

Age effects on predictive eye movements for action

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When interacting with the environment, humans typically shift their gaze to where information is to be found that is useful for the upcoming action. With increasing age, people become slower both in processing sensory information and in performing their movements. One way to compensate for this slowing down could be to rely more on predictive strategies. To examine whether we could find evidence for this, we asked younger (19–29 years) and older (55–72 years) healthy adults to perform a reaching task wherein they hit a visual target that appeared at one of two possible locations. In separate blocks of trials, the target could appear always at the same location (predictable), mainly at one of the locations (biased), or at either location randomly (unpredictable). As one might expect, saccades toward predictable targets had shorter latencies than those toward less predictable targets, irrespective of age. Older adults took longer to initiate saccades toward the target location than younger adults, even when the likely target location could be deduced. Thus we found no evidence of them relying more on predictive gaze. Moreover, both younger and older participants performed more saccades when the target location was less predictable, but again no age-related differences were found. Thus we found no tendency for older adults to rely more on prediction.

train ticket machine people direct their gaze to the virtual button that indicates their desired destination, and then move their hand to that button. Humans are known to shift their gaze toward where they will act next (de la Malla, Rushton, Clark, Smeets, & Brenner, 2019; Mennie, Hayhoe, & Sullivan, 2006; Land, 2009; O’Rielly & Ma-Wyatt, 2020; Voudouris, Smeets, Fiehler, & Brenner, 2018), so if the ticket machine proceeds rather slowly, experienced travelers may anticipate where the next relevant virtual button will appear and direct their gaze, and even their hand, to that location. Such voluntary anticipation could allow a faster selection than simply reacting to the target appearing in the visual periphery (Thomas, Gallagher, & Purvis, 1981; Mennie et al., 2006; Kowler, Rubinstein, Santos, & Wang, 2019; but see also Ryu, Abernethy, Mann, Poolton, & Gorman, 2013). Predictive saccades can be based on various factors, such as the underlying dynamics of the environment (Diaz, Cooper, Rothkopf, & Hayhoe, 2012), contextual information (Li, Aivar, Kit, Tong, & Hayhoe, 2016), or prior experience with similar settings (Aivar, Hayhoe, Chizk, & Mruczek, 2005; Hayhoe, McKinney, Chajka, & Pelz, 2011). Predictive saccades, if directed to the correct location, can be beneficial because relevant visual information that appears at the fixated location will be processed by central, high-resolution vision, rather than by less reliable peripheral vision, fostering prompt use of that information for subsequent action.

Does the reliance on prediction increase with age? The reason to suspect is that the sensory processing of haptic (Overvliet, Wagemans, & Krampe, 2013), tactile (Klever, Voudouris, Fiehler, & Billino, 2019), and visual (Owsley, 2016) signals deteriorates with age. At the same time, movements become slower

Introduction

Humans use visual information to accomplish various daily tasks. In most of these cases, gaze is directed to task-relevant locations before a body movement is executed toward these locations. For example, when interacting with the touchscreen of a

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and more variable (Seidler et al., 2010) and more susceptible to influences from the surroundings (de Dieuleveult, Brouwer, Siemonsma, Van Erp, & Brenner, 2018). Older adults have longer eye movement latencies (O’Rielly & Ma-Wyatt, 2020), larger fixation errors (Peltsch, Hemraj, Garcia, & Munoz, 2011), poorer contrast sensitivity (Oswley, 2016), and a reduced field of view (Ball, Beard, Roenker, Miller, & Griggs, 1988). One way to compensate for such sensorimotor compromises might be to rely more on predictive processes. Indeed, older adults have been reported to rely more on predictive strategies than younger adults do (Wolpe et al., 2016; Klever et al., 2019). For instance, when performing sequential actions, older adults direct their gaze to the location of the next grasping target (Coats, Fath, Astill, & Wann, 2015) or to the next stepping location (Chapman & Hollands, 2006; Curzon-Jones & Hollands, 2018) earlier compared to younger adults. This may indicate that older adults rely more on predictive behavior. However, older adults shifting gaze earlier to the next location of interest relative to an ongoing action may also result from older adults moving their limbs later or more slowly: once they no longer need to look anywhere related to the current movement, they can shift their gaze toward future locations, so this gaze shift may happen earlier with respect to the next action if there is more time between the current and next action. Considering this ambiguity, it remains unclear whether the earlier gaze shifts to future acting locations in aging really reflect predictive behavior or are a byproduct of the dynamics of the ongoing action.

To examine whether the tendency to rely on predictive gaze behavior increases with age, we need to dissociate such a tendency from other factors that influence the timing of the movements. Here, we do so by comparing eye and hand movements during visuomotor tasks with various levels of predictability. Healthy younger and older participants reached to hit a visual target, the location of which was the same in *all* trials of a given condition (predictable), the same in *most* trials (biased), or chosen at *random* on each trial (unpredictable). We are particularly interested in eye movements during the period before the target appears, which is when predictive strategies could be revealed. Participants should be able to predict the target location in the predictable condition and thus fixate that location relatively early, possibly even before the target appears. The timing might depend on how well participants can anticipate the moment the target appears, and need not differ systematically with age. Trying to predict the target location cannot help perform the unpredictable condition, so participants from both age groups can only reliably fixate the target after it appears, with older participants possibly responding less fast. The most interesting condition is when the target location can be correctly inferred in most but not all trials (biased). Will

older adults rely more on predictions in this condition, which could improve performance on most but not all trials? If so, their saccades might have particularly short latencies in this condition, possibly even shorter than those of younger adults.

