Spatiotemporal properties of apparent motion perception and aging

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We used a random-dot two-frame apparent motion paradigm to investigate whether age-related declines in motion perception are caused by deficits in integrating spatial information, temporal information, or both. Two random-dot patterns were presented sequentially on a black screen, separated by a blank inter-stimulus interval ranging from 0.01 s to 0.240 s. From the first to the second pattern, all the dots were shifted to the left or right by an equal displacement ranging from 0.03 deg to 1.64 deg. The spatiotemporal range yielding good direction discrimination performance was greatly reduced with age. For ISIs longer than 0.04 s, older subjects performed less accurately than younger subjects across a wide range of spatial displacements. Older subjects also showed poorer performance for large spatial displacements across a wide range of ISIs. Age-related differences in performance were also found with small displacements; however, these were largely accounted for by age-related declines in visual acuity. Overall, the results show that the maximum temporal interval and maximum spatial displacement over which two frames can be integrated are reduced in older age.

Keywords: motion—2D, apparent motion, aging, spatial integration, temporal integration


Introduction

Motion perception is important for maintaining balance, navigating through the environment, and interacting with familiar objects and people. Interestingly, many aspects of motion perception decline with healthy aging. For example, minimum motion thresholds and motion coherence thresholds increase with age (Gilmore, Wenk, Naylor, & Stuve, 1992; Snowden & Kavanagh, 2006; Trick & Silverman, 1991), speed discrimination is impaired (Norman, Ross, Hawkes, & Long, 2003), and the detection and discrimination of motion direction from random-dot kinematograms declines with age (Ball & Sekuler, 1986; Bennett, Sekuler, & Sekuler, 2007). Older adults also exhibit deficits in more complex aspects of motion perception, such as extracting information from optic flow (Andersen & Atchley, 1995, 1997; Atchley & Andersen, 1998; Warren, Blackwell, & Morris, 1989), detecting the shape of 3D objects from motion (Norman, Bartholomew, & Burton, 2008), and the detection and discrimination of biological movements (Billino, Bremmer, & Gegenfurtner, 2008; Norman, Payton, Long, & Hawkes, 2004; Pilz, Bennett, & Sekuler, 2010). These changes in motion perception may have significant effects on older adults’ performance in everyday activities, such as driving or crossing a street (Andersen, Cisneros, Saidpour, & Atchley, 2000; Conlon & Herkes, 2008; DeLucia & Mather, 2006; Lobjois & Cavallo, 2007).

Despite the well-documented effects of aging on motion perception, it still remains unclear why motion perception declines with aging. Although aging is accompanied by changes in optical factors (e.g., Sloane, Owsley, & Alvarex, 1988; Weale, 1961, 1986, 1988; Winn, Whitaker, Elliott, & Phillips, 1994), these have been shown to be insufficient to account for age-related declines in motion perception (Ball & Sekuler, 1986; Betts, Sekuler, & Bennett, 2009; Norman et al., 2003). Therefore, changes at the neuronal level are likely to be the cause of these effects. Anatomical studies of the retinogeniculostriate
pathway in primates found that the number, volume, and density of neurons do not change significantly with normal aging (Ahmad & Spear, 1993; Kim, Pier, & Spear, 1997; Peters, Nigro, & McNally, 1997; Spear, 1993). However, neurophysiological studies in senescent monkeys and cats have revealed significant declines in neuronal function. For example, senescent neurons in the striate cortex exhibit higher excitability, reduced orientation and direction selectivity, increased levels of neuronal noise, and reduced signal-to-noise ratios (Hua et al., 2006; Schmolesky, Wang, Pu, & Leventhal, 2000; Zhang et al., 2008). Extrastriate neurons in the middle temporal area (MT), which are especially important for motion perception (e.g., Maunsell & Van Essen, 1983; Tootell et al., 1995), show not only increased noise and reduced direction selectivity (Liang et al., 2008; Yang et al., 2008) but also have lower preferred speeds and broader speed tuning functions (Yang, Zhang et al., 2009). These functional changes may in part be mediated by decreased levels of intracortical inhibition (Hua, Kao, Sun, Li, & Zhou, 2008; Leventhal, Wang, Pu, Zhou, & Ma, 2003). Given the importance of V1 and MT neurons in human motion perception (Clifford & Ibbotson, 2002), alterations in neuronal function in aging humans may be similar to the changes observed in aging monkeys as described above.

