Harriet A. AllenSchool of Psychology, University of Birmingham,
Edgbaston, Birmingham, UKClaire V. HutchinsonSchool of Psychology, University of Leicester, Leicester, UKTim LedgewayVisual Neuroscience Group, School of Psychology,
University of Nottingham, University Park, Nottingham, UK



School of Psychology, University of Birmingham, Edgbaston, Birmingham, UK

This study compared the effects of age on the perception of translational, radial, and rotational global motion patterns. Motion coherence thresholds were measured for judging the direction of each motion type as a function of contrast (visibility) and temporal sampling rate in young and elderly participants. Coherence thresholds decreased as dot contrast increased asymptoting at high dot contrasts but were higher in elderly compared to young participants. This equated to global motion impairment in the elderly of a factor of around 2, characterized by a shift of the threshold vs. contrast function along the horizontal axes (dot contrast). The effect of contrast interacted with the temporal sampling rate. Old participants were deleteriously affected by reduced temporal sampling particularly at low contrasts. The findings suggest that age-related changes in global motion perception may be driven principally by deficits in contrast encoding, rather than by deficits in motion integration and suggest a role for increased internal noise in the older visual system.

Keywords: age, motion, contrast sensitivity, optic flow, self-motion, random dot kinematogram

Citation: Allen, H. A., Hutchinson, C. V., Ledgeway, T., & Gayle, P. (2010). The role of contrast sensitivity in global motion processing deficits in the elderly. *Journal of Vision, 10*(10):15, 1–10, http://www.journalofvision.org/content/10/10/15, doi:10.1167/10.10.15.

Introduction

There is considerable evidence that the ability to perform tasks based on motion information declines with age. Older individuals tend to misjudge the speed of moving objects and require faster speeds to accurately discriminate the direction of moving patterns (Scialfa, Kline, & Lyman, 1987; Snowden & Kavanagh, 2006; Wood & Bullmore, 1995). Worryingly, older adults are significantly worse than younger adults at discriminating between moving objects that will collide with them and objects that will miss them, especially when the displays also simulate observer forward motion (Anderson & Enriques, 2006). In addition, Warren, Blackwell, and Morris (1989) have shown that older adults are worse at discriminating their direction of heading than younger adults.

The tasks outlined above rely on the accurate perception of motion patterns termed "optic flow". Regions of the human medial temporal cortex are selectively active for optic flow patterns (Morrone et al., 2000) probably reflecting a human homologue of macaque MST, which contains neurons responsive to these flow patterns (Geesaman & Andersen, 1996; Tanaka & Saito, 1989). Neurons responding to these complex motion patterns combine inputs from lower level motion mechanisms both within and across directions (Gurney & Wright, 1996; Morrone, Burr, & Vaina, 1995; Perrone & Stone, 1998).

A number of studies have used random dot kinematograms (RDKs) to investigate the effects of age on optic flow or global motion processing and have provided good evidence for an age-related performance impairment for translational motion (e.g., Bennett, Sekuler, & Sekuler, 2007; Billino, Bremmer, & Gegenfurtner, 2008; Snowden & Kavanagh, 2006) at least for the very oldest individuals tested (Bennett et al., 2007). When observers are required to integrate multiple local motion signals to encode the global (overall) direction of image motion, older adults required a greater percentage of dots in RDKs to move coherently to be able to discriminate global motion direction (Gilmore, Wenk, Naylor, & Stuve, 1992) and are slower than younger observers to generate the opto-kinetic nystagmus response to these stimuli (Tran, Silverman, Zimmerman, & Feldon, 1998). On the other hand, Mapstone, Dickerson, and Duffy (2008), using high contrast dot stimuli, find little difference between performance for older and younger adults for translational motion.

doi: 10.1167/10.10.15

2

For radial motion (i.e., that from forward self-motion), the findings are less clear with studies finding either no evidence (Atchley & Andersen, 1998), limited evidence (Billino et al., 2008), or clear evidence (Falkenberg & Bex, 2007; Mapstone et al., 2008; O'Brien, Tetewsky, & Avery, 2001) of an age-related impairment. These studies used displays consisting of between 60 (Billino et al., 2008) and 750 (Mapstone et al., 2008) dots simulating movement forward at a range of speeds. Each dot was one or two pixels in diameter and presented as a luminance increment on a darker background. Participants either had to judge whether the focus of expansion was to the right or left of fixation (Billino et al., 2008; Mapstone et al., 2008), whether motion indicated forward or backward selfmovement (O'Brien et al., 2001), or simply detect the pattern (Atchley & Andersen, 1998). By using a motion stimulus that forced participants to use only global motion cues, O'Brien et al. (2001) showed that older adults are particularly impaired (compared to young adults) when only the global motion information is usable. In a complementary study using natural images, Falkenberg and Bex (2007) showed that older adults required a greater increment in stimulus contrast to overcome the addition of visual noise to the stimulus. They suggested that for older adults, lower sensitivity to optic flow patterns was due to reduced neural sampling efficiency and increased internal noise. These studies, finding some evidence for an age-related decline in global motion perception, can be compared to the findings of deficits in more complex tasks that use this motion information. One explanation for these deficits is a decrease in the fidelity of motion information, even when it maintains sufficient quality for simple detection or discrimination tasks.

