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Changes of tuning but not dynamics of contrast adaptation with age

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ABSTRACT

Normal aging results in pronounced optical and neural changes in the visual system. Processes of adaptation are thought to help compensate for many of these changes in order to maintain perceptual constancy, but it is uncertain how stable adaptation itself remains with aging. We compared the dynamics of adaptation in young (aged 19–24 years) and older (aged 66–74) adults. Contrast thresholds for Gabor patterns were tracked during and after 300 s adaptation to vertical and horizontal Gabor patches. The time course of contrast adaptation and asymptotic adaptation magnitude were similar between older and young adults when normalized for their respective baseline thresholds. Older adults showed stronger transfer of adaptation to the orthogonal orientation and there was an asymmetry between the transfer of adaptation between the horizontal and vertical orientations for both groups. These results suggest age-related changes in orientation tuning while the processes of cortical contrast adaptation remain largely intact with aging.

1. Introduction

Visual function declines markedly with aging, as measured by a variety of tasks including visual acuity, orientation discrimination, motion perception and reading speed (Bennett, Sekuler, & Sekuler, 2007; Betts, Sekuler, & Bennett, 2007; Delahunt, Hardy, & Werner, 2008; Li, Patel & Kwon, 2017, also see Owsley, 2016 for review). Sensitivity losses result from both optical and neural changes. For example, optical degradation, such as reduced retinal illuminance and increased lens pigment density, contribute to impairments in spatial contrast sensitivity (Loewenfeld, 1979; Pokorny, Smith, & Lutze, 1987; Said & Weale, 1959; Weale, 1961). However, losses remain even when optical differences are accounted for (Ball & Sekuler, 1986; Bennett, Sekuler, & Ozin, 1999; Betts et al., 2007; Elliott et al., 2009; Elliott, Whitaker, & MacVeigh, 1990; Sekuler, Bennett, & Mamelak, 2000; Spear, 1993).

Senescent changes also affect neural function including gene expression and synaptic regulation (Loerch et al., 2008). Studies of older rhesus monkeys showed that V1 and MT neurons have lower sensitivity to contrast, with MT neurons influenced more by aging than V1 neurons (Yang et al., 2008). V1 neurons also exhibit other age-related changes including reduced optimal spatial frequency, spatial resolution, optimal temporal frequency and high temporal frequency cutoffs (Zhang et al., 2008). In addition, broader orientation and motion tuning (less selectivity) was found for V1, V2 and MT cells in older monkeys (Liang et al., 2010; Schmolesky, Wang, Pu, & Leventhal, 2000; Yu, Wang, Li, Zhou, & Leventhal, 2006). Importantly, all the animals in these studies were examined ophthalmoscopically and had no retinal pathology, glaucoma, or differences in intraocular pressure, suggesting age-related alterations in cortical neuronal responses were not due to optical changes. Higher spontaneous activity and decreased signal-to-noise ratio have also been reported with aging for both monkeys and human (Betts et al., 2007; Fu, Yu, Ma, Wang, & Zhou, 2013; Yang et al., 2008; Zhang et al., 2008). These changes have partly been attributed to decreased proportion of GABA neurons and less effective GABAergic inhibition in the aging brain (Hua, Kao, Sun, Li, & Zhou, 2008; Leventhal, Wand, Pu, Zhou, & Ma, 2003). This reduced inhibition predicts weaker stimulus selectivity of cortical neurons, but psychophysical evidence for this has been mixed. For example, masking studies have found similar orientation tuning between young and older adults (Delahunt et al., 2008; Govenlock, Taylor, Sekuler, & Bennett, 2009). In contrast, Wilson, Mei, Habak, and Wilkinson (2011) used an adaptation paradigm and showed broader tuning bandwidth for face viewpoint in older adults.

At least some of the effects of age-related visual losses could be counteracted by processes of adaptation, which continuously calibrate visual coding to match neural responses for the stimuli the visual system is currently exposed to (Webster, 2015). Importantly this calibration may occur in similar ways whether it is the environment or the observer that is changing. Thus, adjustments through adaptation could discount some of the sensitivity changes resulting from aging. For example, color perception and the relative sensitivity of the different cone classes

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remains fairly constant with aging despite the dramatic changes in the spectral filtering effects of the lens (Hardy, Frederick, Kay, & Werner, 2005; Knoblauch, Vital-Durand, & Barbur, 2001; Werner, Delahunt, & Hardy, 2004; Wuerger & Osorio, 2013).

However, to maintain calibrations in the aging visual system, the processes of adaptation must themselves remain stable. In older observers, alterations in these processes could lead to stronger adaptation (e.g. if the neural responses more readily “fatigue”) or weaker (e.g. if the processes mediating the response changes show less plasticity). Despite the potential importance of maintaining proper adjustments, the properties of adaptation with aging remain largely unexplored. However, studies of cortical adaptation effects suggest that the strength of adaptation remains comparable in older and younger observers (Elliott, Hardy, Webster, & Werner, 2007; Elliott, Werner, & Webster, 2012; Wilson et al., 2011). Moreover, age-related differences in aftereffects could reflect changes in neural sensitivity or tuning rather than changes in adaptability (Wilson et al., 2011). For example, broader tuning predicts less selective aftereffects, and thus measured changes in aftereffects could occur because of changes in the properties of the channels or networks, even if the processes regulating neural sensitivity remain intact. Thus changes in cortical visual neurons (Govenlock et al., 2009; Hua et al., 2008; Pilz, Äijälä, & Manassi, 2020; Schmolesky et al., 2000), or in network properties (King, Fogel, Albouy, & Doyon, 2013; Lee, Grady, Habak, Wilson, & Moscovitch, 2011; Wolpe et al., 2020) could affect how short-term adaptation is manifest. Similarly, a weaker or stronger adaptation effect could occur because of optical or neural factors that affect sensitivity to the stimulus. Consequently to isolate an age-related change in adaptation it is important to equate sensitivity for the observers (Hardy et al., 2005).

