in the analysis. Visual acuity of older adults ($M = 0.98$, $SD = 0.15$) was significantly lower than that of younger adults ($M = 1.28$, $SD = 0.24$). However, visual acuity did not correlate with absolute errors in either of the two age groups with all $p > 0.09$ as indicated by Pearson's correlation. The experiment was approved by the local Ethics Committee of the School of Psychology at the University of Aberdeen (UK) and was conducted in accordance with the Declaration of Helsinki. All participants provided written informed consent.

Stimuli and apparatus

The stimuli and apparatus were the same as in Experiment 1.

Procedure

On each trial, a Gabor was presented in the middle of the screen for 300 ms (Figure 3). After a mask of 200 ms and a brief ISI of 200 ms, participants were asked to adjust a bar on the left side of center to match

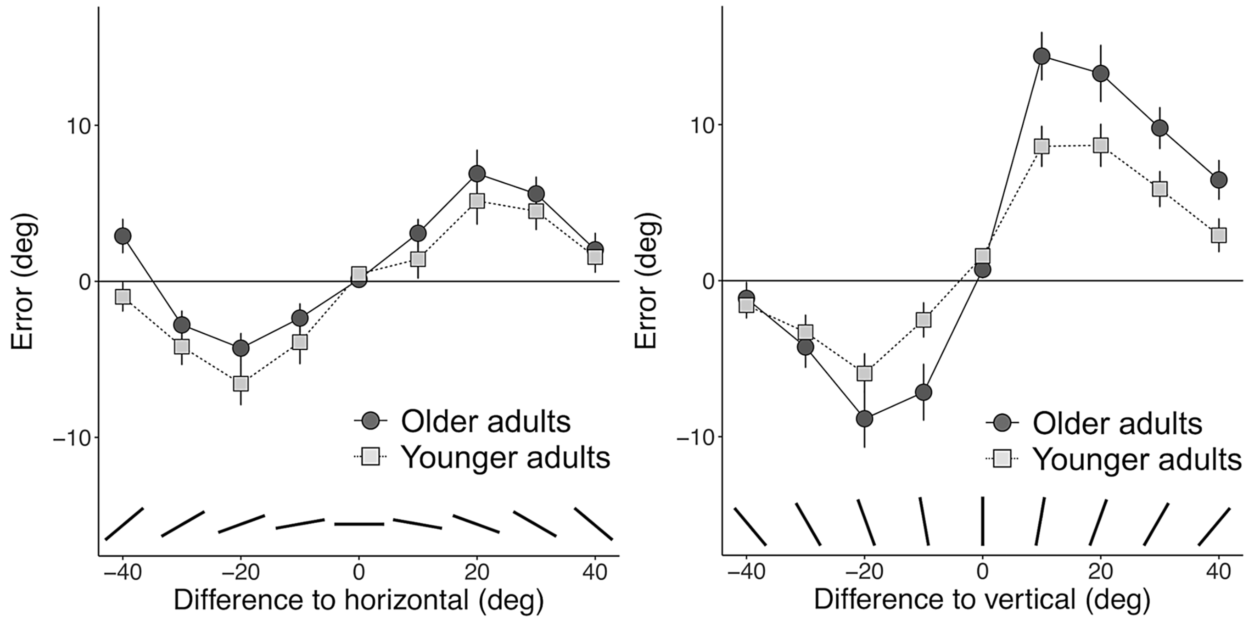

Figure 4. Reproduction errors (deg) for older (dark gray) and younger adults (light gray) for orientations around horizontal (left) and vertical (right). Negative errors indicate errors anticlockwise away from the tested orientation and positive errors indicate errors clockwise away from the tested orientation. Error bars represent standard error from the mean.

the orientation of the previously presented Gabor. We tested 18 orientations in total: vertical (0°), horizontal (90°), and 10°, 20°, 30°, and 40° left and right of those two cardinal orientations. Each orientation was presented 30 times, resulting in a total of 540 trials. The order of presentation was randomized for each participant.

