

Age effects on saccadic adaptation: Evidence from different paradigms reveals specific vulnerabilities

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Saccadic eye movements provide an opportunity to study closely interwoven perceptual, motor, and cognitive changes during aging. Here, we investigated age effects on different mechanisms of saccadic plasticity. We compared age effects in two different adaptation paradigms that tap into low- and high-level adaptation processes. A total of 27 senior adults and 25 young adults participated in our experiments. In our first experiment, we elicited adaptation by a double-step paradigm, which is designed to trigger primarily low-level, gradual motor adaptation. Age groups showed equivalent adaptation of saccadic gain. In our second experiment, adaptation was induced by a perceptual task that emphasizes high-level, fast processes. We consistently found no evidence for age-related differences in low-level adaptation; however, the fast adaptation response was significantly more pronounced in the young adult group. We conclude that low-level motor adaptation is robust during healthy aging but that high-level contributions, presumably involving executive strategies, are subject to age-related decline. Our findings emphasize the need to differentiate between specific aging processes in order to understand functional decline and stability across the adult life span.

of functional resources across the adult life span. Whereas cognitive changes have been extensively studied over the past decades (for reviews, see Baltes, Staudinger, & Lindenberger, 1999; Cabeza, Nyberg, & Park, 2005b; Craik & Byrd, 1982; Hasher & Zacks, 1988; Park & Reuter-Lorenz, 2009; Salthouse, 1996), age effects on sensorimotor capacities have been rather neglected. In particular, age-related changes in plasticity of sensorimotor behavior, which is highly relevant in a continuously changing environment, are not well understood.

Previous studies concerned with age-related differences in sensorimotor plasticity have almost exclusively focused on adaptation of hand and arm movements (i.e., reaching movements). Although findings from cognitive studies consistently indicated a plasticity decline with increasing age, results for reaching adaptation have been ambiguous (e.g., Bock, 2005; Bock & Schneider, 2001; Buch, Young, & Contreras-Vidal, 2003; Heuer & Hegele, 2008b). Overall, only a minor decline of sensorimotor plasticity has been reported; however, the detrimental impact of reduced cognitive strategies during adaptation has been emphasized (Bock & Girgenrath, 2006; Heuer & Hegele, 2008a; Heuer, Hegele, & Sulzenbruck, 2011). We suggest that the investigation of saccadic adaptation is particularly well suited to disentangle age-related vulnerabilities that contribute to plasticity changes.

Saccadic eye movements provide a fundamental possibility to explore our visual environment and offer the opportunity to investigate basic mechanisms of sensorimotor control (Krauzlis, 2005). Indeed, age-related changes in saccadic control have been explored

Introduction

Increased life expectancy and decreased birth rates contribute to massive demographic changes in most developed societies. The mean age of the population is continuously shifting toward the senior range so that it appears imperative to acquire a detailed understanding

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by numerous studies. Results consistently support a pronounced increase of latencies with age but stability of saccade dynamics (Abel & Douglas, 2007; Munoz, Broughton, Goldring, & Armstrong, 1998; Peltsch, Hemraj, Garcia, & Munoz, 2011). A further robust finding is an age-related increase of directional error rates in saccade tasks that require inhibitory control processes (e.g., in the antisaccade task; Gottlob, Fillmore, & Abroms, 2007; Olk & Jin, 2011; Peltsch et al., 2011; Sweeney, Rosano, Berman, & Luna, 2001). In particular, saccade accuracy seems to be maintained stable across the adult life span, even up to an age of 80 years (Munoz et al., 1998). This suggests preserved capacities to compensate for possible age-related changes of ocular muscles or neuronal circuitries that might challenge saccadic accuracy. Age-related changes in plasticity of saccadic control have remained poorly understood. Evidence of robust saccadic adaptation in the developmental course comes from several studies in children and adolescents (Alahyane et al., 2016; Doré-Mazars, Vergilino-Perez, Lemoine, & Bucci, 2011; Lemoine-Lardennois et al., 2016; Salman et al., 2006). Results indicate early maturation of adaptive capacities, showing, for example, reactive amplitude changes already in toddlers. However, only a single study so far has been dedicated to aging of saccadic adaptation and has provided evidence of similar capacities in different adult age groups (Bock, Ilieva, & Grigorova, 2014).

Adaptation of saccadic eye movements is well described and can be considered as a very basic model of sensorimotor plasticity (Hopp & Fuchs, 2004; Péliesson, Alahyane, Panouilleres, & Tilikete, 2010). Saccades allow for bringing relevant visual information rapidly to the fovea, which enables detailed analysis. If inaccuracies are experienced (e.g., due to fluctuations in the oculomotor system), the accuracy of saccades is reestablished by adjusting their amplitude. Adaptive adjustments can be robustly induced in the laboratory by an unnoticed target shift during the saccade that results in a postsaccadic error. This manipulation elicits adaptive amplitude changes that compensate for the experienced error and maintain accuracy of saccades. The retinal error was identified to be the dominant or even exclusive error signal driving this adaptation process (e.g., Wallman & Fuchs, 1998). Given this focus on bottom-up error signals, saccadic adaptation was understood as a low-level mechanism that compensates for accuracy deviations.

More recent findings from a variety of adaptation paradigms, however, have challenged this classical view on saccadic adaptation (for review, see Herman, Blangero, Madelain, Khan, & Harwood, 2013). In several studies, saccadic gain changes were reliably elicited without visual errors. Dissociating retinal error from prediction error (i.e., the discrepancy between predicted and actual movement outcome), there has

been evidence that saccadic adaptation might be primarily driven by prediction errors (Collins & Wallman, 2012; Wong & Shelhamer, 2012). Moreover, it has been shown that saccadic adaptation can be induced even in the absence of any error signal. Amplitude-dependent reinforcement has proved to be sufficient to trigger appropriate gain changes (Madelain, Paeye, & Darcheville, 2011; Madelain, Paeye, & Wallman, 2011). Congruently, saccadic adaptation has been successfully induced using a perceptual task without manipulation of the visual target (Schütz, Kerzel, & Souto, 2014; Schütz & Souto, 2015). Thus, plasticity can be also driven by behavioral goals. In summary, these recent results question whether saccadic adaptation exclusively represents a low-level mechanism that compensates for systematic errors in the oculomotor system. Rather, they suggest that saccades can also be adapted based on high-level mechanisms involving top-down behavioral goals and strategies.

We aimed to investigate how age affects different mechanisms of saccadic adaptation. Because age-related cognitive decline, in particular decline of executive functioning, is well documented (Park & Reuter-Lorenz, 2009; West, 1996), we hypothesize that high-level adaptation mechanisms might be especially prone to age-related decline, whereas low-level mechanisms might tend to be preserved. We chose two established saccadic adaptation paradigms that are supposed to tap into different mechanisms. For each paradigm, we compared saccadic plasticity between young adult and healthy, community-dwelling senior adults.

Experiment 1: Evidence from the double-step paradigm

In our first experiment, we chose the well-known double-step paradigm (McLaughlin, 1967) to induce saccadic adaptation. The typical procedure demands a saccade to a visual target, which is displaced during saccade execution. The target step results in a postsaccadic error, and repeated experience triggers adaptive changes of saccade amplitude within a few trials. Sensitivity for target displacements is reduced during saccades (Bridgeman, Hendry, & Stark, 1975; but see, e.g., Castet & Masson, 2000; Panouilleres et al., 2016), so that conscious perception of the target manipulation can be assumed to play only a minor role in this adaptation process. Efficient stabilization of movement accuracy is driven primarily by postsaccadic errors. Thus, saccadic adaptation in the double-step paradigm is generally considered to reflect a low-level mechanism that enables compensation for systematic

errors and maintains accuracy of the oculomotor system (for review, see Hopp & Fuchs, 2004; Pélişson et al., 2010).

Methods

Participants

A total of 18 young adults (12 women) and 19 senior adults (13 women) participated in the experiment. The participants' age ranged from 22 to 38 years with a mean age of 27.9 years ($SD = 4.7$) in the young adult group and from 52 to 76 years with a mean age of 66.6 years ($SD = 6.0$) in the senior adult group. Recruitment of participants was managed by calls for participation at the University of Giessen and in local newspapers. All participants were paid for participation. Any history of ophthalmologic, neurologic, or psychiatric disorders as well as medications presumed to interfere with oculomotor functioning were screened out by a detailed interview protocol. Visual acuity was measured binocularly, confirming normal or corrected-to-normal for all participants.

