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Motion coherence and direction discrimination in healthy aging

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Perceptual functions change with age, particularly motion perception. With regard to healthy aging, previous studies mostly measured motion coherence thresholds for coarse motion direction discrimination along cardinal axes of motion. Here, we investigated age-related changes in the ability to discriminate between small angular differences in motion directions, which allows for a more specific assessment of age-related decline and its underlying mechanisms. We first assessed older (>60 years) and younger (<30 years) participants' ability to discriminate coarse horizontal (left/right) and vertical (up/down) motion at 100% coherence and a stimulus duration of 400 ms. In a second step, we determined participants' motion coherence thresholds for vertical and horizontal coarse motion direction discrimination. In a third step, we used the individually determined motion coherence thresholds and tested fine motion direction discrimination for motion clockwise away from horizontal and vertical motion. Older adults performed as well as younger adults for discriminating motion away from vertical. Surprisingly, performance for discriminating motion away from horizontal was strongly decreased. Further analyses, however, showed a relationship between motion coherence thresholds for horizontal coarse motion direction discrimination and fine motion direction discrimination performance in older adults. In a control experiment, using motion coherence above threshold for all conditions, the difference in performance for horizontal and vertical fine motion direction discrimination for older adults disappeared. These results clearly contradict the notion of an overall age-related decline in motion perception, and, most importantly, highlight the importance of taking into account individual differences when assessing age-related changes in perceptual functions.

Introduction

Healthy aging in the absence of neurodegenerative diseases is accompanied by a variety of perceptual and sensory changes, including those related to vision (Andersen, 2012; Lindenberger & Baltes, 1997; Owsley, 2011). Visual motion perception has been shown to be especially affected, such that, for example, the abilities to discriminate and to detect low-level motion decrease during healthy aging (Allen, Hutchinson, Ledgeway, & Gayle, 2010; Ball & Sekuler, 1986; Bennett, Sekuler, & Sekuler, 2007; Billino, Bremmer, & Gegenfurtner, 2008; Tran, Silverman, Zimmerman, & Feldon, 1998; Trick & Silverman, 1991), and, related to that, also spatial and temporal processing decline (Pilz, Kunchulia, Parkosadze, & Herzog, 2015; Roudaia, Bennett, Sekuler, & Pilz, 2010). In addition, also high-level motion perception changes, such as the discrimination and detection of biological motion (Agnew, Phillips, & Pilz, 2016; Billino et al., 2008; Norman, Payton, Long, & Hawkes, 2004; Pilz, Bennett, & Sekuler, 2010; Spencer, Sekuler, Bennett, Giese, & Pilz, 2016), or 3D shape from motion (Andersen & Atchley, 1995; Norman et al., 2013; Norman, Bartholomew, & Burton, 2008). Also, the perception of illusory motion has been shown to change with age (Billino, Hamburger, & Gegenfurtner, 2009).

The reasons for deficits and changes in motion perception associated with aging are not fully understood. Neurophysiological studies have shown that neurons in early visual areas are less selective, and have higher spontaneous noise and increased excitability (Leventhal, Wang, Pu, Zhou, & Ma, 2003; Liang et al.,

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2010; Schmolesky, Wang, Pu, & Leventhal, 2000; Yu, Wang, Li, Zhou, & Leventhal, 2006). These changes have been observed from orientation selective neurons in V1 and V2 to motion direction sensitive neurons in area MT, and it has been suggested that they could be involved in the decline of motion perception in healthy older adults (Bennett et al., 2007; Betts, Sekuler, & Bennett, 2007).

To assess age-related changes in low-level motion perception, tasks typically involve the coarse discrimination of motion directions along the cardinal axes (Allen et al., 2010; Billino et al., 2008; Gilmore, Wenk, Naylor, & Stuve, 1992a; Snowden & Kavanagh, 2006; Tran et al., 1998; Trick & Silverman, 1991; Wojciechowski, Trick, & Steinman, 1995). Given the neurophysiological results suggesting increased neural noise and decreased selectivity of cells responding to motion directions, it is reasonable to assume that age-related decline is even more pronounced for fine motion direction discrimination than for coarse motion direction discrimination. So far, only one study has assessed fine direction discrimination in aging. Ball and Sekuler (1986) asked observers to discriminate motion up to 8° clockwise or counterclockwise away from a standard direction. Surprisingly, their initial results showed age-differences for 4° and 6° but not for 2° and 8° difference between control and test stimuli.

Here, we investigated age-related changes in fine motion direction discrimination more systematically over a larger range of angular differences between control and test stimulus.

Interestingly, most studies assessing motion direction discrimination used predefined stimulus durations and determined performance as the motion coherence at which participants could perform the task at a certain performance threshold. However, coherence thresholds vary widely between individuals across all ages (Billino et al., 2008; Tran et al., 1998; Trick & Silverman, 1991). In addition, older adults often need longer stimulus durations to perform a task as well as younger adults (Norman et al., 2004; Pilz et al., 2010; Spencer et al., 2016). Therefore, we controlled for individual differences in motion coherence thresholds and the ability to do the task at a certain stimulus duration. We first assessed participants' ability to discriminate horizontal (left/right) and vertical (up/down) motion at a stimulus duration of 400 ms. Second, we determined motion coherence thresholds for each participant for coarse horizontal and vertical motion direction discrimination. The individually determined coherence thresholds for horizontal and vertical motion were then used to assess participants' ability do finely discriminate motion clockwise away from horizontal and vertical.

