

The effects of aging on the perception of depth from motion parallax

Jessica Holmin¹ · Mark Nawrot¹

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Abstract Successful navigation in the world requires effective visuospatial processing. Unfortunately, older adults have many visuospatial deficits, which can have severe real-world consequences. Although some of these age effects are well documented, some others, such as the perception of depth from motion parallax, are poorly understood. Depth perception from motion parallax requires intact retinal image motion and pursuit eye movement processing. Decades of research have shown that both motion processing and pursuit eye movements are affected by age; it follows that older adults may also be less sensitive to depth from motion parallax. The goals of the present study were to characterize motion parallax depth thresholds in older adults, and to explain older adults' sensitivity to depth from motion parallax in terms of motion and pursuit deficits. Younger and older adults' motion thresholds and pursuit accuracy were measured. Observers' depth thresholds across several different stimulus conditions were measured, as well. Older adults had higher motion thresholds and less accurate pursuit than younger adults. They were also less sensitive to depth from motion parallax at slow and moderate pursuit speeds. Although older adults had higher motion thresholds than younger adults, they used the available motion signals optimally, and age differences in motion processing could not account for the older adults' increased depth thresholds. Rather, these age effects can be explained by changes in older adults' pursuit signals.

Keywords Depth perception · Motion parallax · Aging · Depth thresholds · Smooth pursuit eye movements

Visuospatial deficits in older adults have many adverse effects on health and on social and physical functioning (Crews & Campbell, 2004). Self-reported visual impairment contributes to the incidence of falls in older adults (Lopez et al., 2011) and is a significant predictor of mortality, especially in women (Lee, Gómez-Marin, Lam, & Zheng, 2002). Beyond visual impairment at the ocular level, research on sensory processing in older adults has revealed that perceptual deficits are associated with many negative outcomes, including difficulties with balance (Choy, Brauer, & Nitz, 2008), reading speed (Yu, Cheung, Legge, & Chung, 2010), and driving abilities (Owsley et al., 1998). Given that the population of older adults in the US is projected to nearly double by 2050 (Ortman, Velkoff, & Hogan, 2014), research on understanding age-related visuospatial deficits is especially timely and important. Some aspects of age effects on visuospatial abilities have been relatively well studied (for reviews, see Andersen, 2012; Owsley, 2011). However, very little is known about the effects of age on one important cue to relative depth, motion parallax.

Motion parallax (MP) is produced during observer or scene translation. As an observer moves through the environment, stationary objects appear to move relative to one another, creating relative image motion on the retina. Concomitantly, the translating observer maintains fixation on particular objects in the scene, generating smooth pursuit eye movements (Miles & Busetini, 1992). This combination of retinal image motion and pursuit is used by the visual system to generate a depth percept (Nawrot & Joyce, 2006). The geometric relationship of retinal image motion velocity (change in the angular position of an object's retinal image, $d\theta$), the observer's pursuit eye movement velocity (change in gaze angle, $d\alpha$), viewing

✉ Mark Nawrot
mark.nawrot@ndsu.edu

¹ Center for Visual and Cognitive Neuroscience, Department of Psychology, North Dakota State University, P.O. Box 6050 Fargo, ND, USA

distance to the point of fixation (f), and object distance from fixation (d_{MP}) is described by the motion/pursuit ratio (M/PR; Nawrot & Stroyan, 2009; Stroyan & Nawrot, 2012):

$$\frac{d_{MP}}{f} \approx \frac{d\theta}{d\alpha} \quad (1)$$

The M/PR provides a more useful quantification of depth from MP than “equivalent disparity” (ED) because the M/PR takes into account the role of pursuit eye movements in generating the depth percept. Moreover, the proximal stimulus variables used by the M/PR are dynamic (velocity), thereby better reflecting the dynamic characteristics of MP than do the static spatial displacements used in the quantification of MP with ED. Similarly, these dynamic variables used with the M/PR appear to better describe the underlying perceptual mechanisms of depth from MP. Although ED is useful and intuitive when directly comparing depth percepts from binocular disparity and MP, M/PR is generally a more precise approximation of depth (Stroyan, 2010).

Recent research (Holmin & Nawrot, 2015) has characterized the roles of the motion ($d\theta$) and pursuit ($d\alpha$) signals in limiting depth thresholds in younger adults. However, research on the perception of depth from MP in older adults is scarce. Older adults have a well-documented deficit in motion perception, with higher thresholds for motion detection (Atchley & Andersen, 1998; Bennett, Sekuler, & Sekuler, 2007), motion direction discrimination (Ball & Sekuler, 1986; Snowden & Kavanagh, 2006), and speed discrimination (Norman, Ross, Hawkes, & Long, 2003). The recovery of structure from motion (a perceptual process related to that of depth from MP) is likewise affected by age (Norman, Bartholomew, & Burton, 2008; Norman et al., 2013; Norman, Dawson, & Butler, 2000; Norman et al., 2012), though it is unknown to what degree the neural mechanisms are shared (Nawrot & Joyce, 2006). Aging also affects pursuit eye movements—older adults have poorer pursuit accuracy than younger adults (measured as gains, i.e., eye velocity/target velocity; Sharpe & Sylvester, 1978; Sprenger et al., 2011). Given these deficits in motion and pursuit (the $d\theta$ and $d\alpha$ signals), it follows that older adults might have deficits in the perception of depth from MP, as well.

In view of the logic just outlined, it is surprising that studies of aging and MP have not found any differences in depth perception between younger and older adults. Norman, Clayton, Shular, and Thompson (2004) presented an MP wave stimulus that varied in depth and had older and younger observers adjust the length of a response bar to indicate the magnitude of depth that was shown. Across three different stimulus depth magnitudes (2.0, 4.0, and 6.0 cm), both younger and older observers overestimated the amount of depth presented, but there were no age differences. In another study, observers adjusted a palm board to indicate the perceived

amount of slant presented in MP-defined stimuli (Norman, Crabtree, Bartholomew, & Ferrell, 2009). Again, there was no difference between younger and older observers in the magnitudes of adjusted slant, at any of the four levels of stimulus slant.