Age-related studies on adaptation have tended to focus on steady-state adaptation in the system, and thus leave open the possibility that aging might impact the dynamics or rate of the adaptive adjustments. For example, dark adaptation is slower in older adults because of changes in photoreceptor kinetics (Birren & Shock, 1950; Owsley & McGwin, 1999). However, it is not known whether the dynamics also change for more central, cortical stages of visual processing. In this study our aim was to compare these dynamics in older and young observers by measuring changes in contrast sensitivity with orientation adaptation, a task that is likely to reflect early stages of cortical coding (Gardner et al., 2005; Ohzawa, Sclar, & Freeman, 1985).

2. Methods

2.1. Observers

Nine older adults (Ages from 66 to 74; mean age = 69.8, SD = 2.4; 8 female and 1 male) and nine young adults (Ages from 19 to 29; mean age = 23.3, SD = 4.7; 6 female and 3 male) participated in the experiment. All had normal or corrected-to-normal vision for the viewing distance of the display. Participation was with informed consent and followed protocols approved by the University of Nevada, Reno Institutional Review Board.

2.2. Apparatus and stimuli

Stimuli were displayed on a gamma-corrected Display++ LCD monitor (Cambridge Research Systems) calibrated with a PR-655 spectrophotometer (PhotoResearch). The background of the display was maintained at a mean luminance of 50 cd/m^2 and CIE 1931 chromaticity of $x = 0.30$, $y = 0.31$.

Both adapt and test stimuli were Gabor patches with a spatial frequency of 1.5 cycle/degree. The low spatial frequency was chosen to reduce potential age differences in optical blur. The adapting stimuli had a diameter of 5 degree (SD = 1.25° of the Gaussian kernel) and the test stimuli had a diameter of 4 degree (SD = 1° of the Gaussian kernel). The adapter had a fixed peak Michelson contrast of 90% and was counterphase flickered at 5 Hz. The contrast of the test stimulus was varied in a staircase procedure. Stimuli were presented at the center of the screen (screen size: 50 by 39 deg) and were viewed binocularly from a distance of 75 cm. A 0.25 deg red circle was presented as fixation point throughout the experiment.

2.3. Procedure

The experimental protocol was the same as that of Gao, Webster, and Jiang (2019). Specifically, each session lasted 900 s and consisted of a 200 s pre-adapt, 300 s adapt and 400 s post-adapt period. The adapting orientation remained constant during each run (vertical or horizontal). Thresholds were measured for vertical and horizontal orientations interleaved during the run, and were tracked by separate staircases (2-down, 1-up) for each orientation. Throughout the run, a test stimulus was alternated with the adapt stimulus or a gray screen (pre and post phases) with the following cycle: adaptor or gray screen 1.3 s, 0.25 s gray screen, test 0.2 s, 0.25 s gray screen (see Fig. 1). The initial contrast of the staircase was fixed at 2.5% contrast (0.4 log units). The staircase step size was initially 18.9% (0.075 log units) and changed to 12.2% (0.05 log units) after three reversals, and was then fixed at 5.9% (0.025 log units) after the 6th reversal. Participants were asked to press the left or right arrow key to indicate whether they could tell the orientation of the test stimulus, (a Yes/No task). The contrast of the test stimulus of the next trial would decrease or increase depending on the participant’s response to the current trial. Each participant was tested in two sessions, adapting to a vertical orientation in one and the horizontal orientation in the other. The order of the adapting orientation was counterbalanced across participants.

2.4. Analysis

Baseline threshold was defined as the average of the last 10 reversals for each orientation in the pre-adaptation period. To normalize the settings, the raw time course was divided by the baseline threshold measured in the pre-adaptation period. Thresholds and threshold elevations during adaptation and post-adapt period were assessed as a function of time in separate 3-way ANOVAs comparing age (Young vs. Older) orientation (Vertical vs. Horizontal) and time bin (6 time bins of 50 sec each for adaptation period and 8 time bins of 50 sec each for post-adapt period). To obtain the time constants for the buildup and decay of adaptation, the time course of threshold changes at the adapting orientation was fit by an exponential function $Y_1 = (y_0 - y_t)^*(1 - e^{-t/\tau 1})) + y_t$, where $y_0 - y_t$ represents the amplitude of the function, and $\tau 1$ represents the time constant of the adaptation period. y_t represents the trough response in the buildup phase. The time course of the -adapt period was fit by the exponential function $Y_2 = (Y_1\,(t') - y_p) * e^{-t/\tau 2} + y_p$, where $\tau 2$ represents the time constant of the post-adapt period. y_p means the plateau response in the decay period. t' is a constant 300 in our case so that the starting point of Y_2 (Y_0) equals to $Y_1(300)$.