Experiment 1

Materials and methods

Participants

Seventeen older (62–72 years, $M = 66.2$, $SD = 2.8$, three males) and 27 younger adults (18–29 years, $M = 22.5$, $SD = 3$, seven males) participated in the experiment. All participants were naive as to the purpose of the experiment and had normal or corrected-to-normal vision of 0.8 or above on an Early Treatment Diabetic Retinopathy Study (ETDRS) logarithmic vision chart. All participants had visited an ophthalmologist or an optometrist within the past three years and were free of glaucoma, strabismus, amblyopia, macular degeneration, or cataracts. Older adults were also tested on the Montreal Cognitive Assessment (MoCa; Nasreddine et al., 2005) to assess their cognitive abilities. Three older participants had to be excluded, because two failed the vision test and one did not pass the cognitive screening. All participants were paid £5/hour for their participation. The experiment was approved by the local ethics committee and experiments were conducted in accordance with the Declaration of Helsinki.

Apparatus

Experiments were conducted on an Apple Mac Mini (OS X; Apple, Inc., Cupertino, CA) computer using the PsychToolbox extensions (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) for MATLAB (Mathworks, Natick, MA). Stimuli were presented using a 17-inch Viglen VL950T CRT monitor (Viglen Ltd., St. Albans, Hertfordshire, UK) with a refresh rate of 100 Hz (equivalent to 100 frames per second or fps) and a resolution of 1024 × 786 pixels.

Stimuli

Stimuli were random-dot kinematograms (RDKs) of a circular aperture of 9.4° with 150 dots moving at a speed of 6°/s. All dots had a size of 2 pixels and a limited lifetime of 200 ms (equivalent to 20 fps). The lifetime and position of each dot was randomly allocated at the beginning of each trial. Once the lifetime of a dot elapsed, or the dot moved out of the stimulus region, it was placed at a random position within the aperture, and set to move in the same direction as before. Motion coherence and stimulus duration were individually determined for each participant as described in the following.

Procedure

Participants were seated 60 cm from the screen and their head position was stabilized using a chin rest. The

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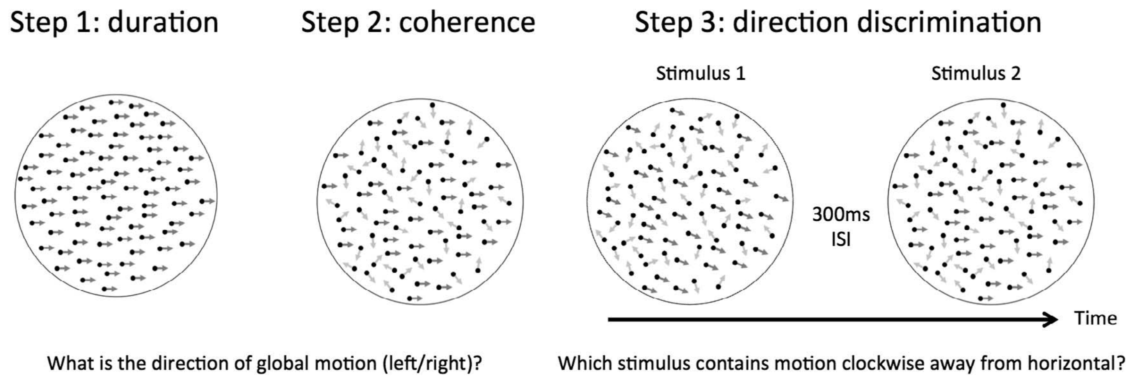

Figure 1. Example of stimuli and trial sequences for all three steps of the experiment for horizontal motion. In step 1, we assessed participants' ability to perform the task at a stimulus duration of 400 ms for 100% motion coherence. In step 2, coherence thresholds were estimated for each participant at a stimulus duration of 400 ms. In both steps, one stimulus appeared on screen, and participants had to determine the global direction of motion. In step 3, two stimuli were shown sequentially on the screen with the individually determined motion coherence. Participants had to indicate which of the two stimuli contained motion clockwise away from target motion (horizontal or vertical).

experiment consisted of two blocks of three steps each (Figure 1), one block for horizontal and one for vertical motion. The order of blocks was counterbalanced across participants. No trial-based feedback was provided in any of the steps. In a first step, we tested whether participants were able to perform the task at a stimulus duration of 400 ms. Participants were asked to discriminate left/right (horizontal), or up/down (vertical) motion, with motion coherence at 100% by pressing "X" for left and "M" for right (horizontal) or "*" for up and "+" for down (vertical) on a standard QWERTY keyboard. Participants performed one block of 20 trials for each of the two motion directions at a stimulus duration of 400 ms. If accuracy was below 85% after a second block of practice trials, the participant was excluded from the analysis. Three older and six younger adults were excluded from further analysis, because they were not able to perform the task.