There are several possible reasons why no age differences were found in either of these studies (Norman et al., 2004; Norman et al., 2009). One possibility, of course, is that age simply has no effect on depth perception from MP. Although older adults show deficits in the two components of depth perception from MP (i.e., motion processing and pursuit), it could be that these deficits are compensated for by the visual system when generating a depth percept, or perhaps that the deficits are too small to have an effect on depth from MP. Another possibility is that the magnitudes of stimulus depth presented to observers by Norman and colleagues were suprathreshold; that is, it is possible that older adults may have higher thresholds for the perception of depth from MP than do younger adults. To illustrate, consider an observer with a deficit in motion processing. This observer might be able to perform a suprathreshold task, such as discriminating 5°/s from 2°/s motion, but show a deficit in motion detection at 1°/s. In a similar vein, older adults might be able to make reliable judgments about the magnitude of suprathreshold MP depth stimuli, but have higher thresholds for detecting or discriminating depth from MP than do younger adults. That is, older adults may be less sensitive to depth magnitudes near the threshold stimulus values. One last possibility is that the effects of age on MP may only be apparent under some stimulus conditions. For example, in Norman et al.’s (2009) study, the velocity at which the MP stimulus translated (generating pursuit eye movements, or $d\alpha$) was 12°/s. In their 2004 study, observers’ head movements were not strictly controlled, so the speed at which observers may have moved their heads (and generated the concomitant pursuit signal in the direction opposite that of head movement; Nawrot & Joyce, 2006) is unknown. It is conceivable that older adults may have lower depth thresholds at some pursuit velocities, such as those used by Norman and colleagues, but might have higher thresholds at other velocities.

In the present study, we sought to characterize depth from MP in younger and older adults across a range of stimulus conditions by measuring depth thresholds at slow, medium, and fast pursuit velocities, as well as measure motion thresholds and pursuit accuracy. We quantified depth thresholds using the simple M/PR ($d\theta/d\alpha$). We also examined how changes (or lack thereof) in older adults’ depth thresholds might be explained using the M/PR model, by asking whether age differences in motion ($d\theta$) and pursuit ($d\alpha$) could explain older adults’ performance in our depth threshold task.

Method

Observers

Groups of 32 younger ($M = 25.3$ years, $SD = 3.8$) and 32 older ($M = 66.3$ years, $SD = 4.7$) adults participated in the experiment. In the older age group, 26 observers were female and six were male. In the younger age group, 17 observers were female and 15 were male. The younger observers were student volunteers from North Dakota State University, who were either paid or given course credit for their participation. The older observers were recruited from the surrounding community and were paid for their participation. All observers gave informed consent to participate.

After giving informed consent, but prior to beginning the study, observers underwent screening for a variety of exclusion criteria. Far visual acuity was assessed using a Snellen visual acuity chart (Graham-Field, Atlanta, GA). Contrast sensitivity was assessed using a Pelli–Robson Contrast Acuity chart (Haag–Streit, Essex, UK). Observers' neurological health status was assessed using a revised form of Christensen, Armson, Moye, and Kern's (1992) health questionnaire. Observers who scored a 20/40 or worse on the (best corrected) acuity test or scored 1.65 or worse on the contrast sensitivity test, or indicated any neurological problems on the questionnaire, were not included in the study. During the study, observers adjusted their corrective lenses for viewing distance, if necessary. The procedures were overseen by the local Institutional Review Board and in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Apparatus

For depth and motion tasks, stimuli were generated using the MATLAB Psychophysics Toolbox (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007) and presented on an Apple 5 K iMac computer with a 27-in. retina display and a resolution of $5,120 \times 2,880$ pixels at 60 Hz. At the 200-cm viewing distance, the monitor subtended 15.4 deg of visual angle, and each pixel subtended 10.8 arcsec. For eyetracking, the stimuli were generated on a Macintosh computer and presented on a 20 in. flat-screen NEC CRT monitor with a resolution of $1,600 \times 1,200$ pixels at 85 Hz. At a 57-cm viewing distance, the monitor subtended 34.8 deg of visual angle and each pixel subtended 90 arcsec. An ASL Eye-trac 6000 (Applied Science Laboratory, Bedford, MA) with D6 remote optics and a sampling rate of 120 Hz was used to measure eye position. The eyetracking system is accurate within 0.5 deg and has a precision of 0.25 deg. The system communicated eye position information to the stimulus computer through a 16-bit analog connection with a National Instruments multifunction I/O board.

The experiment was conducted in a dimly-lit (~ 1 lux) room. During all three tasks, observer movement was restricted by a chinrest, and an eye patch occluded the observers' left eyes for monocular viewing.

Stimuli

These stimuli and methods were modeled after those of Holmin and Nawrot (2015). The depth stimuli were composed of $6,400 \times 43 \times 43$ arcsec black dots positioned randomly on a white background, contained within a 6.3×6.3 deg stimulus window. A small black square (6 arcmin) in the center of the stimulus window served as a fixation point. In separate conditions, the stimulus window translated leftward or rightward at one of three velocities (2.3° , 10.1° , and $25^\circ/s$) to generate pursuit eye movements ($d\alpha$) as the observer maintained fixation on the center point of the translating stimulus. Stimulus window translations began with a positional offset opposite the direction of translation, so that the fixation point at the center of the stimulus window would traverse the vertical midline midway through the window's translation. To generate smooth stimulus window translation, an updated window position was calculated and redrawn every 16.7 ms.