3. Results

3.1. Experiment 1

3.1.1. Baseline threshold

We first explored whether there were age-related differences in contrast detection thresholds without adaptation to the gratings. Left panel of Fig. 2 plots the averaged baseline thresholds measured in the pre-adapt stage for vertical and horizontal orientations for both older and young adults. The right panel of Fig. 2 plots the individual baseline thresholds for vertical and horizontal orientations for both older and young adults. A 2-way ANOVA (age by test orientation) showed that the interaction between the two was not significant ($F(1, 16) = 0.6$, $p = 0.47$, $\eta^2 = 0.03$). There was a marginally significant main effect of age ($F(1, 16) = 4.3$, $p = 0.05$, $\eta^2 = 0.21$) but not for orientation ($F(1, 16) =$

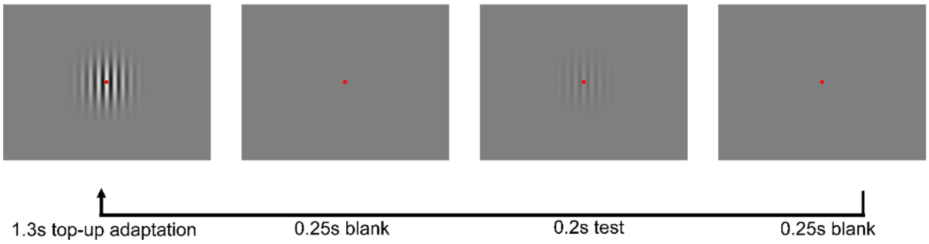

Fig. 1. An example trial during the adapting phase. In the pre-adapt and post-adapt phases, the 1.3 s top-up adaptation was substituted by a uniform gray screen with fixation only.

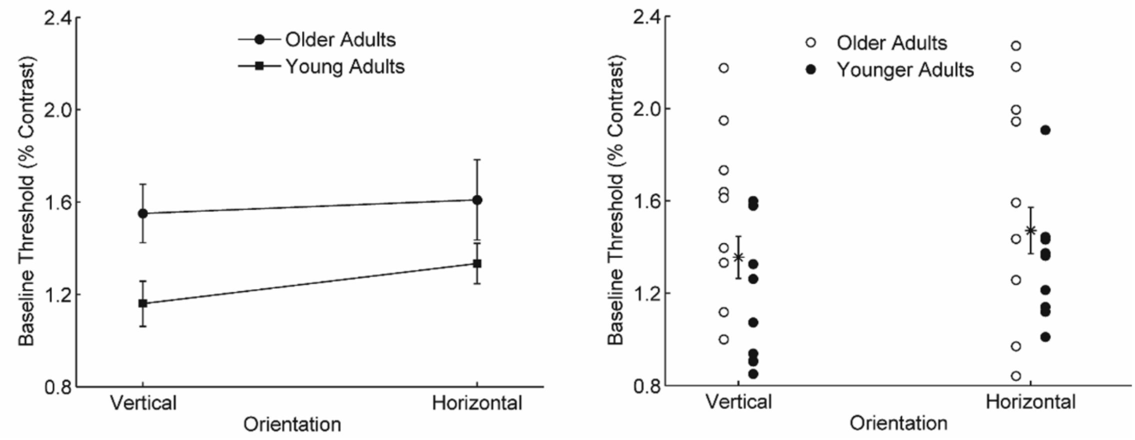

Fig. 2. Baseline threshold. Left panel showed averaged baseline threshold for vertical and horizontal orientation, with circles representing thresholds for older group and squares representing thresholds for young group. In the right panel, open circles show individual baseline threshold for older adults and solid circles show individual baseline threshold for younger adults. Asterisks represent the mean threshold of vertical and horizontal orientations for all participants. Error bars represented one standard error.

2.3, p = 0.15, η^2 = 0.12; Vertical orientation: Mean = 1.36%, SD = 0.39%; Horizontal orientation: Mean = 1.47%, SD = 0.43%). Older adults (Mean = 1.6%, SD = 0.44%) showed a significantly larger baseline threshold than young adults (Mean = 1.3%, SD = 0.28%).

3.1.2. *Threshold elevations at the adapting orientation*

Fig. 3 compares the time courses of contrast adaptation between young and older adults, with the raw time courses of the thresholds during the experiment shown in panel A and time courses as multiples of baseline threshold shown in panel B. To further characterize the threshold changes during the adaptation and post-adapt period, we sampled the thresholds by averaging within 50 s time bins from the start of the adaptation and post-adapt phase (Fig. 4). The relatively long time bin (50 s) was chosen due to the slow buildup and decay of the adaptation effect during the 300 s adaptation period and 400 s post-adapt period. Left and middle panels show results when adapting to the vertical and horizontal orientation, while the right panels shows the settings averaged for the two adapt orientations. (Note for all binned plots the error bars represent ±2 standard errors in order to more clearly illustrate the variability in the settings.)