In a second step, using the same task, we measured motion coherence thresholds for horizontal and vertical motion using the method of constant stimuli for each participant. Forty trials each for seven levels of coherence (10%, 20%, 30%, 40%, 50%, 60%, and 80%) were randomly intermixed. Logistic psychometric functions were fitted to the data for each condition using the psignifit toolbox for MATLAB (Kuss, Jäkel, & Wichmann, 2005; Wichmann & Hill, 2001a, 2001b). Motion coherence thresholds were determined at 82.5% correct performance.

In a third step, using individually determined motion coherences for coarse motion direction discrimination from step 2, participants were asked to perform a fine motion direction discrimination task using a two-alternative forced-choice paradigm. Two RDKs were presented successively. In one RDK, dots moved either horizontally (right, 0°) or vertically (up, 90°), in the other RDK, dots moved diagonally between 1° to 25° degrees clockwise away from horizontal or vertical. Only fine discrimination from upward and rightward but not downward or leftward motion was assessed. RDKs were presented with an interstimulus-interval of 300 ms. In this task, participants had to indicate in which of the two RDKs the dots moved clockwise away from the cardinal axis by pressing "1" if the first interval contained the target motion and "2" if the second interval contained the target motion. Forty trials each for seven levels of angular deviation (1°, 3°, 5°, 8°, 12°, and 25°) were randomly intermixed. Participants performed 10 practice trials with motion coherence at 100% and an angular difference of 45° between control and test stimulus to get familiarized with the procedure of step 3.

Results

Step 1: Stimulus duration

A mixed-design analysis of variance (ANOVA) on duration accuracy with age group (older, younger) as a between-subject factor and motion direction (horizontal, vertical) as a within-subject factor revealed no main effect of motion direction, $F(1, 33) = 0.001$, $p = 0.9$, $\eta^2 = 0$, and no interaction, $F(1, 33) = 1.2$, $p = 0.24$, $\eta^2 = 0.036$, with a mean performance around 95% accuracy in all conditions for both age groups [older adults: horizontal ($M = 0.97$, $SD = 0.06$), vertical ($M = 0.95$, $SD = 0.06$); younger adults: horizontal ($M = 0.96$, $SD = 0.09$), vertical ($M = 0.98$, $SD = 0.04$)].

Step 2: Motion coherence

We assessed individual motion coherences using the method of constant stimuli. A mixed-design ANOVA with age group (older, younger) as a between-subject factor and motion direction (horizontal, vertical) as a

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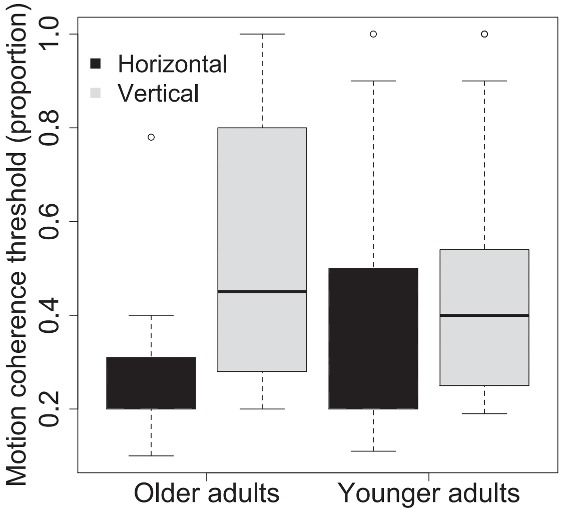

Figure 2. Boxplot of the motion coherence thresholds for older and younger adults for horizontal (left/right) and vertical (up/down) coarse motion direction discrimination. Coherence thresholds were significantly lower for horizontal than vertical motion direction discrimination. There was no main effect of age on motion coherence thresholds and no interaction.

within-subject factor on motion direction thresholds of 82.5% revealed a main effect of motion direction, $F(1, 33) = 11.49$, $p < 0.01$, $\eta^2 = 0.24$, but no main effect of age group, $F(1, 33) = 0.04$, $p = 0.84$, $\eta^2 = 0.001$, and no interaction, $F(1, 33) = 3.33$, $p = 0.077$, $\eta^2 = 0.07$ (Figure 2). Participants generally had lower motion coherence thresholds for discriminating horizontal motion (older: $M = 0.28$, $SD = 0.17$; younger: $M = 0.39$, $SD = 0.27$) compared with vertical motion (older: $M = 0.54$, $SD = 0.29$; younger: $M = 0.46$, $SD = 0.26$).

Step 3: Direction discrimination

Using the individually determined coherence thresholds from step 2 for coarse motion direction discrimination, we assessed participants' ability to finely discriminate motion directions that were clockwise away from vertical or horizontal using a two-alternative forced-choice paradigm. A mixed-design ANOVA with age group (older, younger) as a between-subject factor and motion direction (horizontal, vertical) and angle (1°, 3°, 5°, 8°, 12°, and 25°) as within-subject factors using Greenhouse–Geisser corrected values revealed a significant main effect of angle, $F(5, 165) = 45.018$, $p < 0.001$, $\eta^2 = 0.3$, with performance improving with increasing angular difference between the control and test stimulus, and a main effect of motion direction, $F(1, 33) = 7.34$, $p < 0.001$, $\eta^2 = 0.35$. In addition, there were an age group × motion direction interaction, $F(1, 33) = 5.2$, $p < 0.05$, $\eta^2 = 0.25$, an angle × motion direction interaction, $F(5, 165) = 45.018$, $p < 0.001$, $\eta^2 = 0.01$, and an age group × motion direction × angle interaction, $F(5, 165) = 3.28$, $p < 0.01$, $\eta^2 = 0.02$. Older adults' performance was similar to younger adults for discriminating motion clockwise away from vertical but was strongly deteriorated for motion clockwise away from horizontal (Figure 3).