Stimulus parallax was achieved through relative motion of the dots, translating in opposite directions (shearing), within two different regions of the stimulus window during translation of the entire stimulus window (see Fig. 1). Dots within the bounds of one region of the stimulus moved in the same direction as the stimulus window, thereby generating $d\theta$ in the

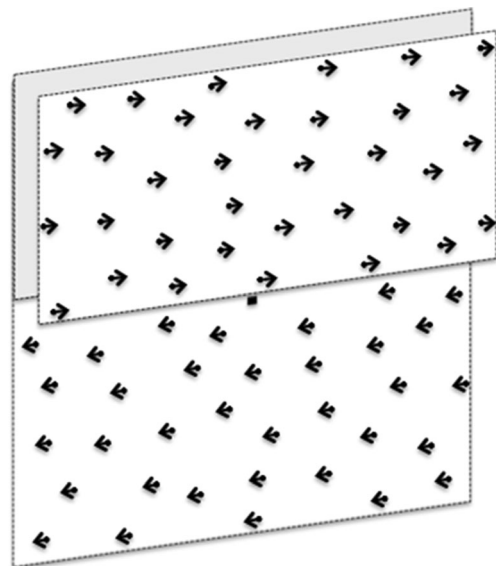


Fig. 1 Schematic of the stimulus used in the depth threshold task. In this example, the background motion is leftward. A rectangle, positioned flush with the horizontal meridian, contains dot motion in the rightward direction. This rectangle appears to be nearer in depth to the observer. Note that in the stimulus, no shadow is visible behind the rectangle in depth; the shadow in the schematic is meant to represent the fact that this rectangle is nearer in depth than the background

same direction as $d\alpha$. This region should appear nearer than the fixation point. Dots within the bounds of the other region moved ($d\theta$) in the direction opposite the direction of stimulus window movement ($d\alpha$), and should appear farther than the fixation point. The two regions corresponded to the upper and lower halves of the stimulus window, and the directions of dot movement within the two regions varied randomly between trials.

To generate this stimulus, on every frame (every 16.7 ms) the dots were shifted laterally, at the same rate as the stimulus window and fixation dot ($d\alpha$: 2.3°, 10.1°, or 25.0°/s). That is, both the stimulus window and the dots appearing within the window were translated every 16.7 ms. To add retinal image motion ($d\theta$) to these dots (which were moving with the fixation spot and should otherwise remain stationary on the retina), dots within the stimulus were further translated seven times (every 100 ms) throughout the 800-ms stimulus presentation. The speed of dot movement relative to the window movement ($d\theta$: 0.013°–0.92°/s) was the same for both directions of dot motion and was determined for each trial using a staircase procedure (see below). The overall perception of the MP stimulus was approximately that of a square-wave grating composed of smoothly moving dots.

In our depth threshold stimulus, parallax was defined by the relative (shearing) motion of dots within the stimulus. To allow for a direct comparison of $d\theta$ values between motion thresholds and depth thresholds, we designed a motion stimulus that was likewise defined by shearing motion (modeled after Snowden, 1992). The motion stimulus was identical to the depth threshold stimulus (i.e., same dot density, contrast, and retinal motion), but was stationary in the center of the screen. Similar to the depth threshold stimulus, the dots in the region above fixation moved to the left or right, and the dots in the region below fixation moved in the direction opposite that of the dots in the upper half of the stimulus. In the depth threshold stimulus, there was no retinal image motion when the dots within the stimulus moved at the same speed as the fixation point; retinal image motion was added every 100 ms. Similarly, in the motion stimulus, the dots moved once, halfway during the stimulus presentation, at 100 ms; the minimum magnitude of displacement that could be presented on a given trial was 10.8 arcsec. It is important to note that although the motion threshold stimuli and depth threshold stimuli were as similar as possible (excepting the presence of pursuit and stimulus duration), in no case did observers report a depth percept in viewing the motion stimulus, nor did either of the authors. The motion stimulus contained only shearing motion, with the dots in the lower and upper regions of the stimulus moving at the same speed; this lack of a relative velocity gradient coupled with the absence of a pursuit signal diminished any cues to depth.

In the pursuit condition, the pursuit target was a single white dot presented on a black background. At the 57-cm

viewing distance, the target subtended 0.23×0.23 deg. The target was translated leftward or rightward every 11.76 ms (85 Hz) at one of three velocities (2.1°, 10.6°, and 25.5°/s).

Procedure

Depth thresholds A trial began when the fixation spot was presented in the center of the screen. Following a button press by the experimenter to initiate a trial, the fixation spot jumped to the left or to the right to indicate the starting position of the stimulus translation. The magnitude of the fixation point jump was calculated from the pending stimulus velocity, such that the stimulus, when it appeared, would cross the vertical midline halfway through its translation. Following a variable interval from 0.5 to 3.5 s, the stimulus window appeared and began to move. The direction of stimulus window movement (left or right) was randomly determined on each trial. The order of condition presentation was determined using a Latin square. Observers maintained fixation in the center of the translating stimulus window throughout the 800-ms duration trial. To simplify data collection, we did not enforce fixation using an eyetracker in this task, as Nawrot and Stroyan (2009) did not find a difference in depth judgments between conditions in which fixation was objectively enforced and those in which observers were given verbal instructions to maintain fixation. Note that observers remained stationary, and MP was generated with stimulus dot movement tied to stimulus window translation, rather than with stimulus dot movement yoked to the observer's head movement. The same mechanisms of pursuit that are crucial for recovering depth from MP operate under both head-stationary and head-translating conditions; however, other somatosensory and vestibular signals that arise during head movements, including translational vestibulo-ocular reflexive (tVOR) eye movement, are not necessary for recovering unambiguous MP depth information (Nadler, Nawrot, Angelaki, & DeAngelis, 2009; Nawrot & Joyce, 2006; Nawrot, Ratzlaff, Leonard, & Stroyan, 2014). Keeping the observer's head stationary eliminates these unnecessary signals.