Several studies have used random-dot kinematograms in a two-frame apparent motion paradigm to investigate the spatiotemporal constraints on motion mechanisms that correlate information across space and time (e.g., Baker & Braddick, 1985b; Braddick, 1974; Lappin & Bell, 1976). The stimuli used in these studies were two random-dot patterns presented sequentially, with the second pattern consisting of dots that were displaced uniformly from their positions in the first pattern. In many cases, the two patterns also were separated by a blank inter-stimulus interval (ISI). The spatiotemporal limits of motion perception were investigated by varying the displacement and ISI. Only within certain ranges of displacements and ISIs, for example, does the two-frame stimulus evoke a perceiving of continuous motion, allowing observers to discriminate the direction of displacement accurately. Braddick (1974) showed that the motion percept is lost when the dot spatial displacement exceeds 20 arcmin, providing the first evidence for the existence of a maximum spatial displacement, or Dmax, over which motion integration occurs. Other studies found that Dmax decreases for ISIs longer than 40 ms, and that motion discrimination in the two-frame paradigm is impossible when the two frames are separated by more than ~100 ms (Baker & Braddick, 1985a, 1985b; Bours, Stuur, & Lankheet, 2007; Lappin & Bell, 1976; Morgan & Ward, 1980). Finally, Dmax depends on stimulus parameters such as eccentricity, area, density, and grain size (Baker & Braddick, 1982, 1985a; Chang & Julesz, 1983a, 1983b; Eagle & Rogers, 1997; Lappin & Bell, 1976; Nakayama & Silverman, 1984). It has been suggested that the perception of motion in the two-frame paradigm is mediated by low-level motion detection mechanisms (e.g., Snowden & Braddick, 1990), a view that is supported by neurophysiological studies showing that spatiotemporal limits for direction selectivity in MT and V1 neurons are similar to the spatial and temporal limits observed in behavioral experiments (Baker & Cynader, 1986; Churchland, Pribe, & Lisberger, 2005; Mikami, Newsome, & Wurtz, 1986; Newsome, Mikami, & Wurtz, 1986).

Here, we employed a two-frame random-dot apparent motion paradigm (e.g., Baker & Braddick, 1985b; Lappin & Bell, 1976) to investigate whether age-related declines in motion perception are caused by a decreased ability to integrate spatial information, temporal information, or both. By varying the distance of spatial displacement and the duration of the blank ISI, we examined the spatial and temporal limits of apparent motion perception in older and younger subjects. We also examined the effect of reduced retinal illuminance and poorer visual acuity on performance in this task, as both factors are known to affect visual function and also vary with age.

### Methods

#### Subjects

Twelve younger (5 males, 7 females, age range: 20–29 years) and twelve older subjects (7 males, 5 females, age range: 62–72 years) took part in this study. Four younger subjects (2 males) also later participated in a control experiment on the effect of retinal illuminance on performance. The younger subjects were McMaster University undergraduates and the older subjects were residents of the Greater Hamilton Area. All subjects gave written consent to participate in the study and were compensated for their time at a rate of $10/h. Subjects’ near and far acuities were measured using the SLOAN Two Sided ETDRS Near Point Test and the 4 Meter 2000 Series Revised ETDRS charts (Precision Vision, LaSalle, Illinois, USA). Contrast sensitivity was estimated using the Pelli–Robson Contrast Sensitivity Test. Subjects wore their best optical correction for each distance when required. All subjects showed normal or corrected-to-normal acuity and contrast sensitivity. Older subjects had lower visual acuity than younger subjects, consistent with age-related declines in acuity, but their average near and far acuities were better than 20/20. A general health questionnaire was completed by all the subjects and none of them reported having any visual problems such as cataracts or glaucoma. The Mini-Mental State Examination was also administered to all the older subjects to screen for cognitive impairment. All the subjects scored above the normal cut-off score of 26/30. Table 1 summarizes these measures.
Apparatus

Each subject was seated in a dark room in front of a 21-inch Apple Studio Display monitor (model M6204) at a viewing distance of 60 cm. A desk lamp provided dim illumination in the room during the experiment. Each subject’s head position was stabilized using a chin rest. The monitor subtended 29.5/23.0 deg of visual angle and had a resolution of 1024/756 pixels with a refresh rate of 100 Hz. Stimuli were generated and presented using a Macintosh G4 computer running OS X, version 10.4.11. The experiment was programmed in Matlab (Version 7.2) using the Psychophysics toolbox (version 3.0.8; Brainard, 1997; Pelli, 1997). A standard QWERTY Macintosh keyboard was used to collect subjects’ responses.

Stimuli

The stimulus consisted of 300 white dots (0.06 x 0.06 deg, or 2 x 2 pixels) randomly positioned inside a black 6.4 deg square region centered on the middle of the screen. Thus, average density was 7.4 dots/deg^2. Dot luminance was 67.4 cd/m^2 and the background luminance was <1 cd/m^2.

On each trial, two dot patterns were presented sequentially in the center of the screen. The second pattern was identical to the first, except all the dots were displaced uniformly either to the right or to the left. Dots that moved out of the square stimulus region were wrapped around and appeared again on the other side of the stimulus region. The amount of displacement and the ISI were varied independently.

The experiment started after a 30-s period of adaptation, during which subjects fixated the black screen. Each trial began with a small white fixation cross in the center of the screen. It remained on for 3 s and then disappeared for 0.25 s before the appearance of the first pattern. Both patterns were presented for a duration of 100 ms separated by an ISI, during which time the entire screen was black. Subjects were instructed to fixate on the fixation point at the beginning of each trial. After the two patterns disappeared, they were asked to press a key labeled “R” located on the right side of the keyboard when they saw the dots move to the right or to press a key labeled “L” on the left side of the keyboard when they saw the dots move to the left. After the subjects’ key response was recorded, the fixation point reappeared, indicating the start of the next trial (see Figure 1).