In addition, we ran a battery of standard cognitive tasks to exclude pathological age-related decline. Derived measures allowed evaluation of crystallized intelligence, problem solving, mental rotation, task switching, and short-term and working memory. Results in the battery primarily served as backing that we studied age effects in a healthy population and thus we refrain from giving a comprehensive report of measures here. However, in the context of our present study, measures of executive functioning were of particular interest. The following tasks of our battery measured critical capacities: LPS3, a subtest of a major German intelligence test battery, measuring nonverbal problem solving (Horn, 1983); part B of the Trail Making Test (TMT-B), measuring cognitive flexibility (Kortte, Horner, & Windham, 2002; Reitan & Wolfson, 1985); and backward digit and block span measures of the Wechsler Memory Scale (WMS), measuring verbal and visuospatial working memory (Härting et al., 2000). Consistent with current knowledge on cognitive aging (compare Park & Reuter-Lorenz, 2009), these measures were sensitive to aging and differed significantly between adult age groups ($ps < 0.033$).

Methods and procedures agreed with the Declaration of Helsinki (World Medical Association, 2013) and were approved by the local ethics committee. Informed consent was obtained by all participants, and protection of data privacy was provided.

Task and procedure

We applied a standard double-step paradigm to elicit backward saccadic adaptation. Participants were asked

to fixate a black cross ($0.5^\circ \times 0.5^\circ$) presented on a mean gray background. Location of the fixation cross was randomly jittered within an area around the center of the screen extending -5° to 0° horizontally and -3° to 3° vertically. Participants initiated each trial by pressing the space bar. Given stable fixation, the cross turned red and jumped 10° rightward after a delay that varied uniformly between 300 and 400 ms. Participants were instructed to follow the cross with their eyes. Saccade onset was determined online. The experiment consisted of three phases: 50 preadaptation trials, 300 adaptation trials, and 50 postadaptation trials. In the pre- and postadaptation trials, the target cross disappeared as soon as the saccade onset was detected. In the adaptation trials, the cross was displaced backward by 2.5° during the saccade and maintained visible at the new location for 600 to 700 ms, uniformly jittered. To keep the overall length of data collection convenient, in particular for our senior participants, our procedure was supposed to elicit gain changes as efficiently as possible. Because spatial generalization of saccadic adaptation is known to be limited (for review, see Pélişson et al., 2010), we chose a constant saccade vector (i.e., the amplitude and the direction of the target step were fixed). The experiment was divided into a total of seven blocks: a preadaptation block, five adaptation blocks with 60 trials each, and finally a postadaptation block.

Eye-tracking equipment

Stimuli were generated using Matlab with the Psychophysics Toolbox (Brainard, 1997). They were displayed on a 22-in. Samsung SyncMaster 2233BW monitor driven by an Nvidia GeForce 9800 graphics board with a refresh rate of 120 Hz. The spatial resolution was set to $1,680 \times 1,050$ pixels. Participants were seated in a darkened room at a distance of 90 cm in front of the monitor. Eye position was recorded by an SR Research Eyelink 1000 Desktop Mount system (SR Research Ltd., Mississauga, Ontario, Canada) at a sampling rate of 1000 Hz. Viewing was binocular, and participants' heads were stabilized by a chin and head rest. A standard nine-point calibration covering the whole screen was applied before each block, and accuracy was accepted if the validation procedure yielded values of average error not larger than 0.4° and worst error not larger than 0.7° . Each trial started with a drift correction in order to guarantee calibration across data collection. Participants were instructed to keep their sitting position as stable as possible. The experimenter continuously monitored the participants and restarted the calibration procedure when an accidental change in position occurred.

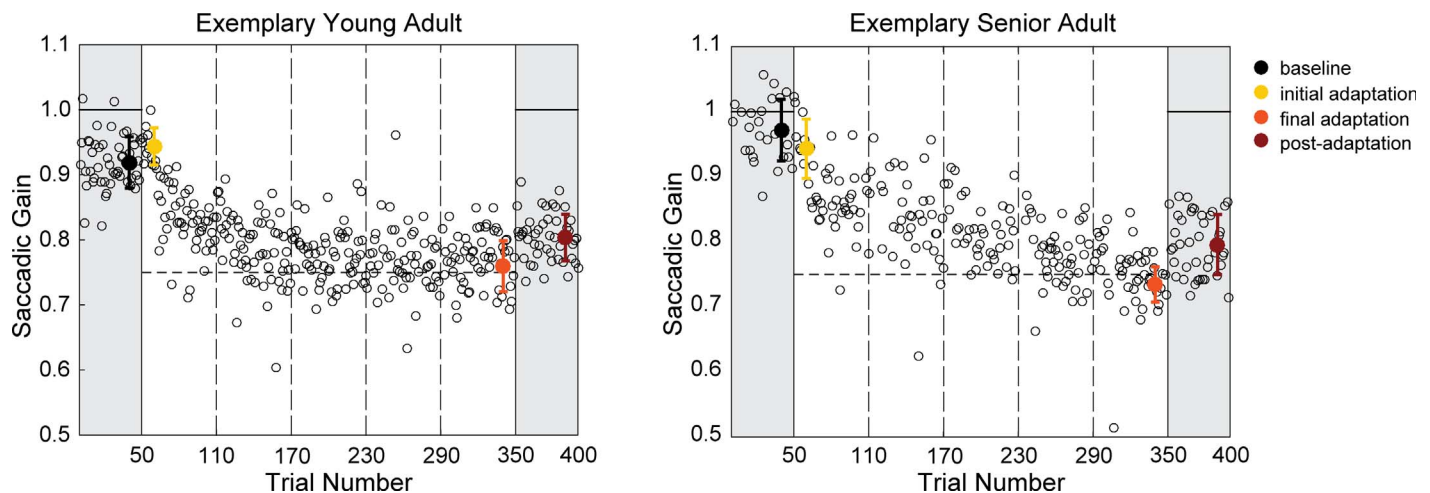


Figure 1. Single-subject data of an exemplary young adult, left panel, and an exemplary senior adult, right panel. Saccadic gain is given as a function of trial number. Black open dots: individual trials; filled dots: average data across specified intervals; error bars: *SD*. Gray-shaded areas indicate preadaptation phase and postadaptation phase; vertical lines: trial blocks; horizontal lines: perfect gain (i.e., eye and target positions match perfectly after the saccade).

Data analysis

Saccade onset during each trial was determined online using a combined velocity criterion. Onset was defined by the time when eye velocity of two consecutive samples exceeded 50°/s and 100°/s, respectively. Subsequently, eye position data were analyzed offline using the Eyelink built-in algorithms. We excluded trials from further analyses if saccades had latencies <80 ms or >500 ms, if they had a duration of <10 ms or >100 ms, or if they had an amplitude <5° or >15°. We excluded on average 15.5% of trials (*SD* = 11.1%) in the young adult group and 22.9% of trials (*SD* = 12.1%) in the senior adult group. The different exclusion criteria contributed to discard rates in both age groups similarly. For young and senior adults, respectively, we discarded 9.8% and 15.6% of trials based on the latency criterion, 4.5% and 6.7% of trials based on the duration criterion, and 7.4% and 16.6% of trials based on the amplitude criterion. Note that a substantial number of trials was excluded based on more than one criterion. Overall, discard rates tended to be higher in the senior adult group than in the young adult group, $t(30) = -1.80$, $p = 0.081$. Data of five observers (two young adults) were dismissed completely because more than 50% of their trials had to be excluded based on our criteria.

We first analyzed saccade gain for four defined trial intervals. The average across all preadaptation trials was used as baseline performance. Note that we observed a decrease of saccade amplitude across the preadaptation phase in the senior adult group, probably because of age-related differences in how participants responded to the target extinction after saccade onset. Given the limited number of preadaptation trials and noise in the individual data, we chose the average

across all trials to derive a robust baseline reference. The results were equivalent when using the first or the second half of trials for baseline levels. For the adaptation phase, we derived two parameters. Initial adaptation performance was derived by averaging across the first 10 adaptation trials; final adaptation performance was derived by averaging across the last 10 adaptation trials. The average across all postadaptation trials was used as measure of postadaptation performance. Gain differences between intervals were considered to be indicative for specific adaptation components. We supposed that the difference between baseline and initial adaptation reflects immediate adjustment, whereas the difference between initial and final adaptation indicates gradual adjustment. The difference between final adaptation and postadaptation performance was taken as a measure of recovery from adaptation.