Observers performed a depth-phase judgment task in which they were asked to indicate verbally the location of the half-cycle of the stimulus (above or below fixation; see Fig. 1) that was closer in depth, relative to the other half-cycle. The observers' responses were recorded on the computer by the experimenter. No feedback was given. The threshold M/PR ($d\theta/d\alpha$) for unambiguous depth perception was found for each direction of stimulus translation (leftward and rightward) in each of the stimulus speed conditions using a staircase procedure with a three-down, one-up decision rule (Wetherill & Levitt, 1965). The initial dot motion ($d\theta$) was set to 0.24°/s, and each step in the staircase increased or decreased dot motion by 0.026°/s. Each staircase ended either when observers had had six reversals, which would track to

the 79 % threshold, or when the ceiling (0.92°/s) had been reached. For the block to end at ceiling, the participant had to reach the ceiling and have no reversals for the following five trials. If a block ended at ceiling and the observer had made fewer than six reversals, the data from that block were not included in the data analysis. Observers completed two blocks of trials for each pursuit direction and each pursuit speed. Each block typically contained 20–40 trials. At the slow and moderate pursuit speeds, all observers were able to generate six reversals in at least one of the two blocks for each pursuit direction. Two of the older observers were not able to perform the task at 25.0°/s and were not included in the data analysis.

Motion thresholds To begin each trial, a fixation spot was presented in the middle of the screen. Following a button press by the experimenter to initiate a trial, the stimulus window was presented, centered on the fixation spot. Observers were to maintain fixation throughout the duration of the stimulus presentation (200 ms). They reported which direction (left or right) the dots in the *top* region (i.e., the region of the stimulus above the fixation point) were moving, and the experimenter recorded observer responses on the computer. No feedback was given. As in the depth threshold task, a three-down, one-up procedure (Wetherill & Levitt, 1965) was used to determine d_{\min} , or the minimum amount of displacement observers needed to reliably discriminate motion direction. Staircases started with a dot displacement of 97.2 arcsec, moved in steps of 10.8 arcsec, and ended with nine reversals. Observers completed two blocks of trials in the motion threshold task.

Pursuit gains The eyetracker was calibrated for each observer using a nine-point calibration of the ASL system, followed by a two-point calibration of the experimental computer's recording of the eye position signal and a final five-point calibration along the horizontal axis of the pursuit target's movement. On each trial, the target was presented in the middle of the screen, and a button press by the experimenter initiated target movement. The experimenter did not initiate a trial until the observer was fixating the centered target. Once the trial was initiated, the target "stepped" either to the left or to the right (Rashbass, 1961), before translating in the direction opposite that of the step. The magnitude of the step varied depending on the pending stimulus velocity, such that for each trial the target would pass through the vertical midline of the screen 100 ms after the onset of translation. The target was erased from the display at 870 ms, and eye position was recorded for an additional 306 ms, giving a trial duration of 1,176 ms. The observer's task was to maintain fixation on the target as it translated. The target translated twice leftward and twice rightward at one of three different speeds (2.1°, 10.6°, and 25.5°/s), for a total of 12 trials per block. The order of pursuit speed presentation

was randomly determined at the beginning of each block for each observer. Observers completed three blocks at each speed, for a total of 36 trials per observer.

Results

Analyses were conducted in Microsoft Excel and SPSS 21 (SPSS II, New York, NY). Depth thresholds were quantified using the M/PR ($d\theta/d\alpha$; Nawrot & Stroyan, 2009). For each of the two blocks, in each of the three conditions, the threshold $d\theta$ (measured in degrees/second) for each direction of stimulus translation (left and right) was determined from the last four reversals. For each observer, the threshold $d\theta$ s for each stimulus direction were averaged across the two blocks to give two mean threshold $d\theta$ s (one for each stimulus direction). A 3 (Pursuit Speed [$d\alpha$]: 2.3°, 10.1°, and 25.0°/s) \times 2 (Age Group: young and old) \times 2 (Stimulus Translation Direction: left and right) analysis of variance (ANOVA) revealed no significant main effect of the direction of stimulus movement, and no interaction with any other variables, in the depth task (all F s < 1). Directional differences were therefore dropped from all further analyses.

The results from the depth task are shown in Figs. 2 and 3. In Fig. 2, the threshold $d\theta$ s found in the depth task are plotted for older and younger observers. Threshold $d\theta$ s were converted to depth measures using the M/PR: In each condition, the ratio of the threshold $d\theta$ s to the pursuit speed ($d\alpha$) that defined that particular condition was calculated (Fig. 3). These M/PR values can be converted to expected relative depth magnitudes (d_{MP}) using Eq. 1 and an expected viewing distance. Similar to binocular disparity, a particular M/PR corresponds to different physical depth magnitudes, depending upon the

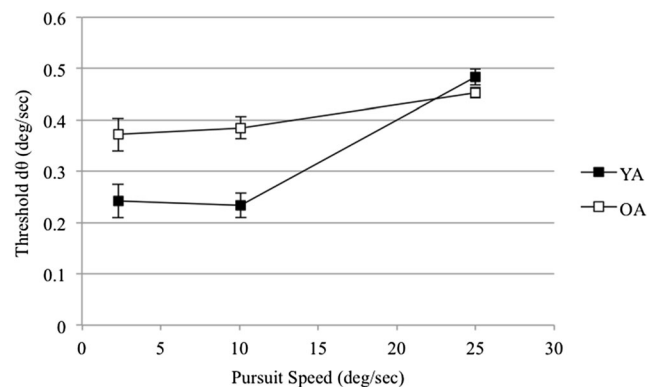


Fig. 2 Threshold $d\theta$ s for younger and older observers. The minimum within-stimulus motion ($d\theta$), in degrees/second, that observers required to perceive depth is plotted against the pursuit speed condition (2.3°, 10.1°, and 25.0°/s) on the x-axis. Black squares represent younger adults (YA), and white squares represent older adults (OA)