To get participants accustomed with the stimuli and experimental procedure, they performed a training block with trial-based visual and auditory feedback before the actual experiment. The training block consisted of 12 trials. The whole experiment took about one hour to complete.

Results

Figure 4 shows identification errors for both older and younger participants for angles around vertical and horizontal. Figure 4 (left) indicates errors for orientations around horizontal, whereas Figure 4 (right) indicates errors for orientations around vertical. Errors were computed as the angular difference between the actual orientation of the Gabor and the orientation of the bar that participants were asked to adjust. Negative errors indicate an adjustment of the bar anticlockwise away from the orientation of the Gabor, and positive errors indicate an adjustment of the bar clockwise away from the orientation of the Gabor.

Absolute errors were submitted to a mixed-design 2 (age group) × 2 (orientations) × 9 (angular difference) ANOVA. Mauchly's test of sphericity indicated that the assumption of sphericity had been violated for the main effect of angular difference and the orientation × angular difference interaction, and degrees freedom were corrected using the Greenhouse-Geisser correction ($\varepsilon = 0.52$ and $\varepsilon = 0.65$, respectively).

The ANOVA revealed main effects of orientation ($F(1,40) = 14.6, p < 0.01$), angular difference ($F(4, 167) = 38.12, p < 0.001$), and the following interactions: age × orientation ($F(1,40) = 5.65, p < 0.05$), orientation and angular difference ($F(5,206) = 11.46, p < 0.001$), and age ×orientation × angular difference ($F(5,206) = 2.9, p < 0.02$). The main effect of age ($F(1,40) = 1.76, p = 0.19$) and the interaction of age and angular difference ($F(4,167) = 1.68, p = 0.16$) were not significant.

Across all age groups, angular errors were smaller for orientations around horizontal (Figure 4 [left]; $M = 4.5°$, $SD = 2.8°$) compared to those around vertical (Figure 4 [right]; $M = 6.7°$, $SD = 3.4°$). Age differences were more pronounced for near-vertical (Figure 4 [right]; Older: $M = 8.1$, $SD = 3.6$, Younger: $M = 5.7$, $SD = 2.9$), than for near-horizontal orientations (Figure 4 [left]; Older: $M = 4.2$, $SD = 1.8$, Younger: $M = 4.8$, $SD = 3.4$).

To further quantify the three-way interaction between age, orientation, and angular difference, we conducted independent *t*-tests between both age groups at each angular difference (Table 2). Significant differences between age groups mainly occurred at close-to-vertical orientations. Taken together, our results replicate the oblique effect by showing that, across all age groups, orientation reproduction was worse for oblique

		Error					CI	
Angle	Age group	*Mean*	*SD*	t value	p value	Cliff's delta	Low	High
Horizontal								
−40°				$t(36.4) = 2.79$	0.008^{**}	0.51	0.15	0.75
	Younger	3.49	2.82					
	Older	4.17	3.30					
−30°				$t(39.5) = 0.98$	0.33	0.06	−0.3	0.4
	Younger	4.82	4.99					
	Older	3.81	2.55					
−20°				$t(38.4) = 1.7$	0.12	0.19	−0.12	0.47
	Younger	7.26	5.76					
	Older	4.71	3.40					
−10°				$t(37.7) = 0.94$	0.35	0.014	−0.3	0.35
	Younger	5.20	5.70					
	Older	3.53	2.72					
0°				$t(36.8) = -0.6$	0.55	−0.08	−0.4	0.26
	Younger	1.35	1.31					
	Older	1.28	1.29					
10°				$t(39) = 1.1$	0.27	0.25	−0.08	0.54
	Younger	4.80	3.62					
	Older	4.24	2.24					
20°				$t(38.9) = 0.83$	0.41	0.18	−0.18	0.49
	Younger	6.69	5.77					
	Older	6.99	6.25					
30°				$t(39.8) = 0.7$	0.49	0.1	−0.24	0.42
	Younger	5.79	4.36					
	Older	5.84	4.20					
40°				$t(37.8) = 0.32$	0.75	0.14	−0.21	0.45
	Younger	3.53	3.43					
	Older	3.45	3.40					
Vertical								
−40°				$t(35) = -0.33$	0.74	0.01	−0.35	0.36
	Younger	3.09	2.89					
	Older	3.48	2.66					
−30°				$t(36) = -0.56$	0.58	0.07	−0.40	0.27
	Younger	4.88	3.83					
	Older	5.35	4.38					
−20°				$t(31.8) = -1.3$	0.19	−0.22	−0.53	0.15
	Younger	6.58	5.44					
	Older	9.45	6.90					
−10°				$t(29) = -2.2$	0.03^{*}	0.33	−0.6	0.03
	Younger	4.71	3.44					
	Older	8.03	6.55					
0°				$t(34.4) = -1.3$	0.2	−0.37	−0.66	0.03
	Younger	1.89	1.71					
	Older	1.40	1.87					
10°				$t(36.2) = 2.9$	0.006^{**}	0.48	0.11	0.73
	Younger	9.07	5.53					
	Older	14.39	6.42					
20°				$t(33.5) = 2.1$	0.05^{*}	0.36	−0.02	0.65
	Younger	9.58	5.08					
	Older	13.44	7.30					
30°				$t(36.5) = 2.3$	0.03^{*}	0.42	0.05	0.69
	Younger	6.57	4.55					
	Older	10.25	4.53					
40°				$t(36.3) = 2.2$	0.03^{*}	0.4	0.04	0.67
	Younger	4.70	3.38					
	Older	7.25	3.99					