Methods

Participants

A total of 24 younger and 21 older adults were invited to participate in this study. Out of these 45 participants, nine were excluded from further analyses because of technical issues during data collection (failure to calibrate the eye-tracker or software failure). Our final sample included 36 participants, consisting of 18 younger ($M = 24 \pm 3$ years; range 19–29 years; three male) and 18 older adults ($M = 63 \pm 6$ years; range 55–72 years; seven male). All of them had normal or corrected-to-normal vision and were free from any known neurological or musculoskeletal issues at the time of the experiment. According to the German translation of the Edinburgh Handedness Inventory (Oldfield, 1971), 34 participants were right-handed, and two were ambidextrous. Older adults were screened for cognitive impairment using the Montreal Cognitive Assessment, applying a cut-off score of ≥ 26 (Nasreddine et al., 2005). This test is used to assess mild cognitive impairments, which could be indicative of pathological conditions, such as dementia. Younger adults were recruited through internal mailing lists of the Justus Liebig University Giessen and were compensated either with 8€/h or with course credits. Older adults were community-dwelling and were recruited through personal contacts of the authors, a recruiting list, and public announcements. Older adults were compensated with 8€/h. The study was approved by the local ethics committee of the Justus Liebig University Giessen. All participants provided informed consent according to the World Medical Association (2013, except for §35, pre-registration) before the beginning of the experiment.

Apparatus

Participants were seated in front of a table, facing a ViewPixx3D 23" monitor (1920 × 1080 px, 521 × 230 mm, 60 Hz; VPixx Technologies Inc, Saint Bruno, QC, Canada). A numeric keyboard was placed 13 cm in front of them, aligned with their midline. Participants rested their heads on an adjustable chinrest during data collection. The chinrest was 53 cm from the center of the monitor. Eye movements of the participant’s right eye were recorded at 500 Hz using the Eyelink II (SR

Research Ltd., Ottawa, ON, Canada), except for one participant whose eye movements were accidentally recorded at 250 Hz. The position of an infrared marker fixed to the right index fingernail was recorded at 250 Hz with an Optotrak Certus (Northern Digital, Waterloo, ON, Canada). The experiment was controlled in MATLAB 2019b (MathWorks Inc, Natick, MA, USA). The presentation of visual stimuli, as well as the recording of eye movements, were controlled by Psychtoolbox (Version 3.0.16) (Brainard, 1997), and kinematic data were collected using the Motom Toolbox (Derzsi & Volcic, 2018).

Procedure

Participants were asked to sit in front of the monitor and read the task instructions. The eye tracker was then calibrated with the standard nine-point calibration procedure implemented in Eyelink II (validation accuracy of $\leq 1^\circ$). The experiment was conducted in a dimly lit room. Each trial of the tasks described below involved the presentation of a centrally presented fixation cross ($0.87^\circ \times 0.87^\circ$) and of a laterally presented target square ($2.9^\circ \times 2.9^\circ$). The target square was presented 16.41° to the left or right relative to the fixation cross.

Because aging can reduce visual sensitivity (Owsley, 2016) and impair peripheral vision (Ball et al., 1988), we first conducted a contrast sensitivity test. Each participant's contrast sensitivity was assessed in a psychophysical forced-choice experiment before starting the main experiment. Participants were asked to fixate a light gray fixation cross that was presented on a darker gray background and then press a button with their right index finger to start the trial. A target square was presented 800 ms after the trial started for a duration of 800 ms, pseudorandomly left or right of the fixation cross. Twenty gray levels between black and dark gray were tested, one level per trial. Each gray level was presented six times in a pseudorandom order for a total of 120 trials. Participants had to keep on fixating the cross and then report whether they saw a target square on the left or right by pressing a button with the respective index finger. Their performance on this task was used to determine the luminance value for the target of the main experiment: we wanted a value that would make it beneficial, but not essential, to move one's eyes toward the target before moving the arm. How we selected the individual contrast levels is explained in the section below. We felt that we should account for individual differences in contrast sensitivity to ensure that finding any systematic difference in prediction between the groups can be attributed to an overall inclination to predict, rather than to participants learning to match the extent to which they predict to how beneficial prediction can

be for their individual contrast sensitivity during the experiment.

After the contrast sensitivity test, participants read instructions about how to perform the main experimental task. They were instructed to hit the square with their right index finger as quickly as possible. The targets in the main task of the experiment had the gray level obtained from the contrast-sensitivity test. The steps of a single trial were illustrated to the participants on paper. After clarifying any questions they had, participants performed three practice trials with the target in each of those trials being presented randomly at one of the two possible locations. Participants could perform more practice trials if necessary. Once both they and the experimenter confirmed that the participant had understood the task, the main experiment started. The task was split into three blocks, one for each condition (predictable, biased, unpredictable). The blocks were presented in counterbalanced order across participants and each block consisted of 50 trials. For each of the conditions, the target square was presented either to the left or right of the central fixation cross (as in the above-mentioned contrast sensitivity test). In the predictable condition, the target always appeared at the same location, whereas the 50 trials were randomly distributed in a 40/10 and 25/25 ratio for the biased and unpredictable condition, respectively. For each participant, the prevailing target location in the biased condition was the same as that in the predictable condition. For 17 participants the prevailing target location was on the left and for 19 it was on the right. Participants did not receive any specific information about the differences between the three blocks. The experimenter did not comment on participants' speculations about the details of each block, but any questions that the participants had about this were answered after the end of the experiment.

Within each trial, participants had to reach and hit the target square as quickly as possible with their right index finger. Participants placed their right index finger at a start button (an "enter" key on a numpad) that was 15 cm in front of them, aligned with their midline, and 36 cm from the monitor. Participants initiated the trial by pressing this start button with their right index finger while fixating a circle ($\varnothing 1.41^\circ$) displayed at the center of the monitor. Their gaze direction at the moment of the button press was used to correct for any drifts of the eye tracker. After this, participants had to fixate a cross that appeared 6.48° below the fixation circle. This cross was visible for 900 ms, after which it disappeared, leaving an empty gray background. We considered the moment when the cross disappeared to be when the actual trial started because participants were free to move their eyes once the fixation cross disappeared. The empty monitor was presented for 1000 ms and was followed by the presentation of the target to the left or right of the previously presented