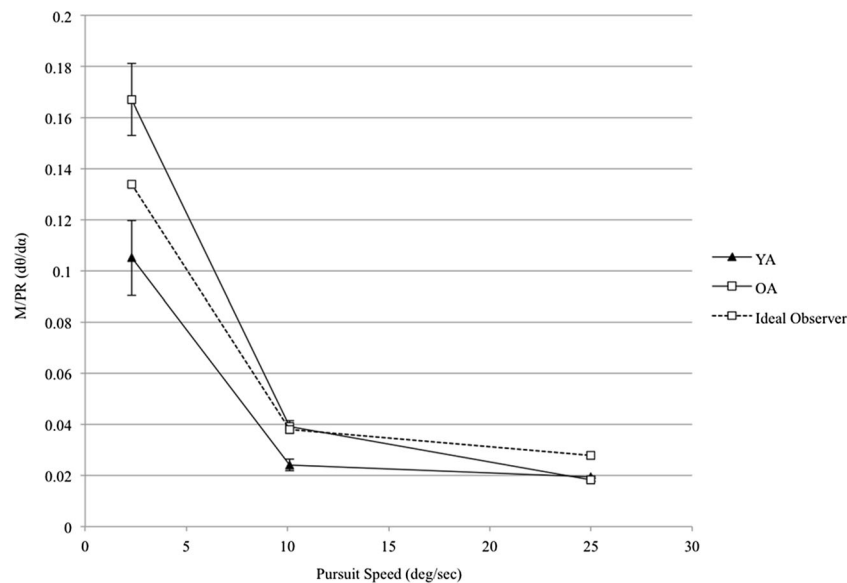


Fig. 3 Depth thresholds ($d\theta/d\alpha$) for older and younger observers. Depth thresholds are plotted against pursuit speed ($d\alpha$: 2.3°, 10.1°, and 25°/s) on the x-axis. The data plotted on solid lines represent the obtained

thresholds for younger (YA) and older (OA) adults. The data plotted on the dashed line represent the ideal depth threshold values predicted for OA (see the text)

viewing distance. For example, a threshold M/PR of 0.1 would correspond to a $d_{MP} = 20$ cm at a viewing distance of 200 cm, but a $d_{MP} = 5$ cm at a distance of 50 cm.

A 2×3 mixed factorial ANOVA was conducted on the depth thresholds, with Age Group (young and old) as the between-subjects factor and Pursuit Speed (2.3°, 10.1°, and 25.5°/s) as the within-subjects factor. Older adults had significantly higher thresholds than younger adults overall [$F(1, 59) = 10.58, p < .01, \eta^2 = .03$; all η^2 values are complete η^2]. We also observed a significant main effect of speed: as pursuit speed increased, depth thresholds decreased [$F(1.04, 61.42) = 121.63, p < .01, \eta^2 = .66$]. There was also an interaction between age and speed [$F(1.04, 61.42) = 7.21, p < .01, \eta^2 = .04$]: At the slowest speed, older adults had significantly higher thresholds than younger adults [$t(62) = 3.04, p < .01$]. Older adults also had higher thresholds than younger adults at 10.1°/s [$t(61) = 4.54, p < .01$]. There was no difference in thresholds between the younger and older adults at the fastest speed, however [$t(60) = -1.58, p = .12$].

Motion thresholds (or d_{min}) were found for each observer using the last six reversals in each of the two blocks and then averaging across the blocks. Older adults' motion thresholds were more than six times higher than those of younger adults [$t(59) = 8.72, p < .01$], as can be seen in Fig. 4. In a simple ideal-observer analysis, it is possible to use these older observers' motion threshold values ($M = 144.70$ arcsec, $SE = 13.41$), found during a one-step/200-ms stimulus duration, to extrapolate the minimum $d\theta$ that older adults would need during a seven-step/800-ms stimulus duration, as in the depth

threshold task. (This extrapolation method is reasonable, given that previous research has shown that when the stimulus duration between displacements is 100 ms or more, adding steps [i.e., more displacements] does not affect motion processing [Snowden & Braddick, 1989, 1990].) The older adults' extrapolated $d\theta$ value was 0.35°/s, which represents the “best” $d\theta$ we might expect older observers to achieve during the depth threshold task, in order to reliably report depth sign. We can also estimate the magnitude of the pursuit signal ($d\alpha$) generated by each observer in response to the stimulus translation in the depth task. The actual $d\alpha$ was estimated for each observer by multiplying the obtained gains in each pursuit task condition (i.e., the gains for 2.1°, 10.6°, and 25.5°/s) by the stimulus speed in each depth task condition, for

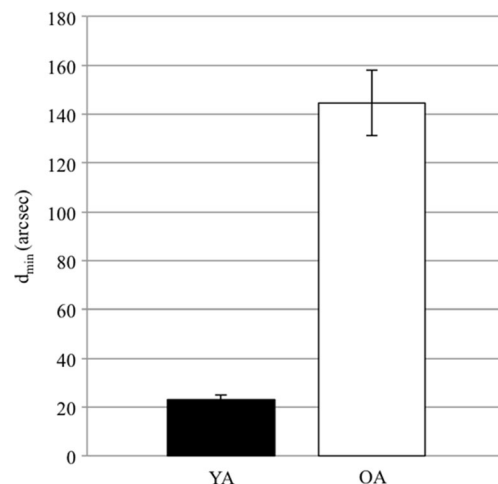


Fig. 4 Motion thresholds (d_{min}) for younger and older observers. Thresholds are plotted as magnitudes of displacement, in arcseconds. YA = younger adults, OA = older adults

each observer. This extrapolated $d\theta$ value and the actual $d\alpha$ can be used to generate an ideal-observer model for older adults—that is, the results we would expect if observers were using all of the information available in the motion and pursuit signals, and combining these two signals optimally. The ideal M/PRs are plotted as the dashed line in Fig. 3.