To assess the age difference for direction discrimination further, we first determined slopes for each motion condition and age group by linearly regressing performance on angle. A mixed-design ANOVA with

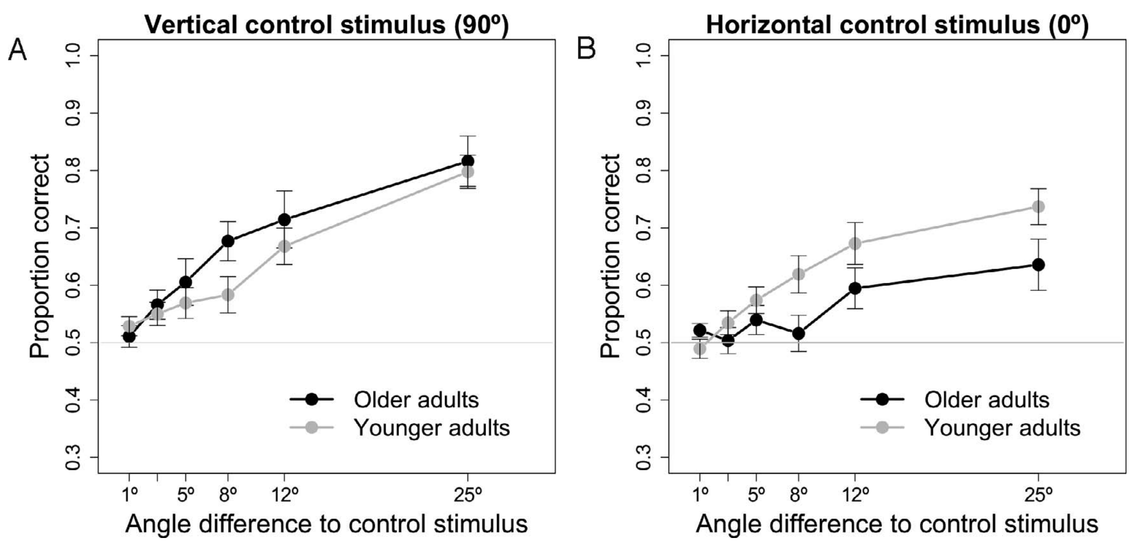

Figure 3. (A) Direction discrimination performance for younger adults (gray) and older adults (black) for vertical control stimuli. (B) Direction discrimination performance for younger adults (gray) and older adults (black) for horizontal control stimuli. Performance increased with increasing difference between control and test stimulus and older adults were significantly worse than younger adults for horizontal control stimuli. There was no age difference for vertical control stimuli. Error bars represent standard error from the mean.

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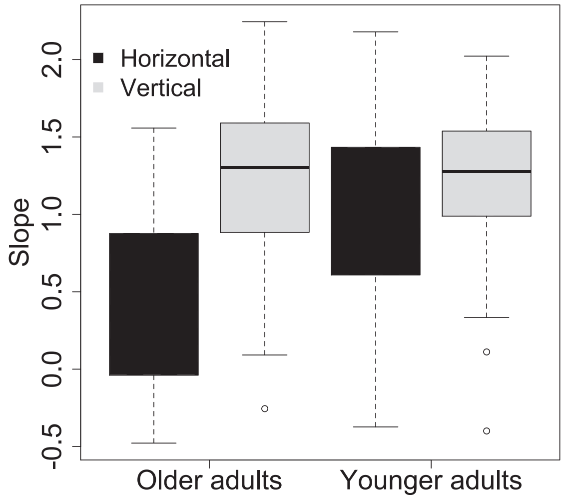

Figure 4. Boxplot of the regression slopes for older adults (left) and younger adults (right) for horizontal and vertical control stimuli for fine motion direction discrimination.

age group as between-subject factor and motion direction and within-subject factor revealed no main effects of age group, $F(1, 33) = 1.1$, $p = 0.3$, $\eta^2 = 0.03$, and no age group × motion direction interaction, $F(1, 33) = 3.5$, $p = 0.07$, $\eta^2 = 0.2$, but a main effect of motion direction, $F(1, 33) = 9.3$, $p < 0.01$, $\eta^2 = 0.2$. Slopes for horizontal (older: $M = 0.55$, $SD = 0.65$; younger: $M = 0.99$, $SD = 0.65$) were smaller than slopes for vertical (older: $M = 1.2$, $SD = 0.7$; younger: $M = 1.12$, $SD = 0.60$; Figure 4).

Second, we performed correlations between motion coherence for coarse motion direction discrimination in step 2 and slopes for fine motion direction discrimination in step 3 to determine the relationship between motion coherence and direction discrimination performance. There was a significant correlation between motion coherence thresholds and slopes for older adults for horizontal motion direction discrimination, $R^2(13) = 0.55$, $p < 0.05$, but no significant correlation between motion coherence and performance for older adults for vertical motion direction discrimination, $R^2(13) = 0.51$, $p < 0.06$. Correlations for younger adults were not significant [horizontal: $R^2(20) = 0.14$, $p < 0.33$; vertical $R^2(20) = 0.26$, $p < 0.26$].