The accuracy of direction discrimination of the dots was measured for 8 levels of ISI (0.01, 0.02, 0.04, 0.06, 0.08, 0.10, 0.16, or 0.24 s) and 7 levels of spatial displacement (DISP; 0.03, 0.06, 0.16, 0.32, 0.51, 0.64, or 1.28 deg). Each condition had 40 trials (20 trials per direction) resulting in a total of 2240 trials. All trials were randomly intermixed and presented in 4 blocks of 500 trials and a fifth block of 240 trials. All subjects completed the experiment in one session lasting approximately 90 min, including 4 breaks. In each break, cumulative feedback on the subject’s performance was provided.

Results

Figure 2 shows mean response accuracy of younger and older subjects in all conditions, plotted for each level of DISP in Figure 2A and for each level of ISI in Figure 2B. As expected, accuracy varied significantly across conditions in both age groups. Crucially, the effect of age on performance was not constant and also varied with the levels of DISP and ISI.

This observation was verified with statistical analyses, performed using the statistical computing environment R (R Development Core Team, 2008). Response accuracy (i.e., proportion correct) was arcsin-transformed and

Table 1. Mean (standard deviation) age, near and far ETDRS decimal acuities, Pelli–Robson contrast sensitivity, and Mini-Mental State Examination (MMSE).

<table>
<thead>
<tr>
<th>N</th>
<th>Age</th>
<th>Near acuity</th>
<th>Far acuity</th>
<th>Pelli–Robson</th>
<th>MMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>12 (5 males)</td>
<td>23.17 (2.82)</td>
<td>1.35 (0.21)</td>
<td>1.29 (0.23)</td>
<td>1.94 (0.04)</td>
<td></td>
</tr>
<tr>
<td>12 (7 males)</td>
<td>68.08 (4.44)</td>
<td>1.02 (0.16)</td>
<td>1.13 (0.18)</td>
<td>1.91 (0.09)</td>
<td>29.56 (0.45)</td>
</tr>
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Figure 1. Example of a typical trial in the current experiment. All dots were displaced the same distance ranging from 0.03 to 1.28 deg from frame one to frame two. The ISI varied from 0.01 to 0.24 s.
Figure 2. (A) Performances of younger and older subjects as a function of dot displacement are shown for separate levels of inter-stimulus interval. (B) Performances of younger and older subjects as a function of inter-stimulus interval are shown for separate levels of dot displacement.
analyzed with a 2 (Age) × 8 (ISI) × 7 (DISP) mixed-design analysis of variance (ANOVA). The Geisser–Greenhouse correction, ε, was used to adjust degrees of freedom of within-subjects tests to correct for violations of the sphericity assumption. In such cases, the adjusted p-values are reported. The main effects of Age, ISI, and DISP were significant, as were the two-way interactions between ISI × DISP and DISP × Age. The ISI × Age interaction was not significant, but the three-way interaction between ISI × DISP × Age was highly significant. Table 2 lists all the statistical analyses.

To analyze the interactions, we examined the effects of age as a function of ISI and DISP separately. Figure 2A shows the effect of DISP at different levels of ISI. In general, accuracy in the younger group was almost perfect within the normal range for their age group, acuity was, such that in those conditions, an age difference was apparent at all ISIs. For the largest DISP of 1.28 deg, both groups showed near chance performance across all ISIs.

The effects of ISI and DISP are jointly represented in the contour plots of Figure 3. The color scale represents the accuracy at each combination of ISI and displacement, and the contour lines link conditions with equal bands of accuracy. As can be seen in Figure 3A, young subjects’ region of best performance spans small and medium displacements for a large range of ISIs. However, the older subjects’ region of best performance is greatly reduced, notably along the ISI (y-axis) dimension (Figure 3B). The difference between younger and older subjects’ performances is depicted in a difference plot in Figure 3C. The yellow horseshoe shape in the plot highlights the combinations of ISI and spatial displacement that produce the greatest age differences in performance. In summary, older subjects show deficits in three regions: at small displacements (≤0.06 deg) across a wide range of ISIs, at large displacements (0.6–1 deg) across a wide range of ISIs, and at medium ISIs (i.e., 0.06–0.16 s) across a wide range of spatial displacements.

Previous studies of the effect of aging on motion perception reported greater declines in older women compared to older men (e.g., Gilmore et al., 1992; Pilz, Bennett et al., 2010; Raghuram, Lakshminarayanan, Khanna, 2005; Trick & Silverman, 1991). Figure 4 plots performance of males and females separately in a set of conditions where age differences were most prominent. As can be seen from the figure, there was no evidence of sex differences in performance in our task. We verified this observation with a Sex × ISI × DISP repeated-measures ANOVA on response accuracy of older subjects. Neither the main effect of Sex nor any interactions with Sex were significant (in all cases $F \leq 1.5, p > 0.24$), confirming that older men and women showed similar performance across conditions.