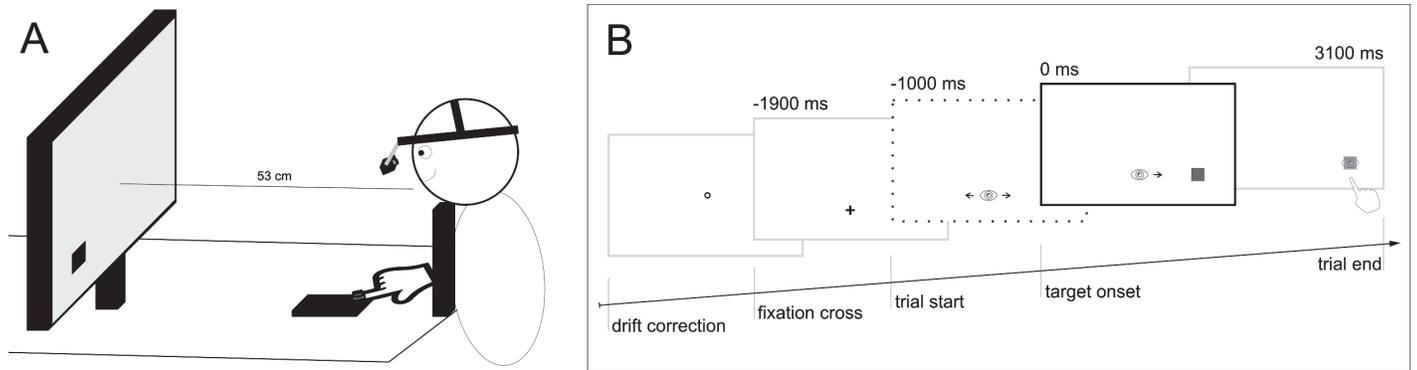


Figure 1. Illustration of the experimental design. (A) Sketch of the experimental setup. (B) Timeline of a single trial. After successful drift correction, a fixation cross was presented for 900 ms. The trial started when the cross disappeared (dotted frame), leaving an empty gray screen. The target appeared 1000 ms after fixation cross offset (bold outlined frame; 0 ms). Participants had to hit this target with their right index finger as quickly as possible. The frame background is illustrated in white, instead of the actual color gray, for better visibility.

cross. The target remained at its location for 3100 ms. Each trial lasted 5000 ms for a total of 10 minutes per condition. The whole experimental procedure, including assessments, took approximately 90 minutes. A schematic illustration of the setup and the timeline of a single trial is presented in [Figure 1](#).

Contrast sensitivity analysis

Contrast sensitivity was evaluated using the `psignifit 3` function ([Wichman & Hill, 2001](#)) in MATLAB 2019b. Each participant's responses to the detection of the target square were fit to a logistic function. We considered only those trials in which the participant's eyes did not move further than 4.69° away from the fixation cross, which was so for 99% of the trials of younger adults and 98% of the trials for older adults. For each participant, we estimated the gray level that would result in 80% correct responses from the psychometric function. This gray level was then used for the target in the main experiment. Standardizing target detectability at the individual level reduces the chance of different gaze strategies between age groups arising from poorer peripheral vision in older participants. Two older participants' behavior on this task was too inconsistent to determine a suitable gray level, perhaps because they did not follow the instructions during the contrast sensitivity test correctly, and so an individual contrast sensitivity could not be calculated. The target's gray level for these two participants was set to the average gray level found for two older adults and five younger adults in a pilot experiment. For the other participants, we chose the gray level that was detected with a probability of 0.8 of their own maximal probability of detection. On average, the contrast sensitivity thresholds were lower for the

younger than the older adults (average Michelson contrast 0.01 ± 0.001 compared to 0.03 ± 0.013 , respectively).

Eye movement analysis

Eye movement analysis was performed in MATLAB 2022a. We first low-pass filtered the raw gaze data with a second-order Butterworth filter using a cut-off frequency of 30 Hz. Saccade onset and offset were based on two-dimensional gaze speed using a threshold of $35^\circ/\text{sec}$. We only considered saccades with amplitudes larger than 2° between onset and offset as determined with the velocity threshold.

To obtain a first insight into our participants' behavior, we calculated the Euclidian distance between gaze position and the center of the current target for each sampling moment and averaged the performance across all trials, separately per condition and participant. Since the start position of the eyes was between the two possible target locations, the initial distance was always around 16° . However, distances can become larger than this value, for instance when a participant makes a saccade to the incorrect target location. A distance close to 0° denotes that the participant is looking at the presented target.

Predictive saccades are saccades that occur before (or very shortly after) target presentation. However, not every saccade that is initiated before the target presentation has to be truly predictive. For instance, when the target location is unpredictable, participants may shift their gaze back and forth between the two possible target locations to increase the chance of seeing the target soon after it appears ([Figure 2](#)). To see whether participants predictively shift their gaze to the target as well as whether they use an exploratory gaze