When the test grating had the same orientation as the adapting grating, Fig. 4A shows raw thresholds averaged over 6 time bins during adaptation and over 8 time bins during post-adapt period, with adapting to vertical orientation in the left panels and adapting to horizontal orientation in the right. The raw thresholds during the adaptation period were assessed with a mixed design three-way ANOVA, with age group, time bin, and adapting orientation as independent variables. This revealed a main effect of time bin (F (5, 80) = 97, $p < 0.001$, $\eta^2 = 0.86$) and age (F (1, 16) = 7.3, p = 0.016, $\eta^2 = 0.31$) but not of orientation (F (1, 80) = 0.9, p = 0.36, $\eta^2 = 0.\ 05$). The only significant interaction was found between time bin and age (F (5, 80) = 7.9, p = 0.013, $\eta^2 = 0.33$). Posthoc comparisons with Bonferroni correction showed that the young and older observers did not differ during the first 3 time bins (0–150 s) but diverged at later times with significant differences for the bins from 150 to 300 s (Time bin 150–200 s: older adults: Mean = 5.19%, SD = 1.30%; young adults: Mean = 4.03%, SD = 0.87%, t(34) = 3.1, $p < 0.02$; Time bin 200–250 s: older adults: Mean = 5.62%, SD = 1.45%, young adults: Mean = 4.08%, SD = 0.93%, t (34) = 3.80, $p < 0.002$; Time bin 250–300 s: older adults: Mean = 5.51%, SD = 1.26%, young adults: Mean = 4.07%, SD = 0.61%, t (34) = 4.3, $p < 0.001$). Thus, at later stages of the adaptation period, older adults consistently showed larger contrast detection thresholds at the adapting orientation compared to young adults. However, as noted below, these differences did not occur after normalizing for the differences in the baseline thresholds.

For the post-adapt period, a mixed design three-way ANOVA for raw thresholds again showed a main effect of time bin (F(7,112) = 161.9, $p < 0.001$, $\eta^2 = 0.91$) and age (F(1,16) = 8.5, p = 0.01, $\eta^2 = 0.35$) but not of orientation (F(1,112) = 1.2, p = 0.29, $\eta^2 = 0.\ 07$). The only significant interaction was again found between time bin and age (F (7, 112) = 8.1, $p < 0.001$, $\eta^2 = 0.34$). Post-hoc comparisons with Bonferroni correction showed significant larger contrast detection threshold for older adults compared to young adults across all time bins (all $ps < 0.05$). For both older and young adults threshold of first time bin (0–50 s) was significantly larger than the later ones (all $ps < 0.05$). Thus, the larger contrast detection threshold of older adults during the later stage of adaptation was persistent throughout our 400 s post-adapt period.

Because there was a difference between baseline threshold between older and young adults, we also analyzed thresholds after normalizing by the baseline thresholds. Fig. 4B shows these normalized thresholds averaged over the same time bins and for adapting orientations as in Fig. 4A. After normalization, older adults tended to have a larger adaptation effect when adapting to horizontal while a weaker