Furthermore, we fitted an exponential model to the gain data in all adaptation trials for each participant. We applied a model with three free parameters (Souto, Gegenfurtner, & Schütz, 2016):

$$S(t) = \alpha + \beta e^{-\lambda t} \quad (1)$$

$S(t)$ gives the fitted saccadic gain for a given trial t . The three free parameters used are the asymptotic level α , the amplitude of adaptation β , and the adaptation rate λ ; $1/\lambda$ corresponds to the exponential rate constant (i.e., the number of trials it takes the function to reach about a third of the initial value). Given the definition of parameters, the difference between α and β provides a measure for immediate adjustment, and β directly reflects gradual adjustment. After removing baseline levels, gain in adaptation trials was fitted iteratively until the best solution was found using a nonlinear

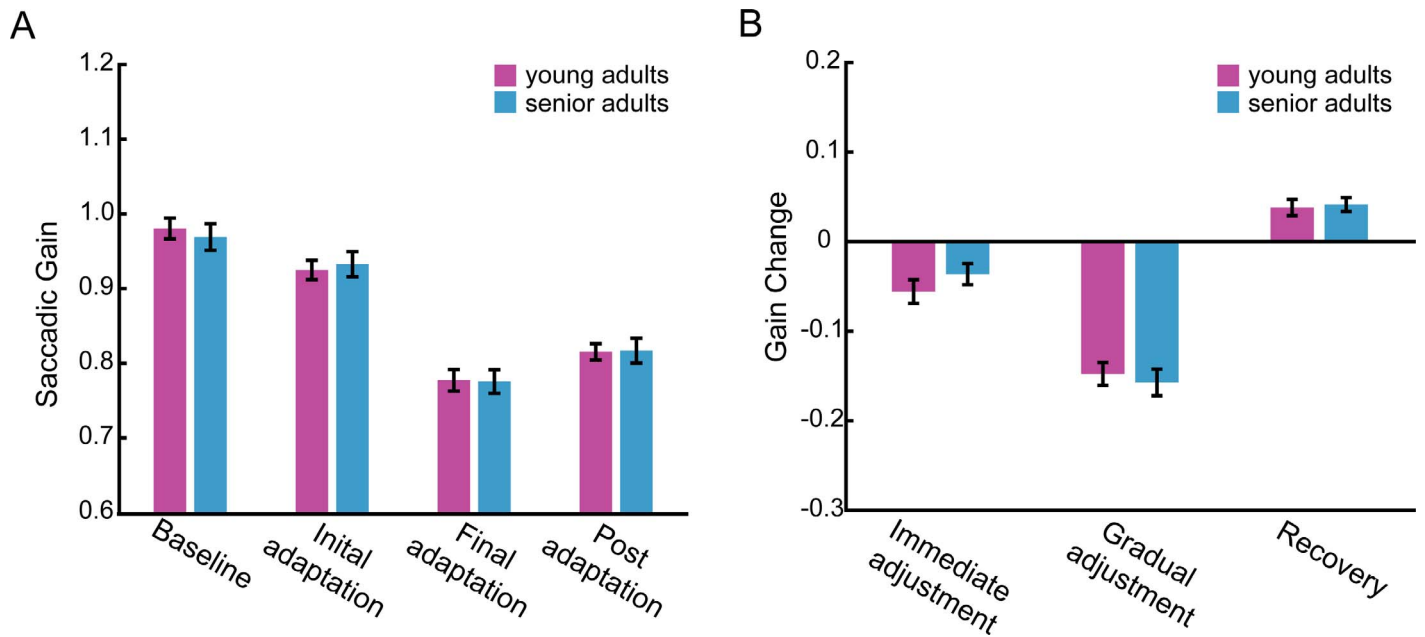


Figure 2. Saccadic gain in the double-step paradigm. (A) Average gain in the specified trial intervals for young adults and senior adults. (B) Changes in gain indicating immediate adjustment, gradual adjustment, and recovery for young adults and senior adults. Error bars: SEM.

least-squares fitting procedure provided by the OPTI toolbox for Matlab (Currie & Wilson, 2012). To obtain robust fits, we constrained α and β to a range of -0.5 to 0.5 and λ to a range of 0.001 to 1 .

Results

The applied double-step paradigm robustly elicited backward saccadic adaptation in both age groups. Figure 1 shows exemplary saccadic gain data across trials for a single young and senior participant, respectively. Data overall appeared similar across both participants. For the young adult, we determined an average gain of 0.92 in the baseline trial interval; by the end of the adaptation phase, the gain was reduced to 0.76 . The senior participant showed a gain of 0.97 in the baseline trial interval and reduced it to 0.73 across the adaptation trials. Note that gain did not increase to baseline in the postadaptation phase because the target was extinguished after saccade onset and did not reappear. Thus, the gain shift reflects retention, rather than the extent of readaptation to baseline.

We analyzed age group differences across the specified trial intervals by a mixed analysis of variance (ANOVA) with the within-subject factor trial interval (baseline, initial adaptation, final adaptation, and postadaptation) and the between-subjects factor age group (young adults and senior adults). If appropriate, we used the Greenhouse-Geisser correction. As a measure of effect size, η^2 is provided, giving the

proportion of variance associated with the particular effect. Figure 2A illustrates saccadic gain results for both age groups and shows saccadic plasticity across the experiment in both age groups. Congruently, the ANOVA yielded a significant main effect of trial interval, $F(3, 90) = 215.83$, $p < 0.001$, $\eta^2 = 0.88$. However, we found neither a main effect of age group, $F(1, 30) < 0.01$, $p = 0.995$, $\eta^2 < 0.01$, nor an interaction effect of both factors, $F(3, 90) = 0.41$, $p = 0.696$, $\eta^2 = 0.01$.

The main effect of trial interval was followed up by post hoc paired comparisons with Bonferroni correction. Results indicated that average gain differed significantly between all specified intervals (all $p < 0.001$). Highest gain was found in the baseline trials ($M = 0.98$, $SD = 0.06$). A significant decrease was already found at the beginning ($M = 0.93$, $SD = 0.06$) and also at the end ($M = 0.78$, $SD = 0.06$) of the learning phase. After removal of the target manipulation, gain increased again but did not reach the baseline level within the postadaptation phase ($M = 0.82$, $SD = 0.05$).

We also explored adaptation across the experiment by directly considering gain differences between the specified trial intervals. Change data are shown in Figure 2B. Additional analyses overall confirmed the results from the initial ANOVA. We used one-sample t tests to evaluate whether changes differed significantly from zero. In both age groups, we observed significant immediate adjustment at the beginning of the learning phase, significant gradual adjustment across the learning phase, and finally significant recovery from adaptation (all $p < 0.005$). This further supports that