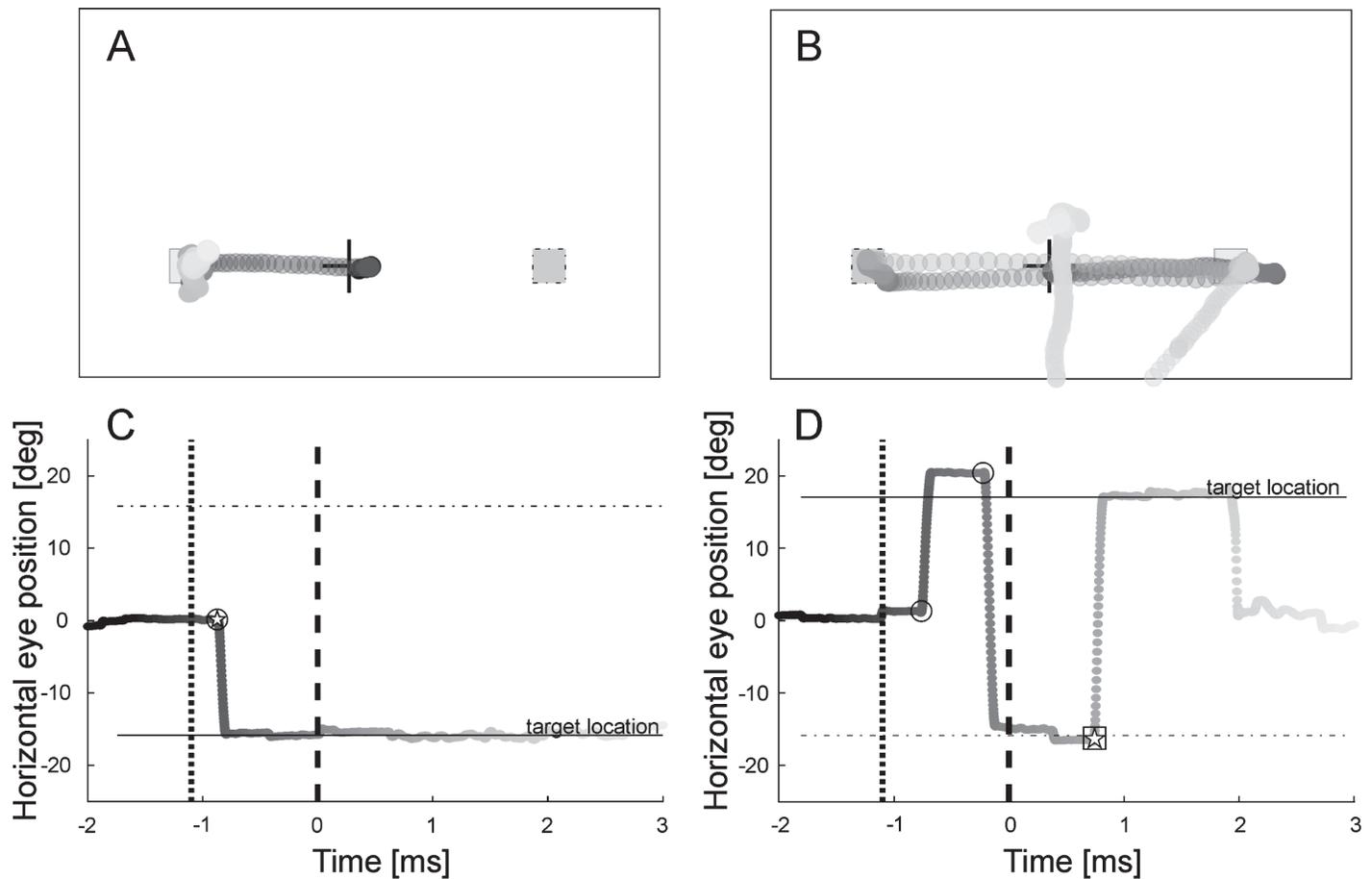


Figure 2. Examples of gaze deployment. (A, B) Gaze orientation on the experimental monitor during a single trial. The shade of gray represents the time and is equivalent to the gradient depicted in C and D. The target with the solid outline is the actual target and that with the dashed outline is the other potential target (that was not visible during that trial). (C, D) Temporal evolution of horizontal eye position in a single trial. Fixation cross offset (dotted line) and target presentation (dashed line) are used to classify saccades as predictive (circle) and reactive (square). The onset of the target saccade is indicated by a star. The solid and dot-dashed horizontal lines show the true target and the alternative target location, respectively. In the predictable condition (A, C), we expect participants to perform an early predictive saccade toward the anticipated target location. In the unpredictable condition (B, D), they might shift their gaze between the potential target positions before the target appears, and then make a final reactive target saccade if necessary.

strategy, we started by determining the latencies of both the first saccade and the saccade that brought gaze on the target.

The *latency of the first saccade* was defined as the time of the onset of the first saccade. The *latency of the target saccade* was the time of the onset of the saccade that brings gaze to the true target location. The target saccade was determined in two steps. We first identified saccades that could potentially be target saccades: they had to have an amplitude of at least 5° and to land at least 5° from the fixation cross in the direction of the true target location. If several such saccades were found, we chose the one with the longest fixation because we reasoned that the other saccades with shorter fixation durations might have been exploratory. We express both first and target saccade latencies

relative to the moment of the target presentation because this produces negative and positive latency values for saccades that were initiated before and after target presentation, respectively, making it easier to interpret the results.

Any prediction must be based on learning the probabilities of the target appearing at the two locations. To confirm that our experimental paradigm worked and that our participants learned the probabilities, we tested if there was any *reduction in target saccade latency* during the execution of the predictable condition, which is the condition in which the probabilities should be easiest to learn. We subtracted the median target saccade latency of the first ten from that of the last ten trials of all conditions separately per participant. Thus, a negative change

indicates an earlier initiation of target saccades in later than in earlier trials.

To assess gaze deployment for visual exploration, we determined the number of *changes in saccadic direction*, i.e., how often participants' gaze direction was reversed until the target was finally foveated. To this end, we only considered saccades in the opposite direction than the previous saccades, to exclude gaze shifts that were achieved by consecutive saccades in the same direction. The number of changes is zero if the eye moves from the fixation cross straight to the target, or to the target in several steps in the same direction. Only changes in the saccades' horizontal direction were considered for this variable.

Trials were excluded from the eye movement analysis if no target saccade was detected, for instance because the signals were too noisy, participants kept fixating the initial position or blinked during the saccade to the target, or because they only made a saccade to the wrong side and hit the wrong side. Overall, 2.29% of all trials had to be excluded, split into predictable (3.06%), biased (1.83%), and unpredictable (2.00%) conditions.

Hand movement analysis

Kinematic hand movement data was analyzed in MATLAB 2022a. For each trial, we obtained the three-dimensional position of the infrared marker on the finger and determined movement speed by numerical differentiation of the positional data. Movement onset was determined as the first sample after trial onset with a movement speed exceeding 10 cm/s and the hand being further than 3 cm from the hand start position. Movement offset was determined as the first sample with a movement speed lower than 10 cm/s while the marker was within 10 cm of the monitor. *Hand movement latency* was calculated as the time between the moment of target presentation and movement onset. *Movement time* was defined as the duration between movement onset and movement offset.