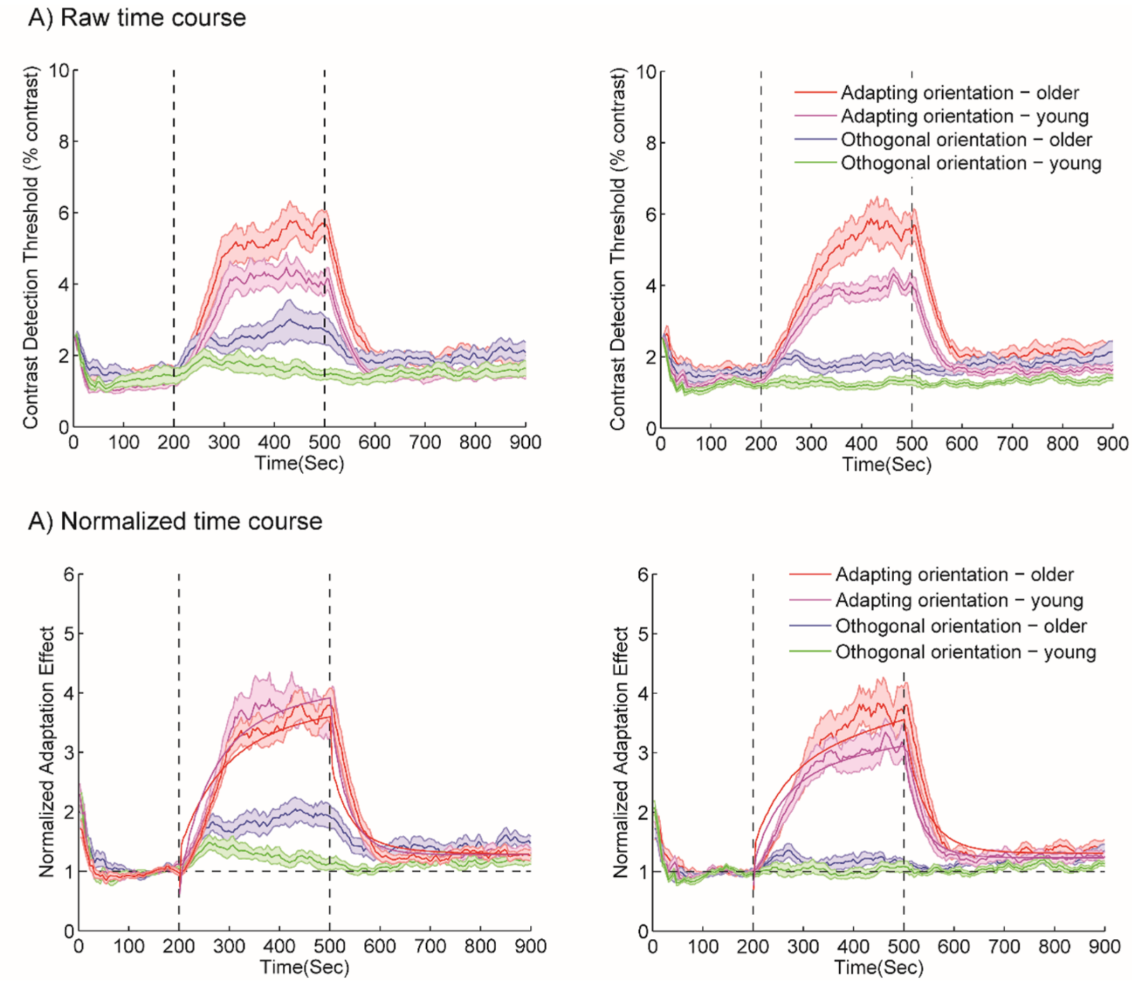

Fig. 3. Time course of contrast adaptation for young and older participants. Panel A showed raw time course and Panel B showed normalized time course. Left panels showed results for adapting vertical orientation and right panels showed results for adapting horizontal orientation. The smooth lines represented the average of the exponential fitting across individuals and the shaded areas represented one standard error.

adaptation effect for the vertical adaptor. This was because the ratio of the baseline thresholds for older vs. young observers differed between the vertical and horizontal orientations.

For the normalized threshold elevations during the adaptation period, a mixed design three-way ANOVA with age group, time bin, and adapting orientation as independent variables only revealed a main effect of time bin ($F(5, 80) = 92.9$, $p < 0.001$, $\eta^2 = 0.85$) but not of age ($F(1, 16) = 0.08$, $p = 0.79$, $\eta^2 = 0.005$) or orientation ($F(1, 80) = 3.9$, $p = 0.07$, $\eta^2 = 0.19$). Posthoc comparisons with Bonferroni correction showed that threshold elevations in the later four time bins (100 – 300 s) were significantly larger than those of the first two time bins (0–100 s). This indicated that the two groups showed a similar time course of the buildup and reached a similar level of asymptotic adaptation. Similarly, a mixed design three-way ANOVA for threshold elevation (as multiples of baseline threshold) in the post-adapt period only revealed a significant main effect for time bin ($F(7, 112) = 113$, $p < 0.001$, $\eta^2 = 0.88$). Posthoc comparisons with Bonferroni correction showed that threshold elevations in the later six time bins (100 – 400 s) were significantly smaller than those of the first two time bins (0–100 s). This indicated that the two groups showed similar time course of the decay and reached similar levels of residual responses by the end of our 400 s post-adapt period. We also compared the threshold elevations in the last time bin of post-adapt period normalized by the pre-adapt baseline. For both vertical and horizontal adaptors, the ending threshold was significantly (all $p < 0.007$), indicating that the adaptation effect did not decay to baseline within the 400 s post-test for both older and young adults.

In addition, we compared parameters of the exponential fits for the buildup and decay of the adaptation effects. The average fits are shown by the bold lines in Fig. 3B. The values obtained from the fits to individual observers' results are given in Supplementary Materials (Tables 1-5). For the buildup and decay period, two-way ANOVAs of the 5 parameter values showed no main effect of age or orientation and no interaction (all $ps > 0.19$). However, the lack of effects was likely due to the extreme values of the fits for some of the observers. Thus, we also fit the average time course for the two groups. Table 1 showed the 5 parameters for different adapting orientations for the two groups. When adapting to the vertical orientation, the time constant for buildup was 80.6 s for older adults and 68.2 s for young adults. When adapting to the horizontal orientation, the time constant for buildup was 110.4 s for older adults and 78.7 s for young adults. For older adults, the time constant for decay was 40.9 s and 37.8 s for vertical and horizontal adapters. For young adults, the time constant for decay was 35.5 s and 31.3 s for vertical and horizontal adapters. The exponential fitting of averaged time course indicated that the buildup and decay of adaptation effect was slightly slower for older adults.

In summary, when aftereffects were normalized for the baseline thresholds, the two groups showed a similar time course of the buildup and decay of adaptation, reaching similar amounts of asymptotic adaptation and residual responses. Both older and young adults also showed residual adaptation effects even at 400 s after the adapting period.