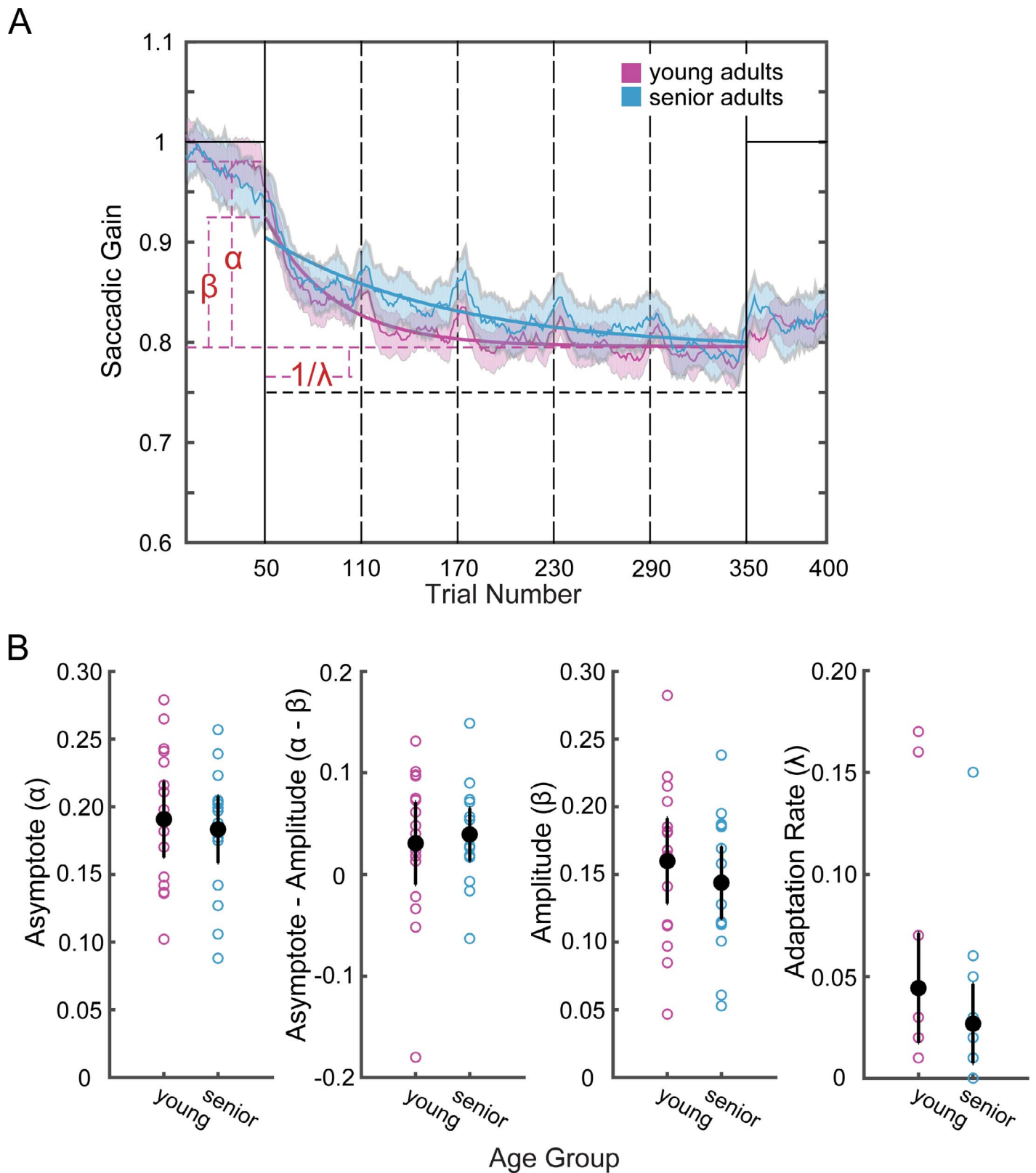


Figure 3. Fitting results for the double-step paradigm. (A) Saccadic gain as a function of trial number. The thin pink and blue lines represent the averaged gain across young and senior adults, respectively. Data are smoothed by a running average with a bin size of 10 trials. Shaded areas: 95% confidence intervals; vertical lines: trial blocks; horizontal lines: perfect gain (i.e., eye and target positions match perfectly after the saccade). The thick pink and blue lines represent the three-parameter model fit for young and senior adults, respectively. The meaning of the parameters is illustrated within the plot for young adults' data; the parameter α gives the asymptote

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of the function starting from the average baseline gain level, and the parameter β gives the overall amplitude of adaptation from beginning of the adaptation phase to its end. The parameter λ gives the adaptation rate, and $1/\lambda$ corresponds to the number of trials it takes the function to reach about a third of the initial value. (B) Estimated model parameters for young adults and senior adults. Panels from left to right: asymptotic level α , difference between asymptotic level and adaptation amplitude $\alpha - \beta$, adaptation amplitude β , adaptation rate λ . Error bars: 95% confidence intervals.

the paradigm robustly elicited learning processes in both age groups. We used one-tailed t tests to clarify whether young adults show more pronounced plasticity than senior adults. Cohen's d is provided as a measure of effect size. It indicates the extent of nonoverlap between two distributions; values of 0.5 are typically considered as a medium effect size. Neither immediate adjustment, $t(30) = -1.14$, $p = 0.132$, $d = 0.40$, nor gradual adjustment, $t(30) = 0.50$, $p = 0.309$, $d = -0.20$, nor recovery from adaptation, $t(30) = -0.29$, $p = 0.386$, $d = -0.10$, were found to be significantly more pronounced in young adults.

Fitting of the data with the three-parameter model yielded consistent results. Figure 3A illustrates saccadic gain as a function of trial number averaged across young adults and senior adults, respectively.

The model fits for the averaged data suggests only minor differences between both age groups. Parameters of the individual fits are provided in Figure 3B. Using one-tailed t tests, we analyzed whether parameters reveal more pronounced adaptation processes in young adults than in senior adults. Results yielded no

significant differences between both age groups, asymptotic level α : $t(30) = -0.43$, $p = 0.334$, $d = -0.15$; difference between asymptotic level and adaptation amplitude $\alpha - \beta$: $t(30) = 0.38$, $p = 0.335$, $d = 0.13$; adaptation amplitude β : $t(30) = -0.83$, $p = 0.206$, $d = -0.29$; and adaptation rate λ : $t(30) = -1.08$, $p = 0.146$, $d = -0.38$. Consistency across the applied analysis approaches was supported by significant correlations between immediate adjustment of saccadic gain and the parameter difference score $\alpha - \beta$, $r(31) = 0.75$, $p < 0.001$, as well as between gradual adjustment of saccadic gain and the parameter β , $r(31) = 0.62$, $p < 0.001$. In summary, fitting results confirmed that young and senior adults show similar adaptation capacities immediately at the beginning of the learning phase and gradually across the learning phase. Furthermore, they provided evidence that the adaptation rate was not affected by age.

We finally explored saccadic latencies in the double-step paradigm by an additional ANOVA. Figure 4 illustrates average latencies for each age group. Increased saccadic latencies represent the most consistently reported age effect on oculomotor control. As expected, age groups differed substantially in saccadic latencies across all trial intervals, with younger adults showing lower latencies, $F(1, 30) = 23.11$, $p < 0.001$, $\eta^2 = 0.44$. Latencies decreased across trial intervals, $F(3, 90) = 4.64$, $p = 0.011$, $\eta^2 = 0.13$. There was no significant interaction between both main effects, $F(3, 90) = 0.11$, $p = 0.957$, $\eta^2 < 0.01$. Furthermore, latencies did not correlate with any of the parameters we derived from fitting accuracy data with the exponential model (i.e., asymptotic level, adaptation amplitude, and adaptation rate). Thus, exploration of latencies yielded support for expected age differences but also showed that these differences do not affect saccadic plasticity.

Experiment 2: Evidence from a perceptual task

In our second experiment, we induced saccadic adaptation by a perceptual task recently introduced by Schütz and colleagues (Schütz et al., 2014; Schütz & Souto, 2015). Whereas in the double-step paradigm, visual errors drive adaptation, the applied perceptual task triggers adaptive changes of saccade amplitude by

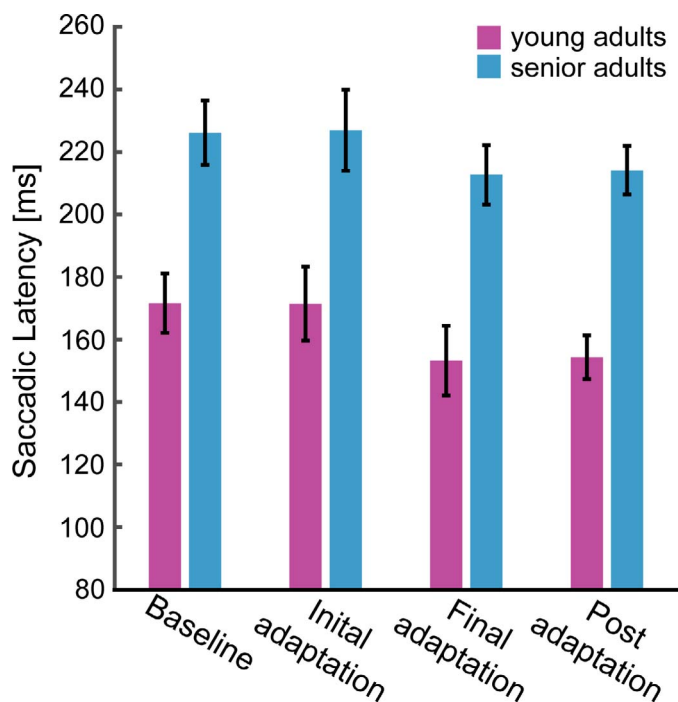


Figure 4. Average saccadic latencies in the specified trial intervals of the double-step paradigm for young adults and senior adults. Error bars: SEM.