Discussion

We tested fine direction discrimination performance for motion clockwise away from horizontal and vertical using individually determined motion coherence thresholds. Surprisingly, we found large age effects. Younger adults performed similar for both motion directions. Older adults, however, showed tremendous decrements for discriminating motion clockwise away from horizontal but had no deficit for discriminating motion clockwise away from vertical. Studies on motion direction discrimination performance in aging that have assessed motion coherence on an individual level are sparse and previous studies have mostly assessed coarse discrimination abilities based on one motion direction (Allen et al., 2010; Billino et al., 2008; Gilmore, Wenk, Naylor, & Stuve, 1992b; Tran et al., 1998; Trick & Silverman, 1991). To our knowledge, only one study so far assessed age-related changes in fine motion direction discrimination across a variety of different directions. Using a same/different task, Ball and Sekuler (1986) asked participants to detect differences in motion directions between two intervals of moving dots. Motion directions between the two intervals differed by 0°, 2°, 4°, 6°, or 8°. Most surprisingly, they found age-related performance differences only at 4° and 6° but not at 2° or 8°. Ball and Sekuler (1986) tested performance for two cardinal and one oblique direction, and found that performance was generally better for cardinal than oblique directions across both age groups. However, unfortunately, they did not compare performance between horizontal and vertical.

Further analyses of our results showed a relationship between slopes for fine motion direction discrimination and motion coherence thresholds for coarse motion direction discrimination for older adults for horizontal motion, which indicated that performance deficits for fine motion direction discrimination were due to low motion coherence thresholds. Based on these results, it seems reasonable to assume that performance for older adults strongly depends on stimulus coherence and therefore should be similar for horizontal and vertical fine motion direction discrimination with high motion coherence. Therefore, in Experiment 2, we used a predefined motion coherence of a comfortable level of 70% motion coherence for all participants to assess direction discrimination performance without differences in motion coherence. We only tested a control group of older adults, because the difference in performance was only present for this age group.

Experiment 2

Materials and methods

Participants

Five older (61–82 years, $M = 68.6$, $SD = 10.11$, two males) participated in the experiment. The same criteria applied for all participants as described already.

Apparatus and stimuli

The same apparatus and stimuli were used as described already.

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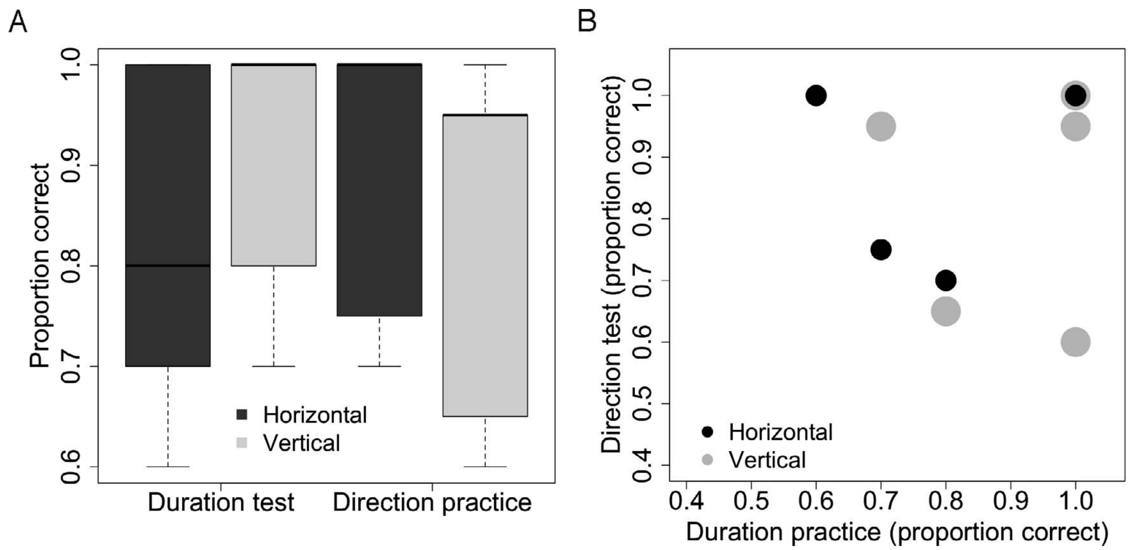

Figure 5. (A) Motion duration pretest (left) and direction practice accuracy (right) for all participants for horizontal and vertical control stimuli. There was no significant difference between conditions. Error bars represent standard error of the mean. (B) Correlogram between duration test and duration practice to highlight the individual differences in performance and the absence of a relationship between tasks and conditions. (Note that three participants performed at ceiling for practice and test, two for horizontal, and one for vertical).