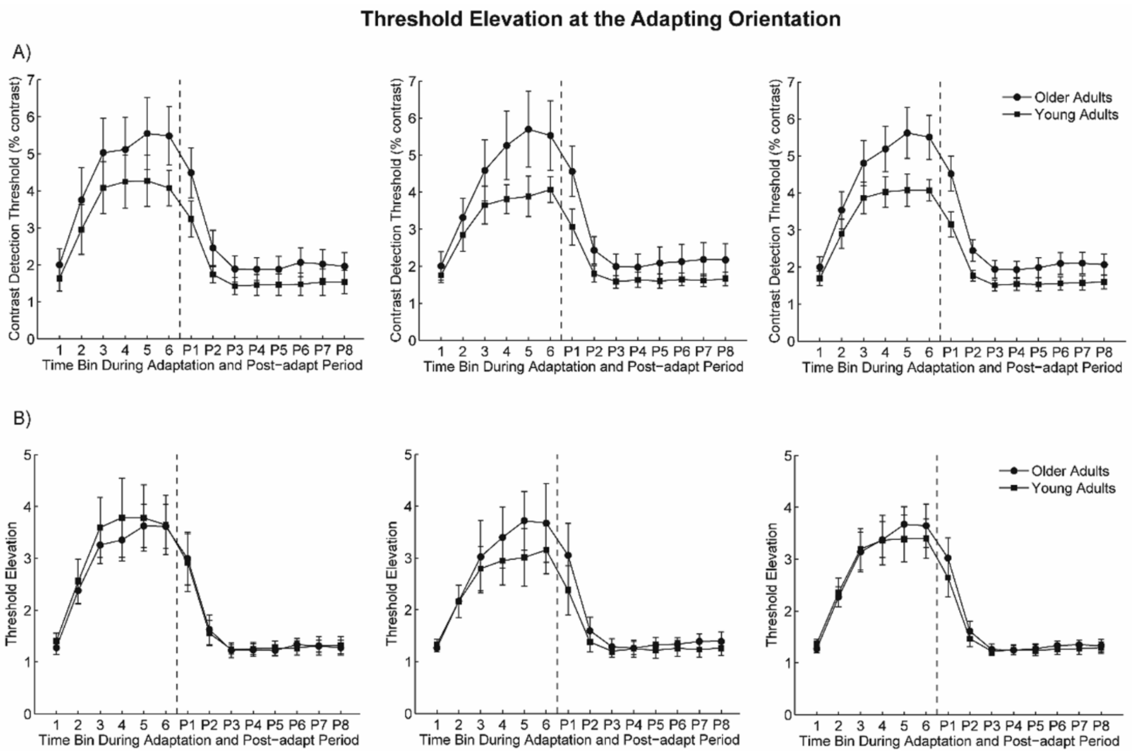

Fig. 4. Threshold averaged for each time bin during adaptation (time bins 1–6) and post-adapt period (times bins P1-P6) for young and older adults. A) Raw thresholds during adaptation and post-adapt period; B) Threshold elevation as multiples of baseline threshold during adaptation and post-adapt period. Left panels showed results when adapting to vertical orientation and middle panels showed results when adapting to horizontal orientation. The right panels showresults when data from adapting vertical and horizontal orientations are averaged. Circles represented threshold elevation for older group and squares represented threshold elevation for young group. The dashed vertical line indicated the separation between adaptation and post-adapt period. Error bars represent ± 2 standard errors.

Table 1
Five parameters obtained from the exponential fitting for averaged time course (normalized).

	Adapting orientation	y0	yt	tau1	yp	tau2
Older adults	vertical	3.8	0.6	80.6	1.2	40.9
	horizontal	4.1	0.7	110.4	1.3	37.8
Young adults	vertical	3.9	0.6	68.2	1.3	35.5
	horizontal	3.2	0.8	78.7	1.2	31.3

3.1.3. Threshold elevations at the orthogonal orientation

Fig. 5 shows the corresponding effects when the adapt and test orientation were orthogonal rather than the same as in Fig. 4. The left and middle panels again show results when adapting to the vertical and horizontal orientation, respectively, while the right panels show the averaged results for the two adapt orientations. The raw binned thresholds are shown in Fig. 5A. For settings during the adaptation period, a mixed design three-way ANOVA of raw thresholds, with age, time bin and orientation as factors revealed that there was a significant three-way interaction ($F (5, 80) = 4.3, p = 0.002, \eta^2 = 0.21$). There was also a main effect of age ($F (1, 16) = 7.8, p = 0.01, \eta^2 = 0.33$) and orientation ($F (1, 80) = 14, p = 0.002, \eta^2 = 0.48$). The two-way interaction between orientation and age was not significant ($F (1, 80) = 0.8, p = 0.38, \eta^2 = 0.05$). Posthoc comparisons showed that during adaptation, older adults had higher contrast detection thresholds for the orthogonal orientation than young adults ($t (214) = 7.2$. $p < 0.001$, older adults: Mean = 2.16%, SD = 0.86%, young adults: Mean = 1.47%, SD = 0.51%). For both groups, the orthogonal threshold change was larger when adapting to vertical than to horizontal ($t (107) = 5.3$. $p < 0.001$, adapt to vertical orientation: Mean = 2.1%, SD = 0.92%, adapt to horizontal orientation: Mean = 1.5%, SD = 0.49%).

For the post-adapt period, there was again a significant three-way interaction ($F (7, 112) = 5.7, p < 0.001, \eta^2 = 0.26$). We found a main effect of age ($F (1, 16) = 6.6, p = 0.02, \eta^2 = 0.29$) and marginally significant main effect of orientation ($F (1, 112) = 4.3, p = 0.056, \eta^2 = 0.21$), but no interaction between the two ($F (1, 112) = 0.0, p = 0.98, \eta^2 = 0.00$). Posthoc comparisons showed that older adults had larger thresholds for the orthogonal orientation than young adults ($t (286) = 8.9, p < 0.001$, older: Mean = 1.91%, SD = 0.57%, young: Mean = 1.40%, SD = 0.37%). For both groups, the threshold was higher when adapting to vertical than horizontal ($t (143) = 2.9$. $p = 0.004$, older: Mean = 1.75%, SD = 0.61%, young: Mean = 1.56%, SD = 0.45%).