### Effect of visual acuity

Aging is accompanied by a decline in visual acuity (Elliott, Yang, & Whitaker, 1995; Pitts, 1982). In the current study, although acuity for older subjects was within the normal range for their age group, acuity was,
on average, lower in older subjects than in younger subjects (Near Acuity: $t(20.4) = 4.31, p < 0.001$; Far Acuity: $t(20.6) = 1.95, p = 0.06$; see Table 1). In this section, we consider whether differences in visual acuity may explain the observed differences in performance between younger and older subjects.

We would expect visual acuity to influence apparent motion discrimination most strongly in conditions in which the spatial displacement separating the two random-dot patterns is small. At larger displacements, other factors like $D_{\text{max}}$ (Braddick, 1974) presumably are responsible for limiting performance, and therefore, acuity should contribute less to age differences in apparent motion. We tested these ideas in the following way. We first evaluated the data collected with small (i.e., 0.03 and 0.06 deg) and large (i.e., 0.51, 0.64, and 1.28 deg) spatial displacements with separate linear models that included main effects of ISI, displacement (DISP), Age, and all of the two-way interactions between each variable. Next, we evaluated both sets of conditions with two new linear models that included visual acuity as a covariate; Acuity $\times$ ISI and Acuity $\times$ DISP interactions were also included. Including acuity as a covariate allowed us to evaluate the effects of age on motion discrimination accuracy after accounting for the effects associated with acuity. If the effects of age were due entirely to the effects of acuity, then significant effects of age found in the first analyses should not be significant in the second analyses. Therefore, we expected that including acuity in our analysis would diminish the effects of age when the spatial displacement was small but not when it was large.

In the case of small displacements (i.e., 0.03 and 0.06 deg), the first analysis revealed a significant main effect of Age ($F(1, 22) = 16.6, p = 0.0005$) as well as a significant Age $\times$ ISI interaction ($F(7, 154) = 2.82, p = 0.008$). When near acuity was added to the model, the analysis revealed a significant effect of acuity ($F(1, 21) = 21.4, p = 0.00014$), but the main effect of Age ($F(1, 21) = 3.09, p = 0.093$) and the Age $\times$ ISI interaction ($F(7, 147) = 0.768, p = 0.61$) were not significant. Similar results were obtained if we used far acuity rather than near acuity, although in this case the main effect of Age (but not the Age $\times$ ISI interaction) was still significant. These analyses show that near and far acuities were indeed related to performance in the motion discrimination task. Moreover, the effects associated with age were no longer significant after statistically adjusting for the effects of near acuity and were reduced but not eliminated entirely after controlling for the effects of far acuity. Hence, a difference in visual acuity probably contributed significantly to the observed age difference in apparent motion in these conditions.

In the case of large displacements (i.e., 0.51, 0.64, and 1.28 deg), the first analysis revealed a significant main effect of Age ($F(1, 22) = 15.96, p = 0.0006$) and a
significant Age × DISP interaction ($F(2, 44) = 11.84, p < 0.0001$). In the second analysis, the main effect of near acuity ($F(1, 21) = 12.46, p = 0.002$) and the acuity × DISP interaction ($F(2, 42) = 10.3, p = 0.0002$) were significant. Importantly, both the main effect of Age ($F(1, 21) = 4.88, p = 0.038$) and the Age × DISP interaction ($F(2, 42) = 4.85, p = 0.013$) were still significant. Similar results were obtained when far acuity was used instead of near acuity. In addition, similar results were obtained when the analyses were restricted to conditions that used spatial displacements of 0.51 and 0.64 deg. These analyses show that visual acuity was associated with performance in the apparent motion task even when the spatial displacement was ≥0.51 deg. However, unlike what was found with small displacements, the effects associated with age remained significant even after controlling for the linear effects of acuity. Thus, in these conditions, it is unlikely that the observed age differences in motion discrimination were due entirely to a difference in visual acuity.

For completeness, we consider the effects of acuity on performance in conditions that used intermediate spatial displacements (i.e., 0.16 and 0.32 deg). In these conditions, age differences in response accuracy were much larger at long ISIs than at short ISIs, suggesting that it is unlikely that age differences in these conditions are due solely to the difference in acuity (Figure 2). The analyses were consistent with this prediction. The first analysis revealed a significant main effect of Age ($F(1, 22) = 12.43, p = 0.002$) and a significant Age × ISI interaction ($F(7, 154) = 4.13, p = 0.0003$). Adding near acuity as a covariate resulted in a significant main effect of acuity ($F(1,21) = 7.18, p = 0.014$), but the main effect of Age ($F(1,21) = 5.01, p = 0.036$) and the Age × ISI interaction ($F(7,147) = 3.05, p = 0.005$) remained significant.