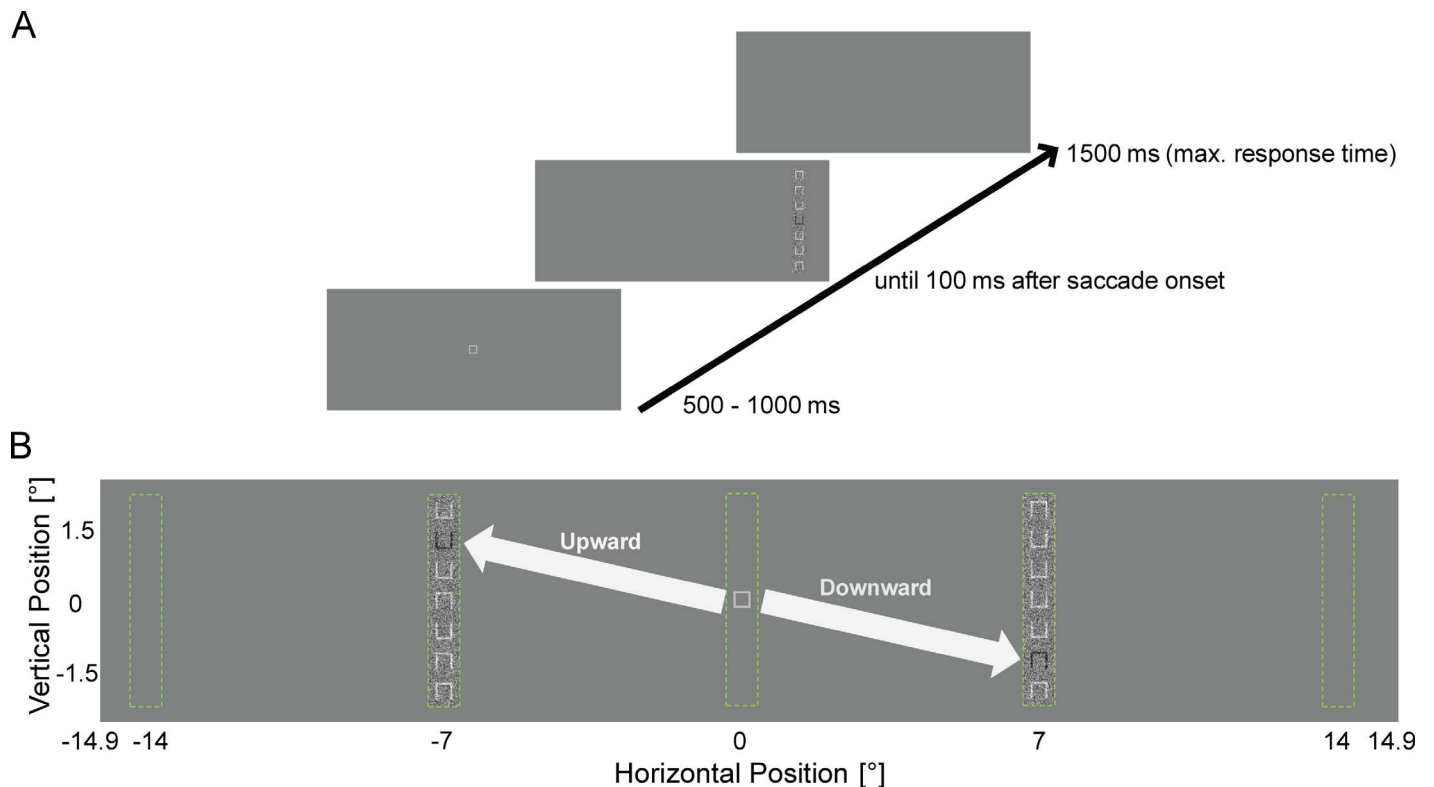


Figure 5. Perceptual task inducing adaptation. (A) General task procedure. After a variable fixation period, a vertical stimulus compound was shown at an eccentricity of 7° either to the left or the right of the fixation square. The fixation square was always shown at the vertical center of the screen; horizontal position was determined by the position of the compound in the previous trial. The discrimination target was a black square within the compound. It had a gap either at the bottom or at the top, and participants had to indicate its location. In baseline trials, the discrimination target was always placed in the center of the compound. (B) Adaptation procedure. In adaptation trials, the position of the discrimination target within the compound was shifted upward or downward in the case of leftward or rightward saccades, respectively. The coupling of shift direction and saccade direction was counterbalanced across participants. Dotted rectangles illustrate possible locations of the stimulus compound.

a behavioral goal. This task specifically allows for the study of high-level mechanisms that contribute to saccadic plasticity because amplitude is shaped by top-down goals, not by bottom-up visual errors. Given age-specific vulnerabilities, saccadic adaptation induced by a perceptual task might be particularly attenuated with increasing age.

Methods

Participants

A total of 17 young adults (11 women) and 16 senior adults (five women) participated in the experiment. The participants' age ranged from 22 to 37 years with a mean of 26.4 years ($SD = 4.6$) in the young adult group and from 64 to 83 years with a mean age of 71.3 years ($SD = 4.8$) in the senior adult group. The recruitment procedure and screening protocol were equivalent to Experiment 1.

Task and procedure

We applied a perceptual task to induce vertical adaptation saccade amplitude. The general task procedure is illustrated in Figure 5A. Participants had to fixate a fixation square ($0.36^\circ \times 0.36^\circ$) presented on a mean gray background. The fixation period was uniformly varied between 500 and 1,000 ms. Subsequently, the fixation square was extinguished and a compound stimulus appeared at an eccentricity of 7° , randomly either to the right or to the left. The compound consisted of seven vertically aligned squares ($0.36^\circ \times 0.36^\circ$) with a line width of 0.05° . Squares were displayed on a random noise background that extended 0.16° beyond them. Contrast of squares and noise background was set to 50%. The compound had a total height of 5.52° and a total width of 0.68° . Position of the fixation square and the stimulus compound followed a random walk across five horizontal positions shown in Figure 5B. The fixation square was always shown at the vertical center of the screen; the

horizontal position was determined by the position of the compound in the previous trial.

Participants were asked to accomplish a discrimination task. The stimulus compound always included six white squares and a unique black square, representing the target. All squares had a gap either at the bottom or at the top. Participants had to decide whether the gap of the target square was at the bottom or at the top. The task was designed to require foveal acuity so that participants had to saccade to the compound to solve the task successfully. Congruently, a significant negative relationship between retinal error and discrimination performance was found in the initial study using the paradigm (Schütz et al., 2014). The compound was displayed for 100 ms after saccade onset, which was determined online. Participants had to indicate their decision within 1500 ms after saccade onset by a key press. If the perceptual judgment was incorrect, negative feedback was provided by a beep.

The experiment consisted of three phases: 50 preadaptation trials, 200 adaptation trials, and 200 postadaptation trials. In preadaptation and postadaptation trials, the target square was always centered in the compound (compare Figure 5A). In adaptation trials, the target was shifted two positions, corresponding to 1.47° , either upward or downward within the compound (compare Figure 5B). The direction of the target shift depended on the saccade direction, so that specific adaptive changes were triggered based on the given context. For half of the participants, rightward saccades were coupled with downward shifted targets and leftward saccades were coupled with upward shifted targets, whereas for the other participants, coupling was the other way around. The specific coupling was counterbalanced across participants within each age group. Notably, the manipulation in the adaptation trials did not induce bottom-up visual errors because the position of the stimulus compound remained stable. Adaptive changes in saccade direction (i.e., rotation upward or downward) were exclusively driven by the demands of the discrimination task. The experiment was divided into a total of five blocks: a preadaptation block, two adaptation blocks, and two postadaptation blocks with 100 trials each. Between blocks, there were breaks of 30 s in which participants were advised to close their eyes.

Eye-tracking equipment

We used exactly the same setup as in Experiment 1 and applied the same calibration procedure.

Data analysis

Saccades were analyzed using the same procedures as in Experiment 1. Criteria for exclusion of trials were

also consistent, except for the saccade amplitude criterion. Given the stimulus layout, we classified saccades with a horizontal amplitude $<3.5^\circ$ or $>10.5^\circ$ as invalid. We excluded on average 9.1% of trials ($SD = 5.2\%$) in the young adult group and 20.7% of trials ($SD = 8.5\%$) in the senior adult group. The different exclusion criteria contributed to discard rates in both age groups similarly. For young and senior adults, respectively, we discarded 3.8% and 10.1% of trials based on the latency criterion, 1.3% and 2.3% of trials based on the duration criterion, and 7.5% and 20.4% of trials based on the amplitude criterion. Note that a substantial number of trials was excluded based on more than one criterion. Senior adults overall showed higher discard rates than young adults, $t(28) = -4.62$, $p < 0.001$, presumably because of the well-known age-related decline in inhibitory control. Discard rates in this experiment were slightly lower than in our first experiment, presumably because the task characteristics (i.e., alternating target positions) triggered less anticipatory saccades. Data of three senior observers were discarded because more than 40% of their trials had to be excluded based on our criteria.

Discrimination performance in the behavioral task was measured across all trial intervals. Young adults performed at ceiling with an average accuracy rate of 98.2% ($SD = 1.1\%$). Senior adults showed a slightly lower accuracy rate of 93.7% ($SD = 3.2\%$) but performed the task appropriately. Most likely because of the restricted accuracy range, we were not able to observe a significant relationship between discrimination performance and retinal error (compare Schütz et al., 2014). We discarded data of one senior observer because his performance was at chance level (48.4%), and thus we assumed that he misunderstood task instructions.