Table 2. Descriptive statistics and results from Welch two sample t-tests between age groups for all tested orientations, Cliff's delta and corresponding confidence intervals (CI). *Notes*: $^{*}p < 0.05$, $^{**}p < 0.01$.

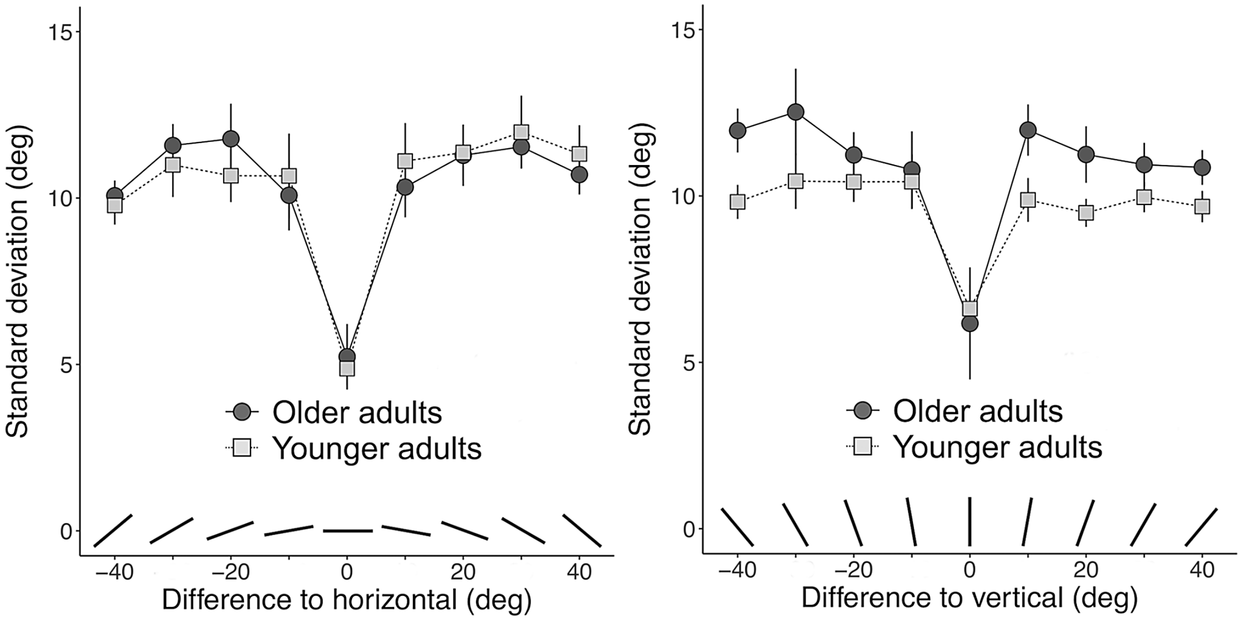

Figure 5. Averaged standard deviations of reproduction errors (deg) for older (dark gray) and younger adults (light gray) for orientations around horizontal (left) and vertical (right). Error bars represent standard error from the mean.