As in the previous cases, very similar results were obtained if far acuity was used as the covariate. In summary, these analyses suggest that accuracy in the apparent motion discrimination task was associated with near and far visual acuities. Moreover, differences in visual acuity accounted for much, if not all, of the age difference in apparent motion discrimination in conditions that used small spatial displacements. However, in conditions that used medium and large spatial displacements, age differences in apparent motion remained even after accounting for differences in visual acuity.

**Retinal illuminance control**

Aging is accompanied by increases in the density of the ocular media and reductions in pupil size (Weale, 1988), which together produce a two- or three-fold reduction in
retinal illuminance between 20 and 60 years of age (Weale, 1963). Retinal illuminance significantly affects acuity (Shlaer, 1937) as well as temporal and spatial summations (Barlow, 1958). Therefore, it is possible that differences in retinal illuminance contributed to the age differences observed in this task. To determine the effect of lower retinal illuminance on performance, we tested a subset of younger subjects at a range of display luminance levels.

Methods

Luminance was varied by placing neutral density filters in front of the display. Placement of one, two, and three neutral density filters reduced the dot luminance to 31.3, 14.9, and 7.0 cd/m², respectively, which corresponded to 47%, 22%, and 10% of the original luminance. Previous studies have shown that these reductions in display luminance reduce retinal illuminance in younger subjects by approximately 0.25, 0.5, and 0.75 log units (Betts, Sekuler, & Bennett, 2007; Winn et al., 1994).

Two subjects completed the experiment with 1 and 2 neutral density filters and two other subjects completed it with 2 and 3 filters. Subjects ran in all the conditions at one luminance level before continuing to the next level and the order of luminance levels was counterbalanced across the subjects. To reduce the amount of time required to complete the experiment, only 5 levels of ISI (0.01, 0.02, 0.04, 0.08, 0.16 s) were presented at all 7 levels of displacement (0.03, 0.06, 0.16, 0.32, 0.51, 0.64, or 1.28 deg), resulting in 35 conditions.

Results

Figure 5 plots the performance of younger subjects as a function of spatial displacement for separate levels of ISI and for different amounts of mean luminance. As can be seen from the figure, varying the luminance of the display did not significantly affect performance. Even with the lowest dot luminance, younger subjects in the control experiment had a higher mean accuracy than older subjects in Experiment 1 in 33 of 35 conditions.

Discussion

Previous studies have found age-related deficits in low-level motion perception (Bennett et al., 2007; Gilmore et al., 1992; Norman et al., 2003; Snowden & Kavanagh, 2006; Tran, Silverman, Zimmerman, & Feldon, 1998; Trick & Silverman, 1991). The current experiments investigated whether these deficits can be attributed to changes in the spatial and/or temporal properties of low-level motion detectors by using two-frame apparent motion displays.
Consistent with previous research, direction discrimination performance was limited by the extent of spatial displacement and the temporal interval between frames (e.g., Baker & Braddick, 1985b; Braddick, 1974; Lappin & Bell, 1976; Morgan & Ward, 1980). For short or medium ISIs, younger subjects showed good performance for small and intermediate displacements, but performance declined rapidly for large displacements (>0.64 deg), consistent with previously reported Dmax values obtained with similar stimuli (Baker & Braddick, 1985b). Interestingly, the range of displacements yielding good performance was reduced in aging. Although older subjects performed as well as younger subjects at intermediate displacements, their performance was impaired at small and large displacements. When the spatial displacement in the two-frame display was smaller than 0.16 deg, older subjects performed worse than younger subjects, but we found that the age difference could be accounted for by differences in visual acuity. For large spatial displacements, older subjects performed worse than younger subjects across a wide range of ISIs, and the age difference could not be attributed to a difference in visual acuity. These results suggest that the maximum spatial displacement (i.e., Dmax) over which the two frames can be integrated is diminished in older subjects.

This experiment also confirmed previous findings of a temporal limit for short-range apparent motion (Baker & Braddick, 1985b; Bex & Baker, 1999; Morgan & Ward, 1980). Younger subjects showed good performance for ISIs below 0.1 s, after which performance dropped for all displacements. This temporal limit was also found to be greatly reduced with aging. Indeed, older subjects performed as well as younger subjects for a range of spatial displacements when ISIs were ≤0.04 s. However, for longer ISIs (0.06–0.16 s), their performance declined significantly for all spatial displacements (see Figure 2A, second row). This suggests that the maximum temporal interval over which the frames can be integrated is also decreased in older subjects.

Several previous studies of motion perception found greater effects of aging in women than in men (e.g., Gilmore et al., 1992; Pilz, Bennett et al., 2010; Raghuram et al., 2005; Trick & Silverman, 1991). However, there was no evidence of sex differences in performance in our task. More research is needed to determine why gender-specific effects of aging are found for some motion perception tasks, but not others (Billino et al., 2008; Snowden & Kavanagh, 2006).