The critical parameter of interest for our analyses was vertical saccade amplitude. Because adaptation was found to be similar in upward and downward conditions, we collapsed data to increase the trial number for our analyses. Note that the presence of specific adaptive changes dependent on saccade direction in both adult groups basically indicates that contextual adaptation is robust to aging. We derived vertical amplitude for baseline, initial adaptation, final adaptation, and postadaptation trial intervals according to the methods used in Experiment 1. We again calculated defined change scores. Amplitude data were further analyzed by fitting the three-parameter exponential model (see Formula 1). We first removed baseline amplitude from all trials and then fitted amplitude in adaptation and postadaptation trials with the model until the best solution was found. We constrained α and β to a range of -5 to 5 and λ to 0.001 to 0.2 .

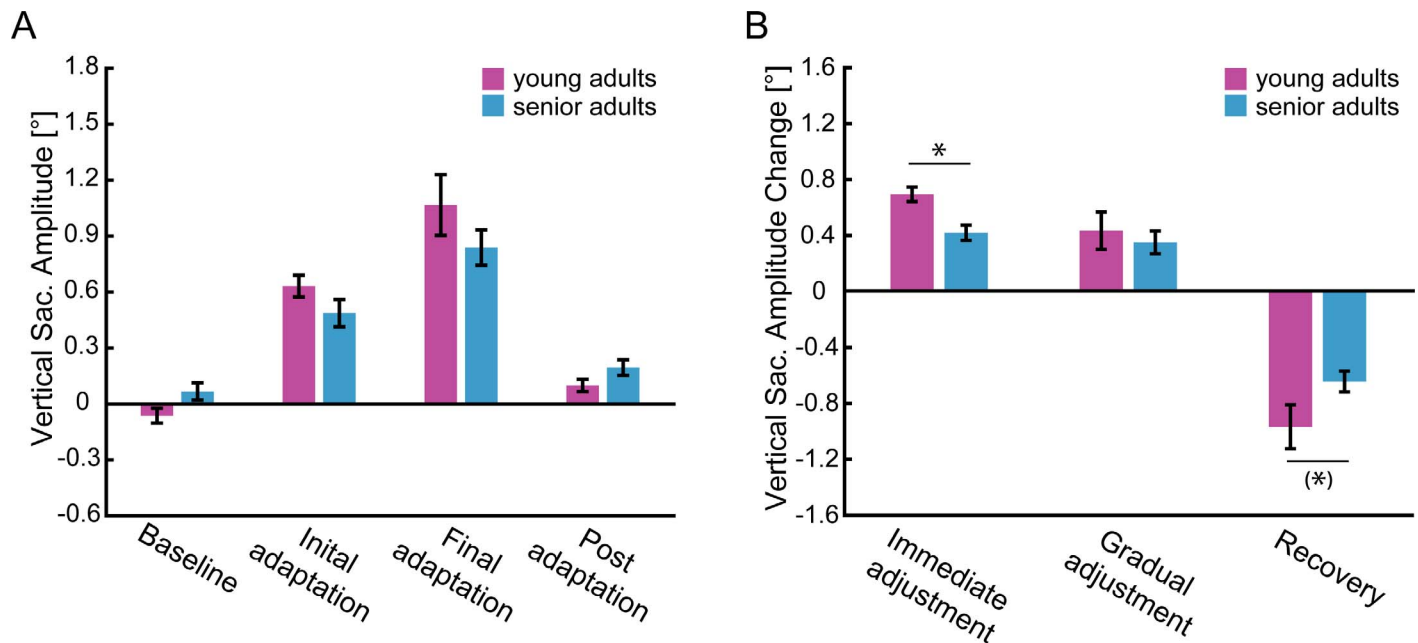


Figure 6. Vertical saccade amplitude in the perceptual task. (A) Average amplitudes in the specified trial intervals for young adults and senior adults. (B) Changes in amplitude indicating immediate adjustment, gradual adjustment, and recovery for young adults and senior adults. Error bars: SEM.

Results

Both age groups showed substantial adaptive changes in vertical saccade amplitude induced by the perceptual task. In the baseline trial interval, vertical saccade amplitude was close to zero, on average -0.06° and 0.07° for young and senior adults, respectively. The young adults increased the amplitude to 1.06° by the end of the adaptation phase; the senior adults reached on average an amplitude of 0.84° . Figure 6A summarizes vertical amplitudes in the different trial intervals for both age groups.

We analyzed amplitude data equivalent to the procedure applied for Experiment 1. ANOVA results showed a main effect of trial interval, $F(3, 81) = 74.74$, $p < 0.001$, $\eta^2 = 0.74$, whereas there was no main effect of age group, $F(1, 27) < 0.21$, $p = 0.650$, $\eta^2 < 0.01$. The interaction effect of both factors just failed to reach significance, $F(3, 81) = 3.17$, $p = 0.068$, $\eta^2 = 0.11$.

We explored adaptive changes further by considering amplitude differences between specified trial intervals. Change data are provided in Figure 6B. For both age groups, all change scores (i.e., immediate adjustment, gradual adjustment, and recovery from adaptation) differed significantly from zero (all $p < 0.001$). Thus, data consistently supported saccadic plasticity across the perceptual task. However, one-tailed t tests yielded specific plasticity advantages for young adults. Senior adults showed less pronounced immediate adjustment, $t(27) = -3.71$, $p < 0.001$, $d = -1.42$, and a trend toward attenuated recovery from adaptation $t(27) = 1.69$, $p =$

0.051 , $d = 0.68$. In contrast, age groups did not differ in gradual adjustment, $t(27) = -0.49$, $p = 0.313$, $d = -0.20$.

Results from fitting of the amplitude data corroborated age-related differences. Figure 7A illustrates vertical saccade amplitude as a function of trial number averaged across young and senior adults. Note that for purpose of illustration, the data for upward and downward conditions are plotted separately here, but analyses are based on collapsed data.

Inspection of model fits indicates that the adaptation process differs between young and senior adults. Individual fit parameters are shown in Figure 7B. We again ran one-tailed t tests to explore age group differences. Asymptotic level α , $t(27) = -2.80$, $p = 0.005$, $d = -1.06$, as well as the difference between asymptotic level and adaptation amplitude $\alpha - \beta$, $t(27) = -2.51$, $p = 0.009$, $d = -0.98$, differed significantly between young and senior adults. Adaptation amplitude β , $t(27) = -0.74$, $p = 0.231$, $d = -0.28$, and adaptation rate λ , $t(27) = -0.50$, $p = 0.310$, $d = -0.20$, were not affected by age. Consistency across analysis methods was confirmed by significant correlations between immediate adjustment of saccade amplitude and the parameter difference score $\alpha - \beta$, $r(28) = 0.63$, $p < 0.001$, as well as between gradual adjustment of saccade amplitude and the parameter β , $r(28) = 0.57$, $p = 0.002$. Overall, model fits provided evidence that young adults show more pronounced immediate adjustment at the beginning of the adaptation phase than senior adults. Gradual adjustment and adaptation rate were found equivalent in both age groups.