orientations compared to cardinal ones. In addition, reproduction was better for oblique orientations near horizontal than for oblique orientations near vertical. More importantly, however, older adults performed worse than younger adults for oblique orientations near-vertical, in particular to the right of vertical, but not for orientations close to horizontal.

We investigated the response variability, which provides a measure of perceptual uncertainty by computing the standard deviation of each participant's reproduction error for each orientation. Figure 5 shows those standard deviations averaged across participants. Standard deviations were submitted to a mixed-design 2 (age group) × 2 (orientations) × 9 (angular difference) ANOVA. Mauchly's test of sphericity indicated that the assumption of sphericity had been violated for the main effect of angular difference and the interactions between age group x angular difference, orientation x angular difference and age group × orientation × angular difference, and degrees freedom were corrected using the Greenhouse-Geisser correction. The ANOVA revealed a main effect of angular difference ($F(4,164) = 19.75$, $p < 0.01$). As can be seen in Figure 5, there is a clear oblique effect with a relatively low variability (higher precision) for cardinal compared to oblique orientations. In addition, the ANOVA revealed an age x orientation interaction ($F(1,40) = 5.3$, $p < 0.05$). Welch two-sample t-tests showed that the age-difference was marginally significant for orientations around vertical ($t(37) = -1.9$, $p = 0.065$; older: $M = 10.8$, $SD = 2$; younger: $M = 9.7$, $SD = 2$) but not for orientations around horizontal ($t(39) = 0.02$, $p = 0.98$; older: $M = 10.2$, $SD = 2$; younger: $M = 10.3$, $SD = 3$).

All other main effects and interactions were not significant and overall, response variability was comparable for orientations around vertical and those around horizontal (age, $F(1,40) = 0.7$, $p = 0.4$, orientation, $F(1,40) = 0.03$, $p = 0.85$, age × angular difference, $F(4,164) = 0.46$, $p = 0.77$, orientation × angular difference, $F(6,223) = 2.08$, $p < 0.06$, age × orientation × angular difference, $F(6,223) = 0.88$, $p = 0.5$).

Discussion

In Experiment 2, we asked participants to reproduce orientations. Our results confirm the results of Experiment 1 in that age-related changes are most prominent for oblique orientations and highlight the selectivity of age-related changes. Reproduction errors for oblique orientations were overall larger than for cardinal orientations, confirming the oblique effect. There was no age difference for cardinal orientations. When comparing errors for oblique orientations near vertical (Figure 4 [right]) and near horizontal (Figure 4 [left]), we observed two intriguing results. First, overall performance was better for oblique orientations near horizontal than for those near vertical. Second, and more importantly, older adults had larger reproduction errors than younger adults for oblique orientations around vertical, but there was no age difference for oblique orientations around horizontal. These results show that age-related changes in performance are much more complex than simply denoting a difference between oblique and cardinal orientations, as shown in Experiment 1. We will discuss these results in more detail within the General Discussion. Interestingly, participants had a bias to respond in directions away from the cardinal orientations as can be seen by negative reproduction errors for orientations counterclockwise away from cardinal and positive reproduction errors for orientations clockwise away from cardinal. This bias seems to be linked to increased response variability and lower precision in responses for oblique compared to cardinal orientations. Interestingly, the difference in response variability between all tested oblique orientations was relatively small. Previous studies have shown that an increased bias away from cardinal orientations relates to increased uncertainty for oblique orientations when judging the average orientation of scattered Gabor patches (Tomassini, Morgan, & Solomon et al., 2010), which is in accordance with our results. With regard to age differences, we found that response variability for oblique orientations around vertical was marginally higher for older compared to younger adults, whereas the age difference was smaller and nonsignificant for oblique orientations around horizontal. In Experiment 1, we only tested oblique orientations close to vertical, and therefore our results suggest that age differences in orientation discrimination for oblique orientations, as observed in Experiment 1, relate to an increased uncertainty in responses. This visual uncertainty is likely related to age-related changes on the neurophysiological level with increased sensory noise for older compared to younger adults, limiting response precision (Girshick et al., 2011).