Fig. 5B plots the corresponding results after again normalizing the settings for the observers' baseline thresholds. We assessed the threshold elevation using a mixed design three-way ANOVA, with age, time bin, and orientation as factors. In this case there was a significant three-way interaction ($F (5, 80) = 4.5, p = 0.001, \eta^2 = 0.22$). There was a main effect of age ($F (1, 16) = 10, p = 0.006, \eta^2 = 0.39$) and orientation ($F (1, 80) = 33, p < 0.001, \eta^2 = 0.67$). The two-way interaction between orientation and age was also significant ($F (1, 80) = 5.6, p = 0.03, \eta^2 = 0.26$). Posthoc comparisons showed that for both old and young adults, adapting to the vertical orientation induced larger threshold elevations on horizontal tests than vice versa (older: $t(53) = 9.1, p < 0.001$; young: $t(53) = 6.5, p < 0.001$). Older adults also showed larger threshold elevations at the orthogonal orientation for both adapting orientations (adapt vertical: $t (106) = 6.6, p < 0.001$; adapt horizontal: $t (106) = 3.6, p < 0.001$). Thus, the 2-way interaction could possibly be driven by the larger threshold elevation for the orthogonal orientation in older adults than in young adults when adapting to vertical orientation.

For the post-adapt period, there was a significant three-way interaction ($F (7, 112) = 5.2, p < 0.001, \eta^2 = 0.25$). We found a main effect of age ($F (1, 16) = 8.8, p = 0.009, \eta^2 = 0.35$) and orientation ($F (1, 112) = 7.3, p = 0.02, \eta^2 = 0.33$), but no interaction between orientation and age ($F (1, 112) = 2.5, p = 0.14, \eta^2 = 0.13$). Adapting to vertical induced

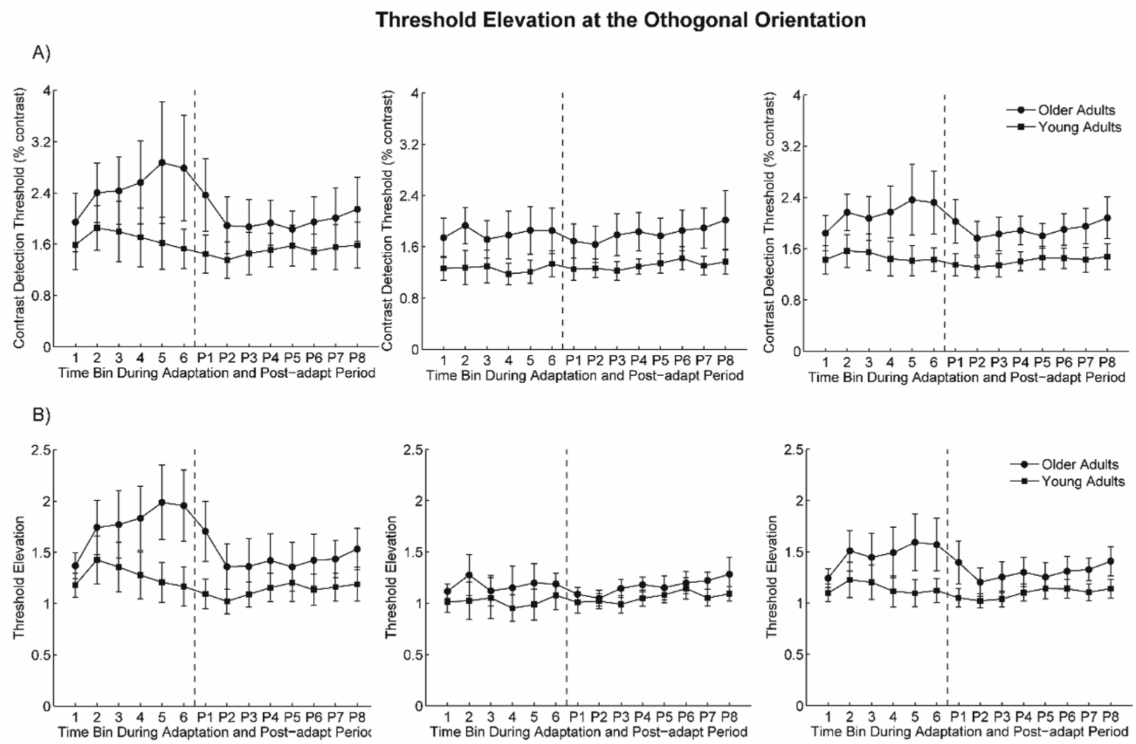

Fig. 5. Threshold of orthogonal orientation averaged for each time bin during adaptation (time bins 1–6) and post-adapt (times bins P1-P6) period for young and older adults. A) Raw thresholds during adaptation and post-adapt period; B) Threshold elevation as multiples of baseline threshold during adaptation and post-adapt period. Left panels showed results when adapting to vertical orientation and middle panels showed results when adapting to horizontal orientation. The right panels show results when data from the two adapting orientations are averaged. Circles represented threshold elevation for older group and squares represented threshold elevation for young group. The dashed vertical line indicated the separation between adaptation and post-adapt period. Error bars represent ± two standard errors.

larger orthogonal threshold elevations than adapting to horizontal, even during the post-adapt period (older: t (53) = 7.2, $p < 0.001$; young: t (53) = 2.6, $p = 0.03$). Both older and young adults also again had more elevated residual thresholds at both adapting orientations (adapt vertical: t (106) = 6.4, $p < 0.001$; adapt horizontal: t (106) = 4.5, $p < 0.001$). The threshold elevation at the end of post-adapt period remained significantly elevated for all conditions (all $p \le 0.05$).