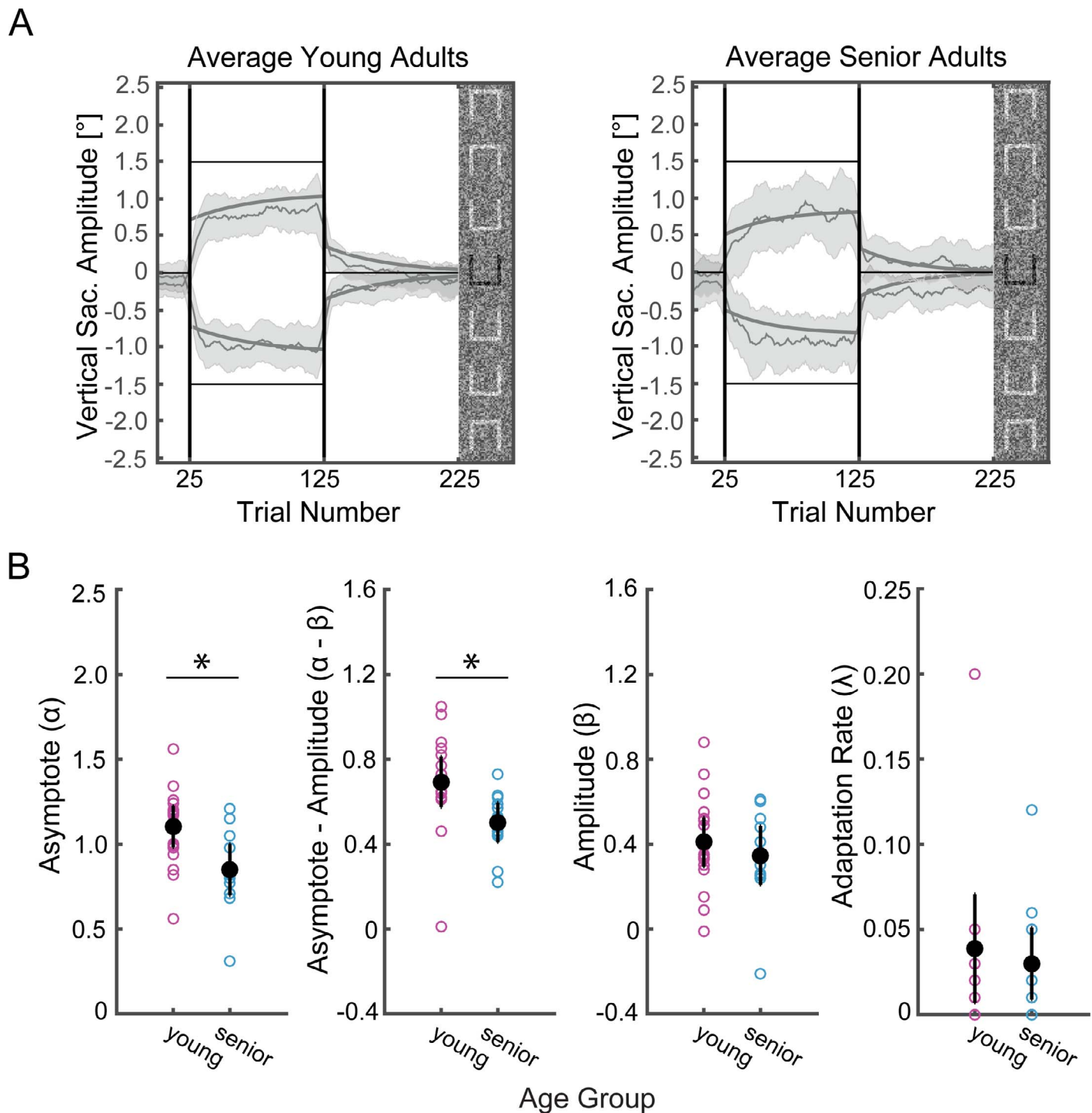


Figure 7. Fitting results for the perceptual task. (A) Averaged vertical saccade amplitude as a function of trial number of young (left panel) and senior (right panel) group. The solid vertical lines indicate onset and offset of adaptation phase; the horizontal line indicates target position. The thin gray lines represent the averaged amplitude across participants. Data are smoothed by averaging across a bin size of 10 trials for display. The shaded regions represent 95% confidence intervals. The thick gray lines represent the three-parameter model fits. Please note that average data for upward and downward conditions are plotted separately for the purpose of illustration, but fits are based on collapsed data as described in the Methods section. Because upward and downward amplitude changes are not perfectly symmetric, overall fits deviate from separate data to some extent. Collapsed data, however, provided the most robust results across all participants. For interpretation of parameters, please see Figure 3A. (B) Estimated model parameters for young adults and senior adults. Panels from left to right: asymptotic level α , difference between asymptotic level and adaptation amplitude $\alpha - \beta$, adaptation amplitude β , adaptation rate λ . Error bars: 95% confidence intervals.

Because we considered in particular immediate adaptive changes in the perceptual task as driven by top-down goals, we aimed to explore their association with standard measures of executive functioning. Multiple linear regression analysis was used to test whether immediate adjustment can be predicted by individuals' performance in the executive tasks included in our cognitive battery (i.e., LPS3, TMT-B, backward digit and block span measures of the WMS [compare methods]). Each of the four predictor variables had a significant zero-order correlation with the parameter immediate adjustment (p 's ≤ 0.038). Using the enter method, we found that the four predictor variables explained 47% of the variance in the magnitude of immediate adjustment, $F(4, 23) = 5.18$, $p = 0.004$, $R^2 = 0.47$. Evaluation of the β coefficients, however, showed that only cognitive flexibility measured by the TMT-B had a significant partial effect in the full model, $t(23) = 3.45$, $p < 0.05$. Overall, the regression analysis further validates that saccadic plasticity in the perceptual task is substantially triggered by high-level mechanisms.

Consistent with our findings in the double-step paradigm, we found a pronounced saccadic latency difference between age groups, $F(1, 27) = 17.34$, $p < 0.001$, $\eta^2 = 0.39$, and a latency decrease across trial intervals, $F(3, 81) = 3.98$, $p = 0.011$, $\eta^2 = 0.13$. The interaction between both main effects was not significant, $F(3, 81) = 0.65$, $p = 0.585$, $\eta^2 = 0.02$. Figure 8 illustrates average latencies for each age group. Latencies did not correlate with any parameter derived from fitting vertical amplitude data with the exponential model (i.e., asymptotic level, adaptation amplitude, and adaptation rate). This replicates the finding of Experiment 1 that saccadic plasticity is not modulated by latency differences.

Discussion

We studied saccadic adaptation in two established paradigms that are supposed to tap into different functional mechanisms. Adaptation in the double-step paradigm is induced by systematic postsaccadic errors and reflects primarily low-level plasticity. In contrast, saccadic adaptation in a perceptual task is triggered by a behavioral goal (i.e., accomplishing a discrimination task) and thus allows insights into high-level processes contributing to plasticity. We explored whether sensorimotor plasticity in both paradigms differs between young and senior adults.

In the double-step paradigm, we found robust plasticity across age groups. Young and senior adults showed similar adaptive changes of saccadic gain at the beginning as well as at the end of the adaptation phase,

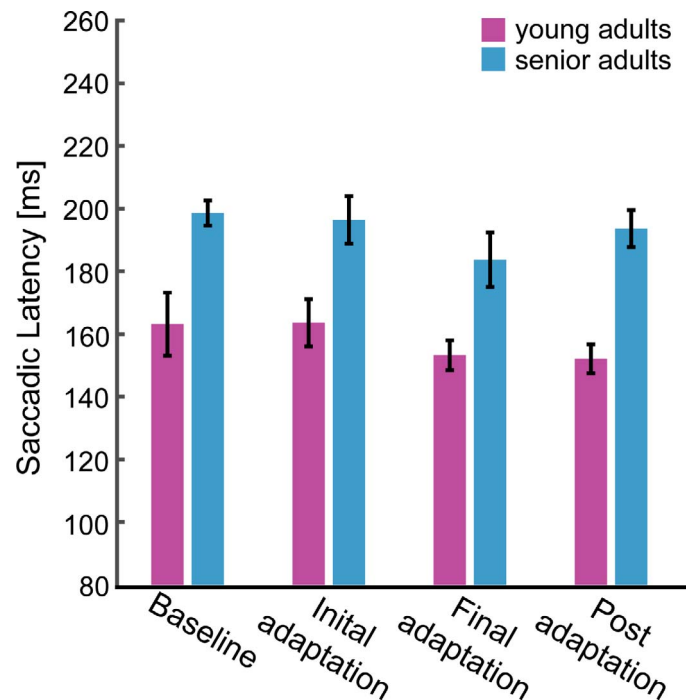


Figure 8. Average saccadic latencies in the specified trial intervals of the perceptual task for young adults and senior adults. Error bars: SEM.

and they did not differ in adaptation rate (i.e., after how many trials they reached a given change criterion). In addition, there was no evidence for age differences in recovery from adaptation when error information was abolished. When adaptation was driven by a perceptual task, age-related differences in plasticity were observed. Although young as well as senior adults showed efficient amplitude shifts, they substantially differed in the contributions of immediate and gradual adjustments to overall adaptation. Whereas immediate adjustments were found to be significantly stronger in young adults than in senior adults, gradual adjustments were not affected by age. Again, age groups showed equivalent adaptation rates. In the postadaptation phase, more pronounced recovery from adaptive amplitude shifts was observed in young adults. Our differential findings in the two saccadic adaptation paradigms contribute to the understanding of specific age-related changes in visuomotor plasticity.

The absence of age effects in the double-step paradigm agrees with evidence provided by the only previous study concerned with saccadic adaptation, suggesting preserved low-level plasticity across the adult life span (Bock et al., 2014). This is in contrast to the heterogeneous pattern of results for reaching adaptation. Several studies have documented an age-related decline of reaching plasticity induced by visuomotor rotations (e.g., Bock, 2005; Bock & Girgenrath, 2006; Buch et al., 2003; Heuer & Hegele, 2008b), but vulnerabilities have been primarily attri-

buted to reduced explicit adjustments. When dissociating explicit and implicit components of reaching adaptation by appropriate paradigms, age effects have been shown to be limited to less efficient use of explicit strategies while sparing implicit adjustments (Hegele & Heuer, 2010a, 2010b, 2013; Heuer et al., 2011; McNay & Willingham, 1998; Roller, Cohen, Kimball, & Bloomberg, 2002). These results consistently indicate resiliency of low-level adaptation mechanisms. Reaching movements and saccadic movements differ fundamentally. Saccades represent extremely fast, ballistic movements that cannot be corrected online after initiation. In addition, because of reduced visual sensitivity during the saccade, awareness of the target manipulation inducing postsaccadic errors is minimized. These characteristics limit the use of explicit strategies during adaptation and allow focused investigation of low-level contributions to visuomotor plasticity.