For the eyetracking analysis, eye velocity was derived from eye position using a two-point central difference algorithm. The data were then low-pass filtered at 40 Hz using a three-term moving average filter. Saccades were identified as velocities greater than $40^\circ/s$ (Burke & Barnes, 2006), and those sections were removed from further analysis. The first 223 ms and the last 306 ms were also discarded, to exclude open-loop pursuit and pursuit after the target had disappeared from the screen. The gains were then analyzed by averaging velocity over the remaining data points (647 ms) and computing the average eye velocity/target velocity.

Figure 5 shows the relationships between the two components of depth from MP ($d\theta$ and $d\alpha$) and depth thresholds, for older adults. The left panel shows each older adult's M/PR, plotted as a function of their motion threshold. Each observer generated three data points: one M/PR per pursuit speed condition in the depth condition (see legend). Because motion threshold (d_{min}) was measured once for each observer, their three data points are stacked vertically. Overall, as pursuit speed increased, depth thresholds decreased, and at the lowest speed (black squares) there seems to be much more variability in M/PRs than at the moderate (white circles) and high (black diamonds) speeds. The right panel shows older adults' M/PRs plotted as a function of pursuit gains (recall that gains were measured for three different pursuit speeds). Again, each observer generated three data points. As in the left panel, the right panel makes apparent that as pursuit speed in the depth task increased, depth thresholds decreased, and there is more variability in depth thresholds in the slowest pursuit speed condition. Relationships between pursuit gains, motion

thresholds, and M/PRs will be explored in the subsequent analyses.

A $2 \times 2 \times 3$ mixed factorial ANOVA, with Age Group (young and old) as a between-subjects factor, Pursuit Direction (left and right) as a within-subjects factor, and Pursuit Speed (2.1° , 10.6° , and $25.5^\circ/s$) as a within-subjects factor, revealed a significant interaction between pursuit speed and age [$F(1.31, 83.13) = 24.45, p < .01, \eta^2 = .09$] in the pursuit task. At a pursuit speed of $2.1^\circ/s$, older adults had higher gains than younger adults; at 10.6° and $25.5^\circ/s$, older adults had lower gains than younger adults (Fig. 6). We observed no effect of pursuit direction, and pursuit direction did not interact with any other variables (all $F_s < 1$).

Although the ideal-observer model (Fig. 3) predicts observers' results if they are combining the two independent sources of information (motion and pursuit) optimally, as described by the M/PR, a regression analysis provides another way to assess how changes in motion, pursuit, and the mechanism that combines them are affected by normal aging. To investigate the effects of age on $d\theta$ and $d\alpha$ on thresholds, difference scores for each older observer were generated for each of the three tasks. Difference scores were calculated by subtracting the mean of the younger adults' scores from each individual older adult's score. For example, in the depth task, for each older adult, the younger adults' mean M/PR in the $2.3^\circ/s$ condition was subtracted from that older adult's M/PR, giving a difference score for each older adult in that condition. The process was repeated for each of the other two conditions in the depth task (10.1° and $25^\circ/s$), for the actual $d\alpha$ s estimated for each observer (as detailed above), and for the motion task. The absolute values of the difference scores were found, and these values underwent a natural log transformation, generating $\log\Delta_{mpr}$, $\log\Delta_{d\theta}$, and $\log\Delta_{d\alpha}$ scores for each older observer (the relationship of $d\theta$, $d\alpha$, and depth thresholds is not linear in the M/PR model; transforming these difference scores enabled us to treat this relationship as linear and

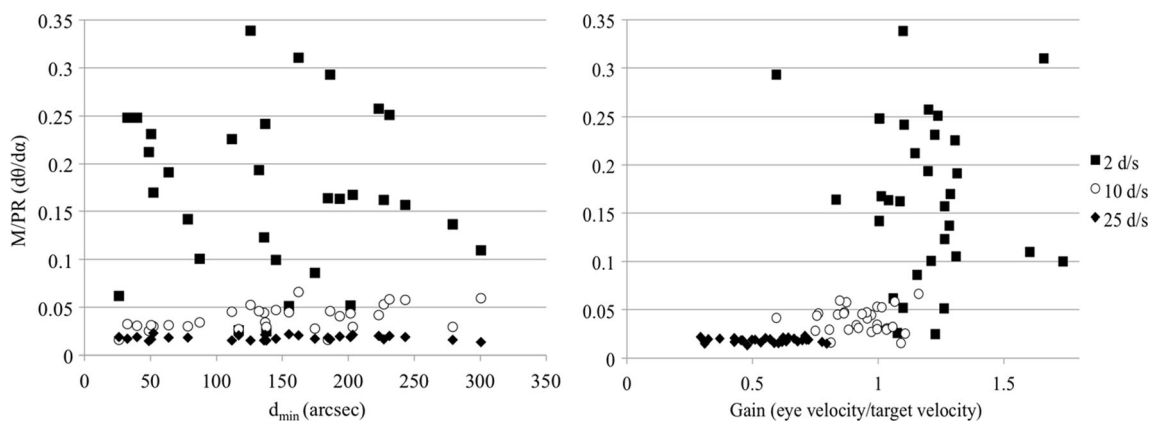


Fig. 5 Relationship of two MP components and depth thresholds, for older adults. In both panels, M/PRs are plotted on the y-axis. The left panel plots M/PRs as a function of motion thresholds (d_{min}), and in the

right panel, M/PRs are plotted as a function of gain. The legend on the right gives the symbols for each of the three pursuit speed conditions in the depth task