Results for both the raw and normalized thresholds thus suggest that when tested at the orientation orthogonal to the adaptor, there was an asymmetry between the transfer of adaptation between the horizontal and vertical orientations. For both vertical and horizontal orientations older adults also showed larger threshold changes and these differences remained throughout the adaptation and post-adapt period, though these differences did not occur when normalizing for the respective baseline thresholds.

4. Discussion

To summarize, in this study we explored the effects of normal aging on the properties of spatial contrast adaptation. Contrast adaptation strongly affects threshold sensitivity and suprathreshold perceived contrasts. It is thought to reflect response changes at early cortical levels, because the adaptation is orientation selective, shows interocular transfer, and is apparent in single unit and fMRI measurements of adaptation in V1 (Blakemore & Campbell, 1969; Blakemore & Nachmias, 1971; Dragoi, Sharma, & Sur, 2000; Fang, Murray, Kersten, & He, 2005). As such this type of adaptation is thought to play a critical role in calibrating early cortical activity for changes in the environment or the observer. We asked how stable the magnitude and temporal dynamics of this adaptation might be with aging. Our results point to changes in tuning of the adaptation in older adults but no apparent changes in the time course.

Compared to younger adults, the older participants showed significantly stronger sensitivity losses for gratings that were orthogonal to the adapting gratings. It is difficult to parcel out whether differences in the tuning of aftereffects reflect stronger adaptation or less selectivity in the adapted channels. However, our results are at least consistent with the possibility that orientation tuning is weaker in older adults. As noted in the introduction, this has been found in measurements of neural tuning functions in older primates and has been postulated to result from a decline in GABA and consequent losses of intracortical inhibition (Hua et al., 2008; Leventhal et al., 2003). An implication of our findings is that adaptive adjustments in cortical responses may therefore be less selective in older adults and therefore less able to calibrate for the specific properties of the stimulus. For example, contrast adaptation may be closely related to adaptation to blur, in which visual coding tends to compensate for the observer's optical aberrations by normalizing spatial vision for the ambient retinal image blur (Sawides et al., 2011; Webster, Georgeson, & Webster, 2002). This blur adaptation is orientation-selective, and could thus play a role in compensating for meridional blur as in astigmatism (Sawides et al., 2010; Vinas, Sawides, de Gracia, Marcos, & Barnes, 2012). The weaker selectivity in older adults could thus impact the extent to which they could compensate for optical aberrations, even though the magnitude of the adaptation to blur might be similar (Elliott et al., 2007).

We also found that these cross-orientation adaptation effects (i.e. the effect of the adaptor on the orthogonal orientation) were asymmetric. Specifically, adapting to vertical orientations induced larger threshold elevations in horizontal test stimuli than vice versa, in both younger and older adults (Fig. 5). This anisotropy may have a similar cause as the horizontal effect, in which sensitivity for horizontal is lower than for vertical, though this difference is primarily found for stimuli with the broad frequency content of natural scenes. These orientation biases may potentially be due to long term adaptation to the prevalence of horizontal contrasts in natural scenes (Essock, DeFord, Hansen, & Sinai, 2003; Hansen & Essock, 2004). For grating stimuli, sensitivity is instead lower for oblique orientations (oblique effect, Appelle, 1972), while thresholds are comparable for vertical and horizontal (Pilz et al., 2020). Our adapting stimuli were Gabor patches and the similar sensitivity we found for vertical and horizontal is thus consistent with previous measurements for gratings. However, while we did not observe significant differences between vertical and horizontal thresholds before adaptation, the short-term post-adaptation differences we found could be consistent with the longer-term adaptation thought to underlies the horizontal effect (Essock et al., 2003; Hansen & Essock, 2004).

Another important finding of our study was that the time course of contrast adaptation remains largely unchanged with aging. Normalized thresholds for tests at the adapting orientation analyzed with time bins indicated that the older and young adults showed similar time course of the buildup and decay of adaptation, reaching similar amounts of asymptotic adaptation and residual responses, though the time constants of group average indicated that in older adults the buildup of contrast adaptation might be more sluggish than that for young adults. Our observation is consistent with the generally similar patterns of adaptation observed previously for cortical adaptation (Elliott et al., 2007, 2011). In particular, both the normalized magnitude of adaptation and the time course were was similar between older and young adults. This suggests that the processes of cortical adaptation may remain largely robust despite the large neural changes resulting from normal aging – or in other words, that the integrity of adaptation processes shows little aging. The rates of adaptation may normally be set to optimally track different rates of environmental change and to distinguish real change from noise (Kording, Tenenbaum, & Shadmehr, 2007; Wark, Fairhall, & Rieke, 2009). This robustness may be critical to allow the visual system to preserve perceptual constancy by discounting the age-related changes in the observer (Elliott et al., 2007, 2011).

5. Conclusions

Our results indicate that the time course of adaptation and asymptotic adaptation magnitudes remain largely unchanged with aging. However, adaptation induced larger sensitivity losses for orthogonal orientations for older adults, suggesting broader orientation tuning with aging. Surprisingly, we also found an asymmetric cross-orientation effect such that adapting to vertical orientations induced larger threshold elevations in horizontal test stimuli than vice versa, in both younger and older adults. Overall, these results are consistent with age-related changes in orientation tuning while the processes of cortical contrast adaptation remain largely intact.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.visres.2021.03.015.

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