Relation to previous motion studies

Several previous studies have examined the effect of aging on motion perception at different speeds (Norman et al., 2003; Snowden & Kavanagh, 2006). In our task, stimulus speed can be determined by taking the ratio of the spatial displacement to the ISI. Doing so reveals that in our experiment the effect of age did not depend on speed per se, but rather on temporal and spatial parameters separately. In Figure 3C, conditions with equal speeds fall along straight lines with slope equal to one and the y-axis intercept inversely proportional to the speed. Looking along the speed lines, it becomes clear that the decline in older subjects’ performance is not constant at a given speed. For example, for two conditions yielding a slow speed of 0.38 deg/s (0.160 s combined with 0.06 deg and 0.08 s combined with 0.03 deg), older subjects showed a 9% decline in accuracy. For 0.04-s ISI and 0.64-deg distance, and 11% for 0.08-s ISI and 1.28-deg distance. This result is not surprising, since performance in our task and in others involving random-dot motion does not depend on speed per se, but rather on the combination of temporal interval and spatial displacement (e.g., Baker & Braddick, 1985b; Pilly & Seitz, 2009; Seitz, Pilly, & Pack, 2008).

Age differences in sensitivity to spatial and temporal stimulus parameters may explain the differential effects of aging on motion perception at different speeds. For example, Snowden and Kavanagh (2006) found that minimum motion thresholds in random-dot displays in older subjects (0.06 deg) were significantly higher than thresholds in younger subjects (0.04 deg). Although Snowden and Kavanagh used continuous motion stimuli, our results using apparent motion displays are consistent with their findings: at short ISIs, our older subjects performed well (>90%) when the spatial displacement was between 0.06 and 0.3 deg, but they performed poorly (<65% accuracy) for displacements smaller than 0.06 deg. Moreover, Snowden and Kavanagh found that older subjects show higher mean coherence thresholds but only for slow, not fast, speeds. Expressed in terms of displacements in the two-frame paradigm used here, their slow speeds corresponded to 0.045- and 0.09-deg displacements, and their high speeds were 0.18- and 0.36-deg displacements. For similar small displacements in our task (0.03 and 0.06 deg), at the shortest ISI of 0.01 s, our older subjects showed 22% and 9% declines in performance compared to younger subjects. However, they showed no decline at longer displacements of 0.16 and 0.32 deg. Given that performance with apparent motion stimuli with short ISIs approximates performance with continuous motion stimuli (e.g., Lappin & Bell, 1976), we suggest that the differential age effect at slow and high speeds in Snowden and Kavanagh’s study may stem from age differences in the spatial constraints on motion perception.

It is important to note that most previous studies of motion perception and aging used motion stimuli with multiple frame exposures, containing several sequential displacements (e.g., Bennett et al., 2007; Gilmore et al., 1992; Norman et al., 2003; Snowden & Kavanagh, 2006; Tran et al., 1998). The dots in our two-frame motion
stimulus underwent only one displacement, providing the minimal stimulus for motion discrimination. Stimuli containing multiple displacements allow the visual system to integrate motion signals over time. For example, direction discrimination performance in random-dot stimuli has been shown to improve as the number of successive displacements increased from one to four or five (Nakayama & Silverman, 1984; Snowden & Braddick, 1989b). This integration is thought to be mediated by the activation of detectors tuned to increasingly large spatial displacements and temporal intervals, and/or by the facilitative interactions of detectors that are tuned to a common direction of motion (Snowden & Braddick, 1989a, 1989b, 1990).

Our experiment only examined the effect of aging on the ability to discriminate motion from a two-frame stimulus. It would be important to examine the effect of additional exposures on age differences in performance in future studies. It may be the case that older subjects show greater benefit than younger subjects from the addition of multiple exposures, which may result in reductions of age differences in performance. Alternatively, the integration processes may decline or remain unchanged, which would increase or maintain the age differences in performance. Current evidence suggests that the latter may be the case. Snowden and Kavanagh (2006) used a stimulus consisting of 4 frames presented for 90 ms each. The dots in the stimulus underwent three successive displacements in the same direction. As mentioned before, older subjects showed large deficits with short displacements, a result that we also found for a single short displacement. Thus, it appears that the impairment at short displacements remains even when three displacements are presented. Similarly, Bennett et al. (2007) found that the age-related decline in sensitivity to coherent motion did not vary as a function of stimulus duration, indicating that adding more exposures, or displacements, affects older and younger subjects’ performances equally. The results of these studies suggest that adding more stimulus exposures would not alter the age differences found in the current experiment. However, this claim necessarily is speculative because it is based on a comparison of studies that used different stimuli and tasks. It is important, therefore, to examine the effect of additional exposures on age differences in performance in future studies.