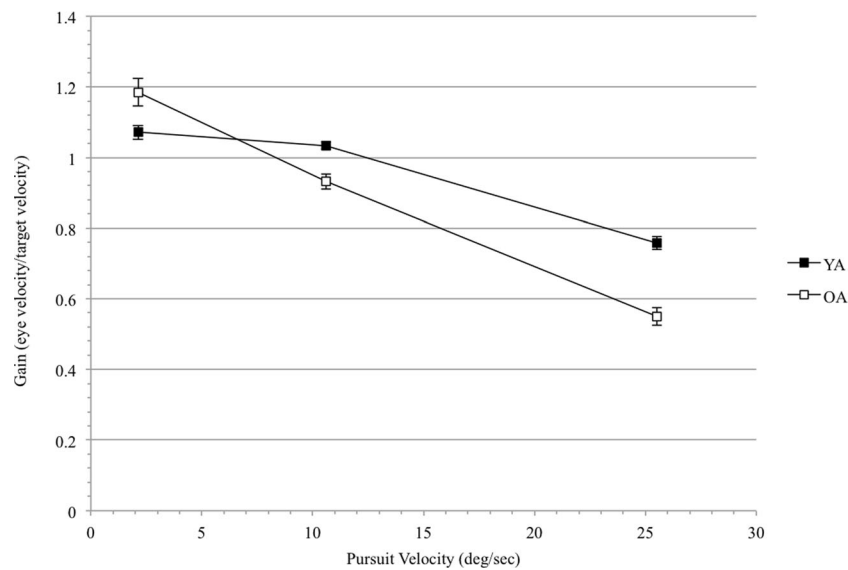


Fig. 6 Pursuit gains for younger and older observers. Gains (eye velocity/target velocity) are plotted against the target speed (2.1°, 10.6°, and 25.5°/s) on the *x*-axis. Black squares represent younger adults (YA),

and white squares represent older adults (OA). Note that a gain of 1.0 represents perfect performance (i.e., eye velocity = target velocity)

perform a regression analysis; Nawrot et al., 2014). A regression analysis was used to assess how well age-related differences in motion perception ($\log\Delta_{d\theta}$) and pursuit ($\log\Delta_{d\alpha}$) accounted for changes in depth perception from MP ($\log\Delta_{mpr}$). The full model was significant ($R^2 = .22$), $F(2, 86) = 11.52$, $p < .01$:

$$\log\Delta_{mpr} = -3.87 + \log\Delta_{d\theta}(0.10) + \log\Delta_{d\alpha}(-0.23). \quad (2)$$

Change in pursuit ($\log\Delta_{d\alpha}$) was a significant independent predictor of change in depth perception ($\log\Delta_{mpr}$) ($p < .01$), but change in motion perception ($\log\Delta_{d\theta}$) was not ($p > .05$). A comparison of the age-related differences in pursuit (Fig. 6) and depth thresholds (Fig. 3) illustrate that both varied together with pursuit speed ($r = -.45$, $p < .01$), thereby resulting in the predictive power of $\log\Delta_{d\alpha}$. In contrast, although we found a large effect of age on motion perception (Fig. 4), there was no correlation of $\log\Delta_{d\theta}$ with $\log\Delta_{mpr}$ ($r = .006$), meaning that some older adults who had larger changes in motion thresholds had smaller changes in depth thresholds, and vice versa. This finding is not unprecedented—Andersen and Atchley (1995) similarly found that older adults' performance on a two-dimensional motion task was not related to their performance on a three-dimensional motion task.

Discussion

Older adults had higher depth thresholds than younger adults in the slow (2.3°/s) and moderate (10.1°/s) MP pursuit speed conditions. When the stimulus was moving at a fast speed

(25.0°/s), older and younger adults had similar depth thresholds. Age had an effect on pursuit and motion processing, as expected. At the three speeds tested in the pursuit task (2.1°, 10.6°, and 25.5°/s), older adults had less accurate pursuit than younger adults. Older adults also had higher motion thresholds than younger adults.

It is interesting to note that, despite age differences in $d\theta$ and $d\alpha$, older observers' obtained thresholds were very similar to the depth thresholds generated by the ideal-observer model (see the dashed line in Fig. 3). Indeed, although their motion thresholds were higher than younger adults', and their pursuit eye movements were considerably less accurate, older adults were apparently using the available motion and pursuit signals in an optimal way. The threshold $d\theta$ s obtained in the slow and moderate pursuit speed conditions of the depth task (and used along with pursuit speed to find the M/PR) were 0.37° and 0.39°/s, respectively (see Fig. 2). These obtained threshold $d\theta$ s are very similar to the optimal motion threshold, 0.35°/s, which was extrapolated from d_{min} and added as a constraint to the ideal-observer model. Older observers' threshold $d\theta$ s were higher in the fastest depth condition than in the slow and moderate depth conditions (Fig. 2), perhaps because older adults' eye velocities were too slow to be able to accurately track the stimulus when it moved at 25.0°/s. The gain at 25.5°/s was 0.55 for older adults, meaning that older adults' average eye velocity was only 55 % of the target velocity. It is not surprising that older adults could not optimally use motion signals at the fast stimulus velocity; they could not move their eyes quickly enough to “keep up” with the stimulus, making motion processing in this stimulus condition difficult (Stone & Krauzlis, 2003). However, although older observers needed stronger motion signals to accurately recover depth sign at

25.0°/s, they still had relatively low depth thresholds at this speed.

The similarity in depth thresholds between younger and older adults at 25.0°/s was due to the fact that younger adults' depth thresholds did not continue to decrease with increasing stimulus speed, as older observers' did (Fig. 3). That is, at 25.0°/s, younger adults required higher threshold $d\theta$ s to recover depth from MP—at this speed, older and younger adults were performing similarly (Fig. 2). This increase in threshold $d\theta$ in younger adults is not entirely unexpected, however; recent research has shown that younger adults require higher $d\theta$ s for depth perception at fast velocities than at moderate velocities (Holmin & Nawrot, 2015), and that younger observers' depth thresholds are stable at moderate and fast pursuit velocities.