This interpretation is also corroborated by the detailed analysis of adaptive shift components. We distinguished between immediate adjustments after the onset of target manipulation and gradual adjustments that develop over the adaptation phase. In the typical double-step paradigm, this distinction can be considered as not well defined because immediate adjustments rely on awareness of the target manipulation. Sensitivity for target displacements, however, is substantially reduced during saccades (Bridgeman et al., 1975; but see, e.g., Castet & Masson, 2000). Thus, immediate adjustments can be expected to contribute only minimally to overall adaptation induced by the double-step paradigm. We indeed observed less than 5% immediate adjustment but about 16% gradual adjustment across the adaptation course (compare also Schütz et al., 2014). Thus, adaptation primarily relied on gradual, automatic processes, whereas fast, high-level processes, which are assumed to be more vulnerable to aging, played only a minor role. We suggest that the still significant immediate adjustments at the beginning of the adaptation phase are most likely based on incomplete intrasaccadic suppression of target displacement (see Bridgeman et al., 1975). Thus, awareness was clearly minimized, but probably not completely abolished, allowing for some high-level contributions to adaptation. However, these contributions were not reliable enough to indicate age-related differences. Overall, our findings indicate that adaptation in the double-step task is dominated by gradual processes and that these processes remain efficient across the adult life span.

Saccadic adaptation induced by a perceptual task provided the opportunity to investigate differential age effects on immediate and gradual adjustments across the adaptation process and results suggest a specific decline of underlying mechanisms. In particular,

immediate adjustments, which are applied to meet the demands of the suddenly manipulated task at the beginning of the adaptation phase, reflect high-level capacities. Notably, task manipulation is completely transparent and thus fully accessible to awareness. Accordingly, in contrast to adaptation dynamics in the double-step paradigm, immediate adjustments in the perceptual task contribute crucially to overall adaptation. In senior adults, immediate adjustments contributed to 50% of the final amplitude change at the end of the adaptation phase; however, in young adults, this contribution reached 65%. This difference indicates that the contribution of immediate shifts to visuomotor adaptation induced by a perceptual task is more pronounced in young adults than in senior adults. Gradual adjustments across the adaptation course were equivalent in both age groups. The advantage of young adults in immediate adjustments was perpetuated at the end of the adaptation phase when young and senior groups had compensated 73% and 57% of the target amplitude manipulation, respectively. Less pronounced amplitude shifts presumably also contributed to the lower discrimination accuracy we observed in senior adults because their saccades were not sufficiently optimized for the behavioral task.

It is well known that aging challenges behavioral and neuronal plasticity (Jones et al., 2006; Lustig, Shah, Seidler, & Reuter-Lorenz, 2009). Thus, the question arises as to which mechanisms contribute to preserved low-level and vulnerable high-level saccadic plasticity. Most basically, we can exclude that our senior age group represented a positively biased sample saved from age-related functional decline. Saccadic latencies in the senior adult group were found significantly increased, consistent with seminal studies on aging of saccadic control (Munoz et al., 1998; Peltsch et al., 2011) and indicating typical age-related slowing of processing speed (Salthouse, 1996). Similar adaptive capacities despite distinctive latency differences moreover corroborate results showing that saccade latencies per se do not influence the magnitude of adaptation (e.g., Schütz & Souto, 2015). However, we were able to predict immediate adjustments by standard measures of executive functioning. This further emphasizes that fast adaptive changes of saccade amplitude reflect high-level adjustments. Executive functioning is widely accepted as a psychological core primitive of functional changes with increasing age (Hasher & Zacks, 1988; Park & Reuter-Lorenz, 2009; Span, Ridderinkhof, & van der Molen, 2004; West, 1996). Our findings show that this impact is also valid for visuomotor control.

Our results can be related to a general model of sensorimotor adaptation that takes into account temporal dynamics of learning processes. Körding,

Tenenbaum, and Shadmehr (2007) modeled sensorimotor adaptation as a combination of fast and slow processes. Whereas fast processes drive rapid adaptive changes that are prone to rapid decay, slow processes contribute gradually over a prolonged timescale to adaptation and decay only slowly (Ethier, Zee, & Shadmehr, 2008). Although our results for immediate and gradual adjustments cannot be directly mapped onto the distinction between fast and slow adaptation processes, some plausible links can be proposed. In our paradigms, immediate adjustments are presumably linked to fast processes. Gradual adjustments might involve both fast and slow processes, but we suppose that they predominantly rely on slow processes. Thus, recovery from adaptation in the double-step paradigm, in which gradual adjustments dominate, can be expected to be rather slow. In the postadaptation phase, when the target was extinguished during the saccade and did not reappear, we congruently determined a reincrease of saccadic amplitude of about 5%, showing a rather slow decay or, in other words, strong retention in both age groups. This pattern indicates that slow adaptation processes are preserved during aging. More pronounced recovery from adaptation induced by a perceptual task in young adults might be based on age-specific contributions of fast and slow process to overall adaptive changes. We speculate that young adults' plasticity relies more on immediate changes, which are supposed to decay rapidly. In contrast, given less efficient use of executive functions, senior adults might rely more on gradual changes, which are supposed to decay slowly. This pattern could contribute to faster recovery from adaptation in young adults than in senior adults. However, modeling of two adaptation components that differ in buildup and decay requires pure retention without sensory feedback. Because visual feedback was available in the postadaptation phase of the perceptual task, the model might not apply to our data directly. Thus, the link between differences in recovery and dominance of specific adaptation components has to remain tentative.

The observed age-related vulnerabilities of saccadic adaptation are functionally based on age effects on involved neuronal substrates. Candidate structures are in particular the cerebellum and the brainstem (Robinson, Fuchs, & Noto, 2002). However, more recently, cortical areas, especially frontal and parietal areas, have also been found to be involved in saccadic adaptation (Blurton, Raabe, & Greenlee, 2012; Gerardin, Miquée, Urquizar, & Péliisson, 2012; Panouilleres et al., 2014). Different areas might contribute to specific adaptation components. Whereas subcortical structures can be assumed to be functionally relevant rather for low-level mechanisms of sensorimotor plasticity, cortical areas might specifically fuel high-

level mechanisms. Age-related detrimental changes have been described in all functionally involved regions (Jernigan et al., 2001; Raz et al., 2005; Sowell et al., 2003), but subcortical decline occurs later than decline in cortical areas. Thus, our finding of preserved low-level visuomotor plasticity but impaired high-level processes in senior adults might reflect differential time courses of regional decline.

In summary, stable saccadic adaptation in the double-step paradigm across the adult age range suggests robust low-level visuomotor plasticity that compensates primarily for visual errors. Because our data do not allow for the dissociation of the contributions of prediction errors and visual errors to adaptation in the double-step paradigm (compare Collins & Wallman, 2012), the particular role of prediction errors cannot be specified. Age effects on saccadic adaptation in a perceptual task specify that although gradual adaptive changes are preserved during aging, fast changes, in particular, are attenuated with increasing age. Thus, the age-related decline of saccadic plasticity is defined by less efficient high-level mechanisms.

General conclusions

Our results provide evidence of differential aging processes in saccadic adaptation. Current theories of age-related functional changes assume a general reduction in processing resources and global decline with increasing age (Salthouse, 1996). Our data highlight that differentiation between specific vulnerabilities and preserved resources is needed. Differential age effects emphasize the often ignored complexity of aging processes and call for comprehensive investigation of subprocesses to improve our understanding of decline and stability (Cabeza, Nyberg, & Park, 2005a).

Resiliency of low-level mechanisms and specific vulnerability of high-level mechanisms in saccadic adaptation moreover provide a link between cognitive and sensorimotor aging. Our findings indicate that psychological core primitives identified for cognitive decline (i.e., executive functioning) apply also to age-related changes in sensorimotor capacities. Saccadic plasticity was not affected by age-related slowing, and there was no evidence for reduced compensation for visual errors; however, we found age-related decline of immediate adaptive adjustments. Thus, not sensorimotor plasticity per se might be reduced in senior adults but rather executive contributions to efficient resource control (compare also Chang, Shibata, Andersen, Sasaki, & Watanabe, 2014).

Keywords: *healthy aging, saccadic eye movements, visuomotor adaptation, plasticity, visual error, executive control*

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