General discussion

In two Experiments, we investigated age-related changes for orientation discrimination. In Experiment 1, we determined discrimination thresholds for two sequentially presented Gabor stimuli for four baseline orientations (horizontal, vertical, 22.5° and 45°) for younger and older adults. Unsurprisingly, there were significant differences in performance between cardinal and oblique orientations for both age groups; thresholds for oblique orientation were overall three times larger than those for cardinal orientations. These results are in line with the oblique effect, a phenomenon that describes the relative deficiency in performance for oblique compared to cardinal orientations. The oblique effect has been confirmed for many visual tasks and stimuli (Appelle, 1972; Hansen & Essock, 2004; Keil & Cristóbal, 2000). Interestingly, however, we found age differences only for oblique gratings, with older participants performing worse than younger participants. For cardinal gratings, older adults performed as well as younger adults.

In Experiment 2, we asked participants to reproduce the orientation of Gabors that were oriented horizontally, vertically, and clockwise and counterclockwise away from those two cardinal orientations. Our results confirm those from Experiment 1. First, they provide strong evidence for the oblique effect in both age groups. Second, and more importantly, they highlight the selectivity of age-related changes to an even greater extent such that the age-difference for oblique gratings was particularly distinct for oblique orientations around vertical.

In comparison to previous studies assessing age differences in orientation perception, our results serve as the missing link between previous neurophysiological (Hua et al., 2006; Schmolesky et al., 2000) and human behavioral studies (Delahunt et al., 2008; Govenlock et al., 2009). Single-cell recordings have found that neurons in primary visual areas have broader tuning curves and are less selective for orientations in senescent cats and monkeys compared to younger ones (Hua et al., 2006; Schmolesky et al., 2000; Yu et al., 2006). Neurophysiological results often translate to human behavior; however, recent studies did not find behavioral evidence for age-related changes in orientation-selective mechanisms (Delahunt et al., 2008; Govenlock et al., 2009; but also see Casco et al., 2017). Several explanations have been proposed. It has been suggested that neural networks involved in orientation selective mechanisms reorganize with age to allow efficient orientation perception despite changes in neural sensitivity (Delahunt et al., 2008). It is further possible that only a subset of neurons in early visual areas contributes to psychophysical orientation judgements (Govenlock et al., 2009), an idea that is supported by neurophysiological studies that found small numbers of neurons that remained selective for orientations in older cats and monkeys (Hua et al., 2006; Schmolesky et al., 2000). However, a third and not necessarily exclusive possibility based on the results from our study is that the previous contradictory results from neurophysiological and human behavioral studies derive from the tested orientations: single-cell recordings were acquired from a variety of neurons tuned to different cardinal and oblique orientations, whereas human behavioral studies primarily concentrated on cardinal orientations, that is, vertical or horizontal. In light of our results, this strongly suggests that age-related neurophysiological changes are most pronounced for cortical neurons tuned to oblique orientations. The effect of aging on orientation selectivity in cortical neurons should be much smaller for cells tuned to cardinal compared to oblique orientations. Even though previous neurophysiological studies have shown that some cells of older animals retain stimulus selectivity (Hua et al., 2006; Schmolesky et al., 2000), to our knowledge, the specific orientations of those cells has so far not been reported.

Because orientation-specific neurons are organized in orientation columns in primary visual areas (Hubel & Wiesel, 1959), it is likely that neurophysiological changes in primary visual cortex are responsible for the age differences as observed in this study. But even though the oblique effect is primarily believed to originate from response properties of neurons in primary visual cortex (Furmanski & Engel, 2000), its neural basis is still unknown, and it needs to be mentioned that also other areas could be involved in the age differences in the oblique effect (Westheimer, 2003).