At all velocities tested, older adults had less accurate pursuit eye movements than younger adults (Fig. 5). An inaccurate $d\alpha$ signal will contribute to higher thresholds, as may be seen in the difference between age groups at 2.3° and 10.1°/s. The similarity between younger and older adults' thresholds at 25.0°/s is not due to an improvement in pursuit performance in older adults; rather, as we described in the paragraph above, younger adults' performance at this speed becomes more like that of older adults.

Although age differences in depth from MP have only been investigated in a few studies, the effects of age on the recovery of shape or structure from motion has received more attention. In the first experiment by Norman et al. (2004), discussed above, older and younger adults discriminated the shape depicted in a random-dot stimulus in an MP display. Here the dot lifetimes—that is, the durations for which individual dots in the stimuli survived before being erased and redrawn in a new position—were varied. Older adults required longer dot lifetimes than younger adults to reliably discriminate the surface shape, and this age difference remained even when the dot lifetime was unlimited. The results of the present study and the first experiment in Norman et al. are not directly comparable, as the recoveries of surface depth and shape information are different perceptual processes (see Norman et al., 2004, for a discussion); this difference is illustrated by the fact that Norman and colleagues found, in the same study, an effect of age for MP-defined shapes, but not for MP-defined suprathreshold surface depth. Older adults also have deficits in recovering structure from motion, as compared to younger adults (Atchley & Andersen, 1998; Norman et al., 2008; Norman et al., 2013; Norman et al., 2000; Norman et al., 2012), though, again, recovering structure from motion and depth from MP are different processes. However, when one considers that both processes require the use of motion information to recover form or surface depth information, and that one of these processes (structure from motion) is well-known to be affected by age, the age effects found in the present study are not unexpected.

Recall that Norman and colleagues (2004; Norman et al., 2009) found no effect of age on MP depth magnitude judgments, whereas the present study found an effect of age on MP depth thresholds. The chief difference in methodology among these studies was in the manner in which MP was generated—in Norman et al.'s studies, observers generated lateral head translations, whereas stationary observers generated lateral pursuit eye movements in the present study. To maintain fixation during head translation, both tVOR and pursuit eye movements are generated (Freeman & Fowler, 2000). However, only the pursuit component is necessary—tVOR does not contribute to the perception of depth from MP (Nawrot & Joyce, 2006).¹ In the present study, we eliminated the unnecessary tVOR signal, leaving the pursuit signal, which generates a vivid and robust depth percept. It is important to note, though, that pursuit eye movements were still being generated in Norman et al.'s studies. Given that the necessary pursuit signals were operating under both the head-moving and head-stationary conditions, it is unlikely that the significant age differences in the present study are a result of the method used to produce the MP stimuli. Instead, the differences in the results of Norman and colleagues' and the present study are likely due to differences in our measures of interest: in the present study we determined factors affecting minimum detectable depth (thresholds), whereas Norman and colleagues studied the perceptual magnitude of suprathreshold stimuli. That is, it would be unusual to study perceived depth magnitudes for stimuli that older observers could not even detect. Therefore, our results are not incompatible with those of Norman and colleagues, but rather, extend our understanding of different aspects of age effects on depth from MP.

It is possible to demonstrate the limits of depth from MP in real-world situations on the basis of the results from the present study. Imagine an observer walking at a rate of 5 km/h. This observer is fixating on an object to the right, orthogonal to the direction in which the observer is walking. If this fixated object is 35 m away (less than the length of an average suburban lawn in the United States), the observer's gaze angle ($d\alpha$) changes at a rate of 2.3°/s, the slowest speed in the present study. A younger observer could reliably discriminate between the fixated object and a relatively nearer or farther distractor object given at least

¹ Readers unfamiliar with pursuit's crucial role in the perception of depth from MP are referred to Nawrot and Joyce (2006) and Nadler et al. (2009), who showed that a pursuit eye movement signal, not a head movement signal or a tVOR signal, provides the extraretinal signal to disambiguate depth from MP. That is, perceived depth from MP changes with changes in pursuit direction, even when head movement and tVOR remain constant. Although Rogers and Graham (1979, Fig. 5, p. 132) are widely taken to have shown the superiority of translational head movement, more recently, Nawrot et al. (2014, Fig. 8, p. 10) demonstrated that perceived MP depth magnitude is reduced in head-translating, relative to head-stationary, conditions because the involuntary tVOR signal generated in the head-translating condition reduces the magnitude of pursuit necessary to maintain fixation.

3.8 m of depth between these objects. Under the same conditions, an older observer could reliably discriminate which object was nearer if the objects were at least 5.6 m apart. Now imagine if the observer were driving at a rate of 50 km/h. If the observer were fixating an object 77 m away (almost the length of a city block), $d\alpha = 10.1^\circ/\text{s}$, the middle speed in the present study. In this case, a younger observer could make reliable judgments about the relative depths of a fixated and a distractor object if the objects were at least 1.54 m apart. In contrast, an older observer could make a reliable depth judgment at 3.8 m, or double the amount of depth required by the younger observer.

To put this result into context, consider the following situation: Looking from one end of a city block to the other, an older adult who is fixating a car that is stopped less than 3 m from a road sign would not be able to tell whether this car is stopped in front of or behind the road sign. This inability to discriminate the relative depths of objects affects a driver's planning and maneuvering. Now imagine an older adult driving past a full parking lot, searching for an empty parking space (the average parking space is approximately 3 m wide). In this situation, older adults would not perceive the space between two cars parked on either side of an empty parking space, and would therefore miss the parking space.

In real-world situations such as the ones described above, the successful recovery of relative depth between objects enables us to act on these objects and plan our movements in the world (Foster, Fantoni, Caudek, & Domini, 2011). Aging affects MP depth thresholds, with potentially substantial consequences for the detection of depth differences in the real world. As the population of older adults continues to grow (Ortman et al., 2014), it will be important to better understand these functional deficits and address how the perception of depth from MP in older adults might be improved.

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