Procedure

All participants performed the same sequence of tasks in two blocks, one for horizontal and one for vertical motion directions. The order of blocks was counterbalanced across participants. Even though we did not assess motion coherence levels individually, we made sure that participants were able to do the motion direction discrimination task at the given stimulus duration and motion coherence for horizontal and vertical motion. Similar to Experiment 1, stimulus duration was set to 400 ms for all tasks and all participants. First, we tested participants' ability to perform the task at a stimulus duration of 400 ms. Participants were asked to discriminate horizontal or vertical translational motion with a motion coherence of 70% by pressing "X" for left and "M" for right (horizontal) or "*" for up and "+" for down (vertical) on a standard QWERTY keyboard. Participants performed one block of 20 trials for each of the two motion directions. One participant was unable to do the task in the first block of vertical trials and one participant was unable to do the task in the first block of horizontal trials. Therefore, both participants received additional training until performance was above 60%.

Second, participants discriminated motion directions using a two-alternative forced-choice paradigm similar to step 3 in Experiment 1. Two RDKs were presented successively. In one RDK, dots moved either horizontally (right, 0°) or vertically (up, 90°), in the other RDK, dots moved diagonally between 1° to 25° clockwise away from horizontal or vertical. RDK were presented with an interstimulus-interval of 300 ms. In this task, participants had to indicate in which of the two RDKs the dots moved clockwise away from the cardinal axis by pressing "1" if the first interval contained the target motion and "2" if the second interval contained the target motion. The angular deviations were slightly changed from Experiment 1 in that each participant now performed 40 trials each for six levels of angular deviation (3°, 6°, 9°, 12°, 24°, and 44°). Those angular deviations were randomly intermixed in two blocks, one for vertically moving control stimuli and one for horizontally moving control stimuli. The order of presentation for the two RDKs was randomized. Before each block, participants performed 20 practice trials for each direction with motion coherence at 70% and an angular difference of 44° between control and test stimulus.

Results

The *t* tests on accuracy for motion duration pre-test and direction practice accuracy did not reveal significant differences between horizontal and vertical control stimuli [motion duration: $t(4) = 0.55$, $p = 0.6$; direction practice: $t(4) = -0.8$, $p = 0.5$, Figure 4]. Figure 4B illustrates the large individual differences between the two motion directions with some participants performing much better for vertical, others performing better for horizontal. Overall, performance in the direction practice also seems to be unrelated to performance in the duration test. It has to be noted that

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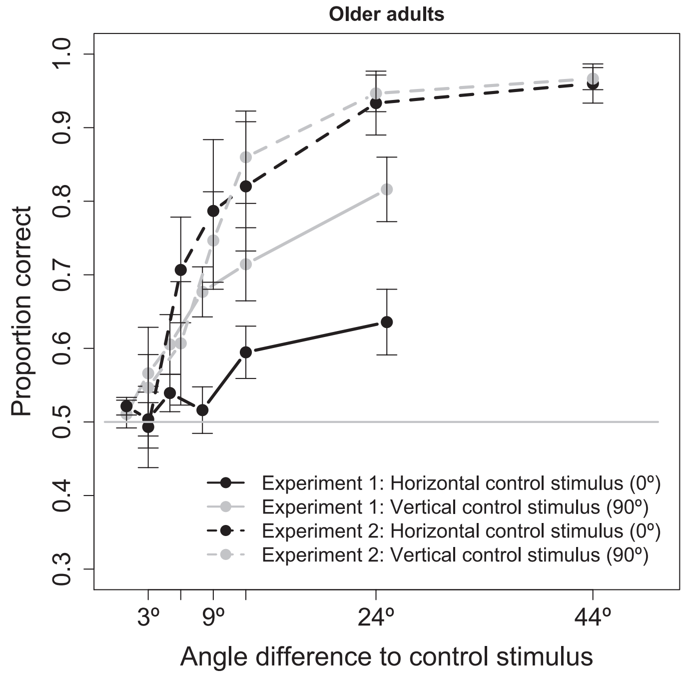

Figure 6. Direction discrimination performance for older adults for horizontal (black) and vertical control stimuli (gray) for Experiment 1 (solid lines), in which individually determined coherence thresholds were used and Experiment 2 (dashed lines), in which motion coherence was set to 70% for all participants.

in Experiment 2, the duration test was performed with a stimulus coherence of 70%, whereas in Experiment 1, stimulus coherence for this task was at 100%. Therefore, performance was overall slightly worse in Experiment 2.

A 2 (motion direction: horizontal, vertical) × 6 (angle: 3°, 6°, 9°, 12°, 24°, and 44°) repeated-measures ANOVA for fine motion direction discrimination revealed a significant main effect of angle, $F(5, 20) = 23.33$, $p < 0.001$, $\eta^2 = 0.7$, with performance improving with increasing angular difference between the control and test stimulus (Figure 6). There was no main effect of motion direction, $F(1, 4) = 0.4$, $p = 0.9$, $\eta^2 = 0.001$, and no interaction, $F(5, 20) = 1.3$, $p = 2.75$, $\eta^2 = 0.02$.

Figure 6 illustrates performance for older adults in Experiment 1 (solid lines) and performance in Experiment 2 (dashed lines). It can be seen that performance in Experiment 1, at which participants performed the task at individually determined motion coherence thresholds is much worse than in Experiment 2, where motion coherence was set to 70%.

Discussion

In Experiment 2, we tested older adults on the same direction discrimination task as in Experiment 1. This time, however, we did not use individually determined motion thresholds but kept coherence at 70% for all participants. Older adults performed equally well for both horizontal and vertical control stimuli.