We excluded trials from the kinematic analyses if we could not calculate hand movement onset or hand movement offset, if movement time was unrealistically short (<300 ms), if hand movement latency or hand movement time exceeded three times the participant's standard deviation, or if no target saccade was detected in that trial. If 20 trials or more from a given block were excluded from the kinematic analysis, then all kinematic data of this participant were excluded because otherwise that participant's data might compromise the overall comparison of kinematic changes across the three conditions. Based on these criteria, eight participants (four younger and four older adults) were excluded because at least 20 trials were excluded in one (four participants), two (two participants), or all

three (two participants) blocks. We excluded these 1200 trials (8 participants \times 3 blocks \times 50 trials) because we could not calculate hand movement onset (16%) or offset (22%), movement time was unrealistically short (6%), hand movement latency or hand movement time exceeded three times the standard deviation in the respective block of trials (1%), or no target saccade was found in that trial (3%). The two participants for whom we could not determine individual peripheral contrast sensitivity thresholds were not among these eight participants.

After removing all the data of the eight above-mentioned participants from the kinematic analyses, we excluded 13% of the trials of the remaining 28 participants: 6% because we could not determine hand onset, 5% because we could not determine hand offset, 1% because the movement time was unrealistically short, 2% because hand movement latency or movement time exceeded three times the standard deviation, and 2% because there was no target saccade. The reason that we could not determine movement onset or movement offset was usually because the hand marker was occluded. We did not observe any unusual kinematic behavior when observing participants perform the task. We also visually inspected the excluded trials and confirmed that participants did reach toward the correct target location. This suggests that participants adhered to task instructions and performed the task as expected, which is why we decided to include the gaze data from these trials in the gaze analyses (except for the trials in which no target saccade was detected, see *Eye movement analysis*).

Statistical analyses

We calculated the median across all valid trials, separately per condition and participant, for *first saccade latency*, *target saccade latency*, *reduction in target saccade latency*, *changes in saccadic direction*, *hand movement latency*, and *hand movement time*. To examine whether participants learned the probability of the target being presented at the same location, we tested whether there was a *reduction in target saccade latency* in the predictable condition with two one-sided one-sample *t*-tests against zero (one per age group).

To investigate how age and the predictability of the target's location influence gaze strategies, we conducted 2 (age group) \times 3 (predictability) mixed analyses of variance on *first saccade latency*, *target saccade latency*, and *changes in saccadic direction*. We also conducted a 2 \times 3 mixed analysis of variance on *hand movement latency* and *hand movement time*. We were interested in an interaction between age and predictability. Specifically, we wanted to determine whether older participants predicted more (i.e., had relatively low latencies) in the biased condition. We reasoned that an

increased inclination to use a predictive strategy would primarily be evident in the biased condition and would be reflected in comparatively short saccade and hand movement latencies. Alpha level for all calculations was set to 0.05. Statistical analysis was performed in JASP 0.18.1 (University of Amsterdam, Amsterdam, The Netherlands) (JASP Team, 2023).

Results

We evaluated whether older adults are more inclined to rely on predictions when allocating their gaze during a visuomotor task, and therefore initiate saccades earlier than younger adults do in the biased condition. Of course, older participants may also initiate their eye movements before target presentation in an attempt to increase their visual sampling and thus increase the chances of seeing the target. If so, we should find more changes in saccadic direction in older adults when the target location is not predictable. We first present descriptive data reporting on the presence of expected effects. This is followed by the analysis of the main dependent variables.

Qualitative gaze behavior

Participants' behavior is qualitatively summarized in Figure 3, which illustrates the average distance between the instantaneous gaze position and the

true target location throughout each condition for both age groups. In the unpredictable condition, the distance to the target obviously only decreases after target presentation. In the predictable condition, both age groups tend to shift their gaze toward the target location before target presentation. Contrary to our hypothesis, in the biased condition (as unexpectedly also in the predictable condition) the older adults seem less inclined than younger adults to shift their gaze predictively toward the more common target location.

Reduction in target saccade latency

To confirm that our paradigm worked as intended and that our participants learned the relative probabilities of the target locations, we checked whether target saccade latencies were shorter in the later compared to the earlier trials of the predictable block, which is the condition in which the probabilities should be easiest to learn. As expected, target saccade latencies were shorter at the end than at the beginning of the predictable condition in both younger ($t_{17} = -3.29, p = 0.002, d = -0.77$) and older adults ($t_{17} = -2.47, p = 0.012, d = -0.58$; Figure 4), which indicates that participants learned that the target was always presented at the same location. They were also shorter at the end than the beginning of the biased condition, albeit to a lesser extent. The average change observed in the unpredictable condition was negligible.