Interestingly, Andersen and Ni (2008) recently examined whether aging is associated with declines in spatial and/or temporal integration by measuring the ability of younger and older subjects to extract 2D shape information from kinetic occlusion information in a random-dot pattern. Shape discrimination performance was measured for a set of coherently moving dots with different density and velocity levels. Shape recognition was poorer in older subjects and the pattern of results suggested that spatial, but not temporal, integration was compromised in older subjects. Specifically, Andersen and Ni found that increasing dot velocity, and consequently the frequency of occlusion events, improved performance equally for the two groups. More importantly, decreasing the individual dot lifetime and the number of frame exposures had a similar detrimental effect on older and younger subjects. These two findings suggested that temporal integration abilities are not affected by aging. This finding appears to differ from our results that suggest an age-related decline in the temporal limits for motion perception. However, it is important to note that our experiment and that of Andersen and Ni examined different aspects of temporal integration. Whereas our results speak to the temporal limits on the ability to extract a coherent motion signal from two successive frames, Andersen and Ni’s results pertain to the ability to integrate motion information over an increasing number of frames. Therefore, we believe that our findings do not conflict with the results of Andersen and Ni.

The results from the current paper provide evidence of decreased functioning of low-level motion detectors. This finding may help explain the pattern of age-related declines seen with different motion perception tasks. In tasks where low-level motion information is especially important, older subjects should show greater declines in performance compared with other motion tasks, where higher level information is available and can be used to compensate for any declines in low-level motion perception. For example, Billino et al. (2008) found large age-related declines in a translational motion task, where subjects were required to discriminate the direction of motion of a subset of dots in random-dot kinematograms. However, the same subjects showed only slight decline in a task requiring the discrimination of the walking direction of a point-light walker. This difference may be due to older subjects’ ability to use higher level information available only in the biological motion stimulus to compensate for their decreased low-level motion perception. A recent study of biological motion discrimination and aging (Pilz, Bennett et al., 2010) provides further support for this hypothesis. Pilz et al. found that older subjects were not able to integrate form and motion information as efficiently as younger subjects when discriminating the walking direction of point-light walkers. This was especially true for inverted walkers. The increased impairment with inverted walkers is consistent with an impairment of low-level motion detectors. Indeed, older subjects may use higher level cognitive mechanisms to compensate for losses in low-level motion perception when viewing familiar stimuli such as upright walkers. However, given that higher level information is not available for less familiar stimuli, older subjects’ performance reflects their inefficiency in processing the available low-level motion information. In another recent study, Pilz, Roudaia, Bennett, and Sekuler (2010) showed that older subjects have difficulties detecting coherently moving targets in dynamic random noise, especially with irregular target forms. Here again, a decreased ability of low-level motion detectors to
integrate information efficiently across time and space might be responsible for age-related decreased performance.

**Potential causes for the observed changes in spatiotemporal limits of apparent motion with aging**

The retinal illuminance control experiment demonstrated that decreasing the luminance of the display by almost 90% does not significantly affect performance at any combination of spatial displacement or ISI. Thus, age-related optical changes that cause a reduction in retinal illuminance cannot account for the observed effects of aging.

Age-related differences in certain tasks may be related to a general slowing of the aging cognitive and perceptual systems (Salthouse, 1996). Our results cannot be explained by the general slowing hypothesis. If it were the case that the aging visual system is simply slower, we would expect older subjects to show the same pattern of performance as younger subjects, except shifted along the time axis toward longer time intervals. Thus, the range of spatial displacements yielding good performance should be the same in older and younger subjects, but older subjects might need longer ISIs to integrate the motion signal. Contrary to this prediction, the current study found that aging resulted in changes to both the spatial and temporal aspects of apparent motion. Furthermore, the results were inconsistent with the hypothesis that aging simply causes the visual system to respond to slower speeds (Raghuram et al., 2005).

Most models of motion detection propose that the stimuli are initially spatially and temporally filtered before reaching the motion detection stage where motion is first perceived (e.g., Reichardt, 1961; van Santen & Sperling, 1984). Here, we consider whether age-related changes in the initial spatiotemporal filters may underlie the observed effects of age in our experiment. The optics of the aging eye may cause older adults to experience increased optical blur (Artal, Ferro, Miranda, & Navarro, 1993). Barton, Rizzo, Nawrot, and Simpson (1996) examined the effect of adding +3.5D optical blur on young subjects’ performance in a motion direction discrimination task using random-dot cinematograms. The effect of blur on performance varied as a function of dot spatial displacement. Blur impaired performance at short displacements (<0.25 deg), had no effect at medium (0.25–0.35 deg) displacements, and improved performance at longer displacements. This is consistent with previous studies showing increased Dmax for apparent motion with low-pass filtered noise patterns (Chang & Julesz, 1983b; Cleary & Braddick, 1990a, 1990b). Based on these findings, an increase in spatial blur in older subjects should lead to poorer performance at short displacements and improved performance at longer displacements. The age effects that we observed only partially follow this prediction. Older subjects do show poorer performance at short displacements, an effect that can be accounted for by reduced acuity, but they still perform poorly at larger spatial displacements. Similarly, if older subjects experience more temporal blur, and reduced temporal resolution (Coppinger, 1955; McFarland, Warren, & Karis, 1958; Misiak, 1951), performance at short ISIs would be expected to suffer because it would be difficult to discriminate the two patterns in time. On the other hand, temporal blur should improve performance at longer ISIs. Contrary to this prediction, older subjects performed best at short ISIs, and their performance declined for medium and longer ISIs. The fact that large age-related declines in performance were found at larger displacements and longer ISIs indicates that the effects cannot be explained solely by increased spatial or temporal blur in older subjects.