These results support the results from Experiment 1 showing that decreased performance for fine motion direction discrimination for horizontal motion in Experiment 1 was most likely due to difference in motion coherence thresholds for coarse motion direction discrimination. It is important to note the large individual differences for the duration test and the direction practice and the similarity in performance across all angular differences.

General discussion

In two experiments, we investigated fine motion direction discrimination in healthy aging. In both experiments, we excluded participants who were unable to perform the task at a given stimulus duration. In Experiment 1, we assessed individual motion coherence thresholds for horizontal and vertical coarse motion direction discrimination, and then assessed age-related differences in fine motion direction discrimination away from horizontal and vertical using those individually determined motion coherence thresholds. Interestingly, there was no overall age-difference for coarse motion direction discrimination. Overall, however, participants performed better for horizontal than vertical motion. For fine motion direction discrimination, both age groups performed equally well for discriminating motion away from vertical. However, older adults' performance was significantly worse for horizontal fine motion direction discrimination. Further analysis showed that the decreased performance for horizontal fine motion direction discrimination in older adults was likely related to small motion coherence thresholds for coarse motion direction discrimination. Experiment 2 supported the relationship between low motion coherence and decreased performance for horizontal control stimuli given that using above-threshold stimulus coherence, older adults performed equally well for fine motion direction discrimination for both motion directions.

Our results suggest a close relationship between stimulus duration, motion coherence, and performance in motion direction discrimination tasks, and strongly contradict the notion of a general age-related decline in motion direction discrimination. In addition, they suggest a performance difference between horizontal and vertical motion direction discrimination, which is rather novel and intriguing given that previous studies on motion direction discrimination in younger adults reported differences between cardinal and diagonal axes

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of motion but not between horizontal and vertical motion directions (Andrews & Schluppeck, 2000; Dakin, Mareschal, & Bex, 2005; Gros, Blake, & Hiris, 1998).

The fact that we did not find age differences for discriminating motion directions is rather puzzling given that previous studies usually report robust age-related differences, especially with regards to coarse motion direction discrimination (Allen et al., 2010; Ball & Sekuler, 1986; Billino et al., 2008; Roudaia et al., 2010; Tran et al., 1998; Trick & Silverman, 1991; Wojciechowski et al., 1995). Even though the interaction between age group and motion direction for coarse motion direction discrimination is marginal, the means indicate that the difference between horizontal and vertical is slightly larger in older adults. In fact, older adults' performance for horizontal motion is on average better than performance in any other condition for both age groups, which strongly supports the absence of age-related performance deficits.

To understand the results presented in this study, it is important to compare them with previous studies on age-related differences in motion perception. The most consistent age differences have been found using correlational designs across the age range (Billino et al., 2008; Tran et al., 1998; Trick & Silverman, 1991). Trick and Silverman (1991), for example, estimated coherence thresholds for adults ranging from 25 to 80 years for coarse horizontal direction discrimination and found an increase of coherence thresholds of about 1% per decade. Assessing performance across similar age ranges, Tran et al. (1998) found an increase of 0.4% per decade, and Billino et al. (2008) even reported an increase of 2.7% per decade. The reason for the comparatively large increase in thresholds per decade as reported by Billino et al. might be the short stimulus duration of 400 ms. Tran et al., for example, used a duration of 10 s, and older adults might have benefitted from the additional processing time. However, it is important to note that all three studies report increasing motion coherence thresholds with increasing age.

Despite the rather consistent results for correlational designs, studies comparing the means of two or more age groups often report mixed results. Gilmore et al. (1992), for example, compared performance of older and younger adults for coarse horizontal direction discrimination and found increased coherence thresholds only for older women but not older men. Allen et al. (2010) assessed effects of age on coarse vertical direction discrimination, measuring motion coherence thresholds as a function of contrast and report age differences that were mainly driven by deficits in contrast encoding rather than motion integration. Wojciechowski et al. (1995) asked observers to discriminate cardinal motion directions in five different locations across the visual field (central, inferior, superior, nasal, and temporal) and found increased motion coherence thresholds for older adults in all but the temporal location. Results from Snowden and Kavanagh (2006) who tested coarse direction discrimination for vertical motion suggest that age effects are limited to slow speeds. Other studies that tested motion perception in aging using procedures other than coarse direction discrimination contribute to the variability of age effects for motion direction discrimination. Ball and Sekuler (1986), for example, tested older and younger adults fine motion direction discrimination abilities at cardinal and diagonal motion directions and found age differences at 4° and 6° but not at 2° and 8° difference between a control and test stimulus. Bennett et al. (2007) assessed motion detection and direction identification for translational motion in various directions in five age groups ranging from 23 to 81 years and found age differences only in the oldest age group ranging from 70 to 81 years. Performance across all other age groups was comparable.