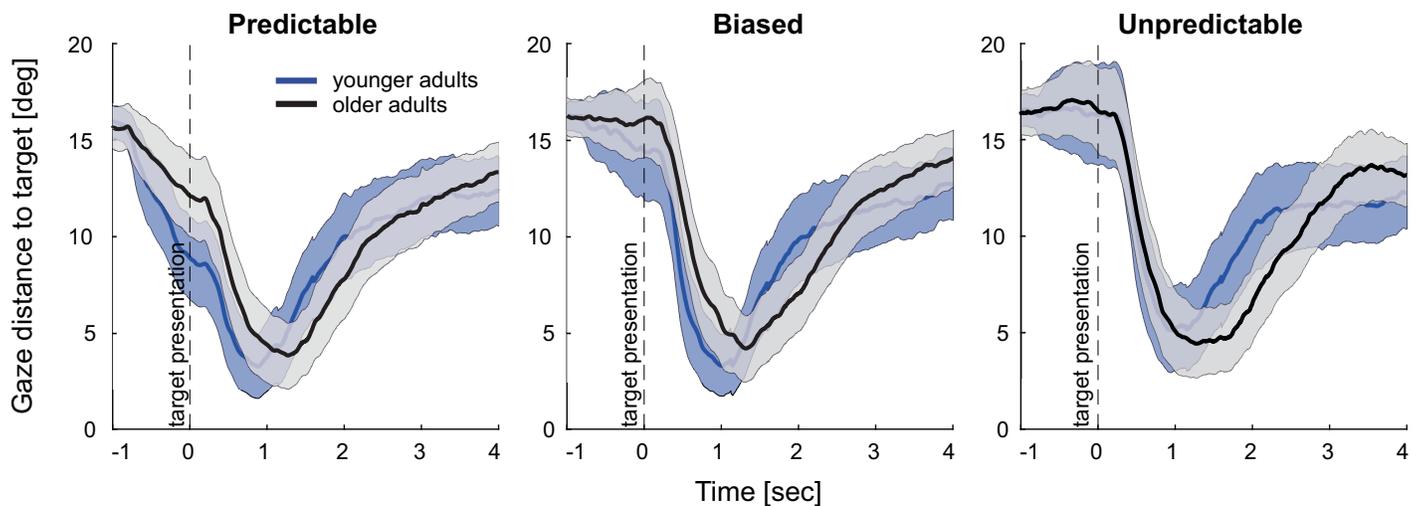


Figure 3. Gaze distance to target location. Time course of the distance between the instantaneous gaze position and the target location. Averages across participants are represented with bold lines for younger adults (blue) and older adults (black). The standard error across participants is represented by the shaded error bars. The distance increases after approximately one second from target presentation because there was no reason to keep gaze on the target for the complete duration of the trial (after the hand reached the target), so participants shift gaze back, presumably to be ready for the next trial.

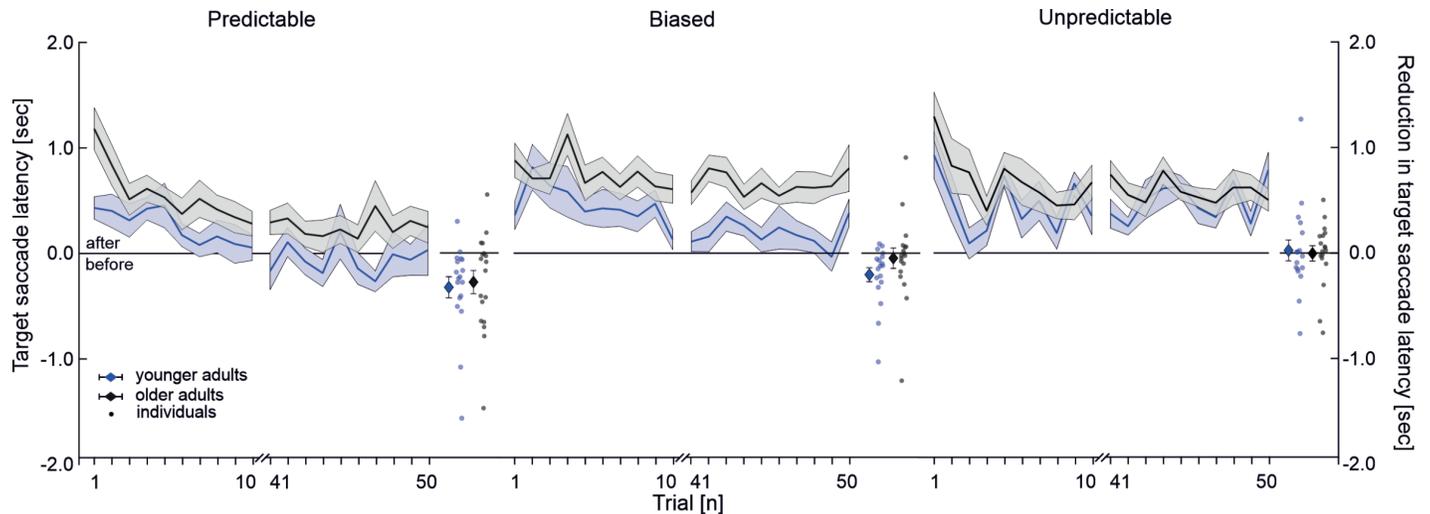


Figure 4. Reduction in target saccade latency. Average target saccade latencies of younger (blue) and older (black) adults during the first and last 10 trials for all conditions. Diamonds on the right side of each panel represent the averaged individual median reduction in latency, with dots indicating individual participants. Negative values indicate shorter latencies in the later than the earlier trials. Note that the values of the diamonds do not correspond with the difference between the mean values of the corresponding curves. They are the means of the median values for individual participants within those curves. This ensures that the exceptionally long latency on some very first trials does not have an excessive influence on the estimated reduction in saccade latency.

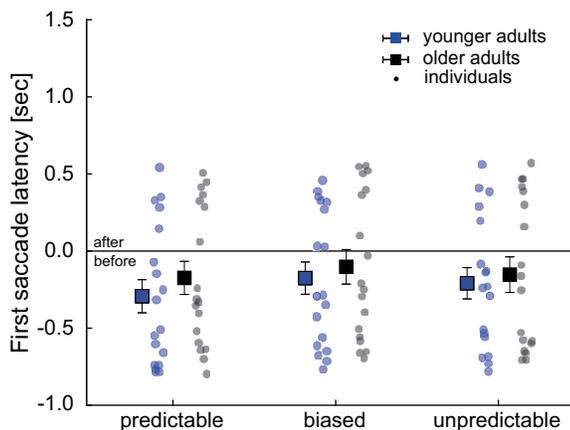


Figure 5. First saccade latencies. Negative latencies indicate eye movements that were initiated before target presentation. Individual median latencies are represented as dots. Means across these median latencies are shown as larger squares together with the standard error.

First saccade latency

Participants often initiated their first saccade before the target appeared. On average, younger participants started their first saccade 294 ms, 176 ms, and 210 ms before target presentation for the predictable, biased and unpredictable condition, respectively (Figure 5). Older participants started their first saccade 175 ms, 103 ms, and 153 ms before target presentation for the predictable, biased and unpredictable condition,

respectively. The latency of the first saccade did not differ significantly between age groups ($F_{1,34} = 0.34, p = 0.563, \eta^2 = 0.01$), or across predictability conditions ($F_{2,68} = 1.84, p = 0.167, \eta^2 = 0.01$), and there was no significant interaction ($F_{2,68} = 0.22, p = 0.807, \eta^2 < 0.01$). Importantly, older adults did not perform saccades relatively early in the biased condition. On the contrary, this was the condition in which their saccade latency was the longest.