Thus, our results suggest that age differences in performance are not solely due to changes in the initial stages of spatial and temporal filtering, and instead reflect a deficit at or after the stage where coherent motion is detected. Two ideas have been put forth to account for the way coherent motion is discriminated in the two-frame apparent motion task. According to the first hypothesis, performance in the two-frame apparent motion task depends on the spatiotemporal properties of low-level motion detectors (e.g., Bours et al., 2007; Braddick, 1974; Snowden & Braddick, 1989a, 1989b). Motion direction is detected by cross-correlating the two dot patterns using pairs of detectors that compare two locations separated by a fixed spatial extent. The input from one location is also delayed by a fixed time delay relative to the other location (e.g., Reichardt, 1961; van Santen & Sperling, 1984). Coherent motion is perceived when the two dot patterns fall within a limited time window, and the spatial displacement falls within the spatial extent of the detector. Thus, the failure of motion discrimination at large displacements (above Dmax) is due to intrinsic spatial limits of the bilocal detectors, which vary according to their preferred spatial frequency and their receptive field size (Baker & Cynader, 1986; Cleary & Braddick, 1990a).

In this framework, our results suggest that the spatiotemporal properties of these local motion detectors change significantly with age. Previous studies using apparent motion displays with humans and primates suggested that apparent motion is mediated by directionally selective neurons in V1 and MT (Mikami et al., 1986; Newsome et al., 1986). More specifically, MT neurons seem to mediate the effects observed at high speeds and large ISIs, whereas both V1 and MT may be involved in mediating the effects at slow speeds and short ISIs (Newsome et al., 1986). To our knowledge, no studies have systematically examined the spatial or temporal limits for generating direction selectivity in senescent neurons. Nevertheless, several recent neurophysiological studies of V1 and MT neurons in senescent primates reveal reduced directional selectivity, higher spontaneous activity levels, decreased signal-to-noise ratios, and lower optimal spatial and temporal
frequencies (Liang et al., 2008; Yang, Liang, Li, Wang, & Zhou, 2009; Zhang et al., 2008). Moreover, the optimal preferred speeds and the speed discriminative capacity in senescent MT neurons are much lower than those of younger neurons (Yang, Zhang et al., 2009). Similar alterations in the aging human visual cortex may be responsible for the decreased spatiotemporal range of apparent motion observed in our older subjects. For example, the decline in older subjects’ performance at long ISIs in the current study might result from a decrease in the optimal temporal delay of the bilocal detectors or from a decrease in their signal-to-noise ratios, which would primarily affect performance at delays further from the optimal delay.

Age differences in solving the correspondence problem?

The decline in performance that occurs in the two-frame apparent motion task at long displacements may reflect an informational limit on the mechanisms that solve the correspondence problem, rather than the spatial characteristics of motion detectors per se (Eagle & Rogers, 1996, 1997; Lappin & Bell, 1976; Morgan, 1992). Specifically, performance in the two-frame task is thought to be constrained by the density of elements in the display rather than the receptive field size of hypothetical motion detectors. Consistent with this idea, Eagle and Rogers (1996) reported that Dmax is proportional to the average spacing between elements, a result that is not easily explained if one assumes a spatial limit on motion detectors. Importantly, this matching operation appears to be carried out after initial spatial band-pass filtering of the stimulus (Eagle & Rogers, 1996, 1997; Morgan, 1992; Morgan, Perry, & Fahle, 1997). According to this framework, our results may be explained by a decrease in the informational limit with age. In other words, older subjects may be less efficient at solving the correspondence problem.

The correspondence process in apparent motion is proposed to be very similar to the process involved in stereopsis (Chang & Julesz, 1983a; Glennerster, 1998). Interestingly, a study investigating stereopsis and aging found that older adults require a higher stereoscopic intraocular correlation than younger subjects to correctly perceive a stereoscopic stimulus (Laframboise, De Guise, & Faubert, 2006). In another study, older subjects showed deficits when discriminating shapes in stereograms with large binocular disparities (0.8 deg) but not medium disparities (0.22 deg; Norman, Norman et al., 2008). Our results in the current study echo these findings, as we find age-related deficits in apparent motion at large but not medium spatial displacements. The existence of age-related declines in stereopsis further supports the possibility that the ability to solve the correspondence problem in motion declines with aging. Further, it raises the possibility that age-related declines in stereopsis and low-level motion perception may have a common cause.

In conclusion, we found an age-related reduction in the spatiotemporal range for direction discrimination from apparent motion displays. This reduction cannot be accounted for by aging optics, but instead points to declines in the functioning of low-level motion detectors.

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