Based on the aforementioned studies, it seems reasonable to assume that age differences in motion direction discrimination vary largely depending on stimulus parameters such as speed, duration, contrast, age and sex of the participants, and the task. However, overall absence of an age difference in our study is still surprising given that many parameters were similar to previous studies. The task for coarse motion direction discrimination has been used many times before (Allen et al., 2010; Billino et al., 2008; Tran et al., 1998; Trick & Silverman, 1991), and age range and sample size were comparable to previous studies (Allen et al., 2010; Ball & Sekuler, 1986; Snowden & Kavanagh, 2006; Wojciechowski et al., 1995). Most of our participants were female, which, based on previous studies, should have emphasized rather than diminished age effects (Gilmore et al., 1992b; Snowden & Kavanagh, 2006). In addition, the stimulus duration was similar to those used in previous studies (Allen et al., 2010; Bennett et al., 2007; Billino et al., 2008). However, it is important to note that we excluded participants who were not able to discriminate motion at high coherence at the given stimulus duration. From other areas such as, for example, biological motion perception, it is well known that stimulus duration affects performance of older adults (Norman et al., 2004; Pilz et al., 2010; Spencer et al., 2016). Effect of stimulus duration on motion direction discrimination might have previously been underestimated, and excluding participants who had difficulties discriminating motion directions at high motion coherence at the defined stimulus duration might have had an effect on the results in this study.

The absence of an overall age difference in our study highlights the importance of taking into account individual differences when investigating perceptual changes in healthy aging, a topic that is becoming

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more and more apparent within the aging literature (Billino et al., 2009; Norman et al., 2013; Pilz et al., 2015; Shaqiri et al., 2015). The results and implications from our study are not only of importance to aging but might also be able to guide research in other areas. Changes in motion perception have been observed in a variety of disorders such as dyslexia (Boets, Vandermosten, Cornelissen, Wouters, & Ghesquière, 2011; Eden et al., 1996; Gori, Seitz, Ronconi, Franceschini, & Facoetti, 2015; Gori, Mascheretti et al., 2015; Kassaliete, Lacis, Fomins, & Krumina, 2015), autism (Koldewyn, Whitney, & Rivera, 2010, 2011; Robertson et al., 2014; Ronconi et al., 2012), and schizophrenia (Chen, Nakayama, Levy, Matthysse, & Holzman, 2003; Spencer, Sekuler, Bennett, & Christensen, 2013). It is generally assumed that deficits in global motion perception in these disorders are related to a dysfunction of areas in the dorsal pathway, especially area MT/V5. However, the exact mechanisms are not very well understood. Considering individual differences when assessing motion perception in the aforementioned populations might help to better understand the mechanisms underlying performance deficits.

In addition to the absence of an age effect, our results suggest performance benefits for horizontal compared with vertical motion direction discrimination. Anisotropies between horizontal and vertical have previously been reported for motion detection (Raymond, 1994; van De Grind, Koenderink, Van Doorn, Milders, & Voerman, 1993) but not motion direction discrimination (Dakin et al., 2005; Gros et al., 1998). Our data suggest that the performance difference between vertical and horizontal is predominantly driven by the group of older adults (Figure 2). However, it is possible that differences in motion coherence thresholds for motion direction discrimination between the two cardinal directions have not been reported, because the effect is difficult to detect within high-performing groups of younger adults. A difference between horizontal and vertical is not that surprising when looking at other areas in vision research that have long reported anisotropies between cardinal directions. Within the attention literature, for example, performance has been shown to be better along the horizontal than the vertical meridian (Carrasco, Talgar, & Cameron, 2001; Mackeben, 1999; Pilz, Roggeveen, Creighton, Bennett, & Sekuler, 2012). In addition, eye movements have been shown to differ for horizontal and vertical motion. Smooth pursuit, for example, has been shown to be more accurate and stable following horizontal than vertical motion (Ke, Lam, Pai, & Spering, 2013; Rottach et al., 1996), and studies on optokinetic nystagmus (OKN) have shown that gain decreases much faster as a function of stimulus velocity for vertical than horizontal motion (Takahashi, Sakurai, & Kanzaki, 1978; van den Berg & Collewijn, 1988). Interestingly, smooth pursuit, OKN, and motion perception share anatomical substrates such as the middle-temporal (MT) and medial-superior temporal area (MST; Lisberger, 2010). It is unlikely that differences in eye movements are directly responsible for our results given that various studies suggest dissociations between eye movements and motion perception (for a review, see Spering & Carrasco, 2015). However, it is reasonable to assume that the aforementioned preferences for information along the horizontal axis over information along the vertical axis share common mechanisms. From an evolutionary perspective, for example, it is reasonable to assume that horizontal information is more relevant given that important information such as approaching cars, people, or animals are more likely to enter our field of view from left or right rather than from above or below. The increased relevance of horizontal information is supported by studies reporting a horizontal bias for contours found in natural scenes (Hansen & Essock, 2004), and neurophysiological studies have shown that more neurons are tuned to horizontal than vertical orientations (Li, Peterson, & Freeman, 2003).

In conclusion, we found overall large differences in coarse motion direction discrimination—participants performed much better for horizontal than vertical motion. Older adults performed as well as younger adults. However, regarding fine motion direction discrimination, older adults were much worse at discriminating directions clockwise away from horizontal than vertical control stimuli, a difference that was strongly related to individual performance for coarse motion direction discrimination. Our results clearly contradict the notion of an overall age-related decline in motion perception, and, most importantly, highlight the importance of taking into account individual differences when assessing age-related changes in perceptual functions.

Keywords: motion perception, healthy aging, visual perception, direction discrimination, motion coherence

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