Target saccade latency

Younger adults had target saccade latencies that were initiated on average 9 ms before the moment of target presentation in the predictable condition (Figure 6). All other target saccade latencies were clearly positive both for younger adults (biased: 261 ms; unpredictable: 372 ms) and older adults (predictable: 364 ms; biased: 576 ms; unpredictable: 542 ms), although there are large individual differences across participants. Not surprisingly, target saccades of both age groups were affected by predictability ($F_{2,68} = 15.53, p < 0.001, \eta^2 = 0.11$): they were shorter for targets at predictable locations. Target saccade latencies were longer in older than younger participants ($F_{1,34} = 9.44, p = 0.004, \eta^2 = 0.14$). Importantly, there was no interaction between age and predictability ($F_{2,68} = 1.90, p = 0.157, \eta^2 = 0.01$). In particular, there was no indication that older adults performed target saccades particularly early (i.e., with short latency) in the biased condition,

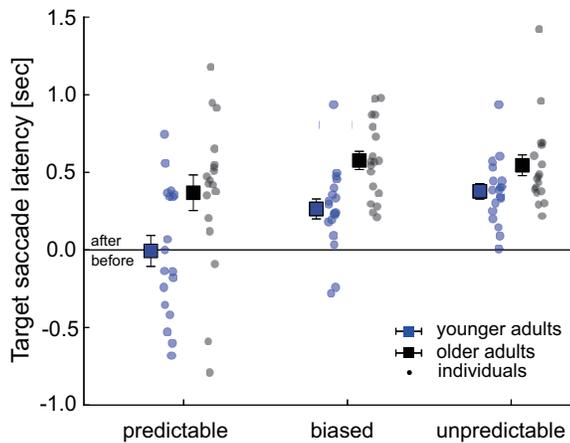


Figure 6. Target saccade latencies. Effects of aging and predictability of the target's location on target saccade latencies. Details as in Figure 5.

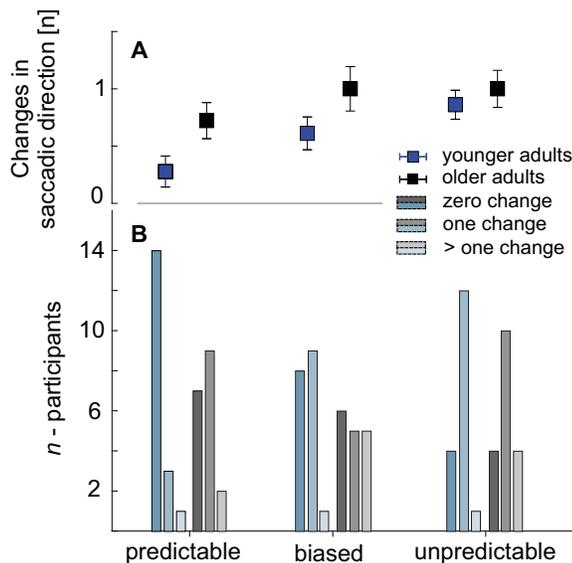


Figure 7. Number of changes in saccade direction. Effects of aging and predictability on the changes in saccade direction. (A) Average of participants' median number of changes per condition and age group. (B) Distribution of participants with zero, one and more than one change in saccade direction.

as one might expect if they were relying more on prediction.

Number of changes in saccade direction

As expected, there were more directional changes in the unpredictable than in the biased and predictable conditions ($F_{2,68} = 10.16$, $p < 0.001$, $\eta^2 = 0.07$; Figure 7), but there was no systematic difference between the two age groups ($F_{1,34} = 3.01$, $p = 0.092$, $\eta^2 = 0.06$)

and no significant interaction ($F_{2,68} = 1.37$, $p = 0.261$, $\eta^2 = 0.01$).

Hand movement performance

Hand movement latency was longer in older adults ($F_{1,26} = 6.81$, $p = 0.015$, $\eta^2 = 0.17$; Figure 8A), and it was influenced by predictability ($F_{2,51} = 8.76$, $p < 0.001$, $\eta^2 = 0.04$). There was no significant interaction between age and predictability ($F_{2,51} = 1.81$, $p = 0.174$, $\eta^2 = 0.01$). Most importantly, there was no indication of hand movement latency being particularly short in the biased condition in older adults. Movement time was not affected by age ($F_{1,26} = 0.12$, $p = 0.730$, $\eta^2 < 0.01$) or predictability ($F_{2,51} = 1.19$, $p = 0.313$, $\eta^2 = 0.01$), and there was no significant interaction ($F_{2,51} = 1.75$, $p = 0.183$, $\eta^2 = 0.01$; Figure 8B).

Discussion

We investigated whether aging leads to stronger reliance on predictive behavior during a visuomotor reaching task. To this end, younger and older participants reached to hit a visual target that could appear at one of two possible locations. In separate blocks of trials, this location was either always the same (predictable), usually the same (biased), or random across trials (unpredictable). As expected, participants learnt to shift their gaze to the target location earlier in the predictable condition. Our older participants showed poorer contrast sensitivity and had greater eye and hand movement latencies. However, we have no evidence of them compensating for such age-related slowing by predictive processes. Neither their gaze nor their hand movements started particularly early in the biased condition, which is where one would expect to see the effect of relying more on prediction (giving rise to performance that is closer to that in the predictable condition). Thus aging does not appear to lead to more reliance on predictive visuomotor behavior, at least in tasks that resemble the one used here.