Our results highlight that orientation perception selectively changes with age. The underlying mechanisms, however, remain unclear. The oblique effect has been related to the relevance and prevalence of orientations in our visual surrounding. The analysis of real-world scenes, for example, has found a prevalence of horizontal and vertical contours in indoor, outdoor and even naturalistic scenes (Coppola, Purves, et al., 1998; Keil & Cristóbal, 2000). Visual experience has been shown to affect the development of the visual system (Barlow, 1975; Mitchell, 1978) to an extent that observers' internal model for orientation perception matches the local orientation distribution in real-world scenes (Girshick et al., 2011). Our results indicate that this development continues into older age, which would further suggest that the visual system ages optimally given the visual input it receives (Moran, Symmonds, Dolan, & Friston, 2014).

In addition to the general performance difference between cardinal and oblique orientations in interaction with age, results from Experiment 2 add another intriguing result: performance was better for oblique orientations near horizontal than for those near vertical, an effect that was enhanced for older adults. A general advantage for processing horizontal over vertical and oblique information has been shown in a variety of other domains such as attention (Carrasco, Talgar, & Cameron, 2001; Pilz, Roggeveen, Creighton, Bennett, & Sekuler et al., 2012), motion perception (Pilz, Miller, & Agnew, 2017; Pilz & Papadaki, 2019) and the accuracy of eye movements (Ke, Lam, Pai, Spering, Brown, & Raymond, 2013; Rottach, Zivotofsky, Das, Averbuch-Heller, Discenna, Poonyathalang, & Leigh, 1996). However, not many studies have investigated performance for orientations near horizontal or near vertical, and the question of why we are better at processing information near horizontal is not a trivial one. In ferret visual cortex, for example, an increased area of cortical volume has been shown to be allocated to horizontal and near-horizontal orientations (Coppola & White, 2004; Coppola et al., 1998), which has been suggested to reflect the demonstrated increased scene content for horizontal and near horizontal orientations (Hansen & Essock, 2004; Keil & Cristóbal, 2000). Behaviorally, it has been found that orientation categorization is more precise at near-horizontal compared to near-vertical orientations (Quinn, 2004). The above studies strongly suggest that an advantage in discriminating, categorizing, or replicating orientation near horizontal is based on the prevalence of those orientations in our visual environment.

In this study, an extensive ophthalmologic assessment before the experiment was not conducted, and older participants were merely screened for optical deficits such as cataract, glaucoma, and macular degeneration. Therefore we are unable to fully exclude the possibility that age-related changes in optical factors and an accompanying reduced retinal illuminance affected our results. For example, the density of the crystalline lens increases with age (Xu, Pokorny, & Smith, 1997). Furthermore, drusen, an early sign of macular degeneration, develop with increasing age (Vinding, 2009). Given that most age-related optical changes develop over time, it is possible that at least some older participants from this study already experienced some decline in retinal illuminance without having been officially diagnosed with a cataract or macular degeneration. However, previous studies found that changes in retinal illuminance did not account for age-related changes in tasks related to apparent motion or orientation perception (Betts, Sekuler, & Bennett, 2007; Roudaia, Bennett, Sekuler, & Pilz, 2010). Crucially, it needs to be noted that the changes observed in our study were highly selective to some orientations. If changes in retinal illuminance affected orientation perception, we would have expected a general age-related decline in performance across all tested orientations.

In conclusion, our results show that orientation perception selectively changes with age, such that age-differences are most pronounced for oblique orientations, in particular those close to vertical. These results provide a missing link between neurophysiological studies that found an age-related decline in orientation perception and behavioral studies in humans that did not find such effect but only tested cardinal orientations. Our results show that changes in orientation perception do not relate to a general decline of perceptual abilities and suggest that age-related changes relate to a lifelong adaptation to the visual environment.

Keywords: orientation perception, healthy aging, oblique effect, cardinal, oblique, visual perception

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