Participants of both age groups initiated their first saccades away from the fixation cross before the target was presented (Figure 5). The first saccade sometimes brought gaze to the target location, but it did not always do so. These first saccades could indicate a predictive strategy, with the prediction sometimes being correct and sometimes wrong, but gaze might also shift for exploratory purposes. The presence of such exploratory saccades would explain why the latency of the first saccade was often negative in the unpredictable condition. However, there can also be predictive saccades in an unpredictable condition. A result of initiating saccades before the target appears

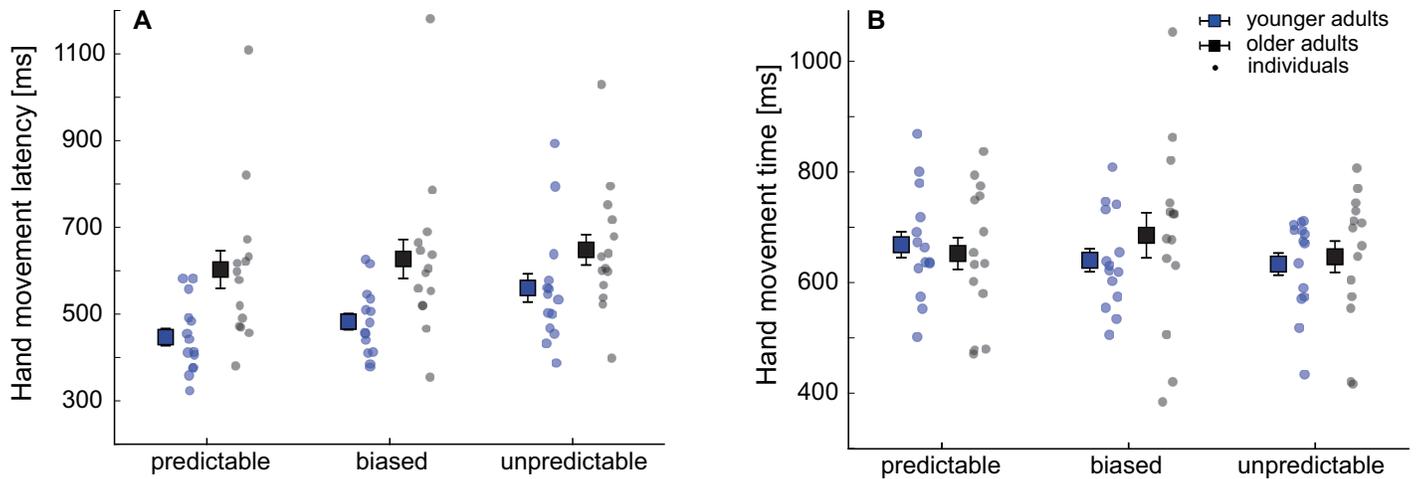


Figure 8. Hand movement results. Effects of aging and predictability of the target's location on (A) hand movement latency relative to target onset and (B) hand movement time. Details as in Figure 5.

when the target location is not predictable is that there will likely be saccades in more than one direction. This is indeed observed, but with no consistent difference in the number of changes in saccade direction between the age groups (Figure 7). Because of the fixed target presentation time relative to trial onset, participants could easily anticipate when the target will appear (Pirogovsky et al., 2013), and therefore initiate a (predictive or exploratory) eye movement just before target presentation to speed up target detection, especially when the target location is unpredictable. Our older participants did not systematically perform more such exploratory saccades than the younger participants.

Older adults generally have reduced (peripheral) acuity and our contrast sensitivity tests are in line with this. Because of this poorer acuity, older adults may make more exploratory saccades in their daily life. However, such exploration would be a result of their reduced visual acuity, rather than a fundamental change in strategy. More generally, older adults might rely more on prediction in daily life because they have access to less or to less reliable sensory information. What we show is that they do not tend to rely more on prediction irrespective of the sensory input. Rather, not finding that older participants rely more on prediction might be a consequence of us having tailored the stimuli in terms of their detectability to each individual's sensory perception levels.

We also examined the latencies of the saccades that finally brought gaze to the target. Target saccades were identified as the ones with the longest fixation around the true target location. Such fixations are particularly long because people keep fixating on the target as they move their hand towards it. By relying on the fixation duration, we can distinguish between exploratory saccades that happened to temporarily shift gaze

towards a possible target location and saccades that functionally shifted gaze to the actual target location, where a functional gaze shift is one that shifts gaze to a target that the hand subsequently moves towards, so that gaze during that fixation can help guide the hand to the target.

In the biased condition, participants might have occasionally performed saccades based on a wrong prediction, bringing gaze to the wrong location with a predictive saccade. In particular, participants might have regularly made predictive saccades in the more common direction on trials in which the less common target appeared. Since making saccades to the wrong side can be expected to delay making saccades to the actual target, target saccades in such trials would have particularly long latencies. By relying on the median target saccade latency across trials, our data are not very sensitive to the presence of occasional saccades based on wrong predictions in the biased condition. Not surprisingly, both age groups shifted their gaze to the correct target location earlier in the predictable compared to the biased and unpredictable conditions (Figure 6). In some individual cases, the median latency in the biased and unpredictable conditions was still negative, or so short that the oculomotor command must have originated before the target appeared (Calancie et al., 2022), so some of these saccades are certainly predictive.

Why did our participants not always use predictive gaze shifts when reaching to hit targets of partly or completely predictable locations? In our study, there was not much pressure to foveate the target fast, other than that it might help hit the target as quickly as possible, as instructed. Given the fact that the target remained visible for 3100 ms, there was ample time to perform the task without necessarily making any predictions. Instead, opting for a predictive saccade might bring

with it the risk of making an incorrect prediction that would bring gaze further away from the correct target location. In such a case, the target would appear further away in the periphery and thus would be harder to see, which is particularly critical for low-contrast targets such as those used in our experiment. An incorrect saccade would make it necessary to perform a subsequent saccade in the opposite direction, which would be of a larger amplitude. In such instances, the costs are higher than if participants had simply kept gaze at the central fixation cross and then reacted to the peripheral target. Thus some participants may not have considered the benefit of making predictive saccades to outweigh the cost of performing subsequent corrective saccades.

On average, older participants initiated their hand movements later, although they did not appear to perform these movements slower than younger adults. Older participants may have not initiated their eye movements as fast as possible, even when the target position was predictable, because the advantage of doing so is relatively small. Decreasing the latency of saccades may not be particularly important in our task because there is enough time to move the eyes and reach the target to guide the hand towards it after the hand has started moving. It may therefore be informative to test young and older participants on a more temporally demanding task, where predictive behavior may be more beneficial than simply reacting to visual information. We conclude that when reaching to hit stationary visual targets, older adults do not compensate for being slower than younger adults by performing more predictive eye movements.

Keywords: aging, gaze deployment, prediction, action, reaching

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