In a parallel stream of research, it is well established that spatial and temporal contrast sensitivity declines with age, especially at medium and high spatial frequencies and high temporal frequencies (e.g., Elliott, Whitaker, & MacVeigh, 1990; Ross, Clarke, & Brown, 1985; Wright & Drasdo, 1985). This age-related loss is likely to be due to both a decline in neural efficiency and optical factors (Pardhan, 2004). By using supra-threshold stimuli, many of the studies reviewed above were not able to test whether global motion sensitivity, even above absolute visibility threshold, is influenced by a lack of contrast sensitivity rather than by degradation in motion integration mechanisms. Conversely, those that used relatively small dots may have particularly impaired older adults with poor acuity. Intriguingly, those studies that reduced the motion stimulus, either by having fewer visible dots (Billino et al., 2008) or measuring contrast sensitivity in noise (Falkenberg & Bex, 2007) have found situations where performance of older and younger adults can be matched. This suggests that there might be an early stage deficit, prior to global motion processing mechanisms, that could explain the age-related performance decline with global motion. Given the known age-related decline in contrast encoding (sensitivity), this seems a likely explanation.

In addition to declines in contrast sensitivity, temporal sensitivity also declines with age. Temporal acuity, in terms of gap detection is worse in older, than younger, adults (Humes, Busey, Craig, & Kewley-Port, 2009). Blake, Rizzo, and McEvoy (2008) measured older and younger adults' abilities to discriminate shapes defined by temporal structure differences (e.g., flicker rate in figure and ground). Older adults were impaired, compared to younger adults. Similarly, Andersen and Ni (2008) found that older adults were worse than younger adults at discriminating shapes defined solely by dot disappearance and reappearance. Conflicting explanations were offered, citing either slowing of the temporal impulse function with age (Blake et al., 2008) or decreases in spatial integration (Andersen & Ni, 2008).

Thus, an apparent decline in motion processing may not be due to a deficit in motion processing per se. We systematically investigated the contribution of lower level aspects of visual performance such as contrast or temporal sensitivity to motion perception in the elderly. Contrast sensitivity losses have profound implications for low-level spatial tasks but also impact on tasks higher up the visual processing stream, including those that require the accurate perception of motion. Here we test the influence of varying the visibility (contrast, Experiment 1, following the logic of e.g., Edwards, Badcock, & Nishida, 1996) and temporal quality of motion information (Experiment 2) on older and younger adults' abilities to judge translational and radial motions. In addition, we directly measure performance with rotational global motion patterns, which have not yet been studied in this context. To preempt our results, we found that both contrast and temporal quality affect motion discrimination in older adults.

Methods

Observers

Ten younger (mean age = 21 years, SD = 2.8) and ten older (mean age = 73 years, SD = 3.4) observers were tested. Testing was monocular; participants used their preferred eye (typically right eye) and used the same eye throughout. All had normal or corrected-to-normal visual acuity (as measured by their optician) and reported no problems with binocular or color vision or ophthalmological problems. Older participants were recruited from the University of Birmingham, School of Psychology's regular volunteer panel who take part as normal controls in neuropsychological assessments. Older participants were screened for major head injuries and dementia using the mini mental state examination (Folstein, Folstein, & McHugh, 1975). All experimental methods adhered to the tenets of the Declaration of Helsinki and were approved by the University of Birmingham Ethics Committee.

Apparatus and stimuli

Stimuli were generated using a Macintosh G4 and were written in C using OpenGL and the Xcode development environment available from Apple. They were presented on a P255f Professional Series monitor (refresh rate 75 Hz) that was gamma-corrected with the aid of internal look-up tables. Testing took place in a dimly lit room where the monitor was the only light source. Stimuli were either translational, radial, or rotational RDKs (see Figure 1). These were presented in a 12° diameter circular window at the center of the display (viewed at 92 cm). Dots were presented on a homogenous gray background (68 cd/m²). The visibility of the dots (expressed as Michelson

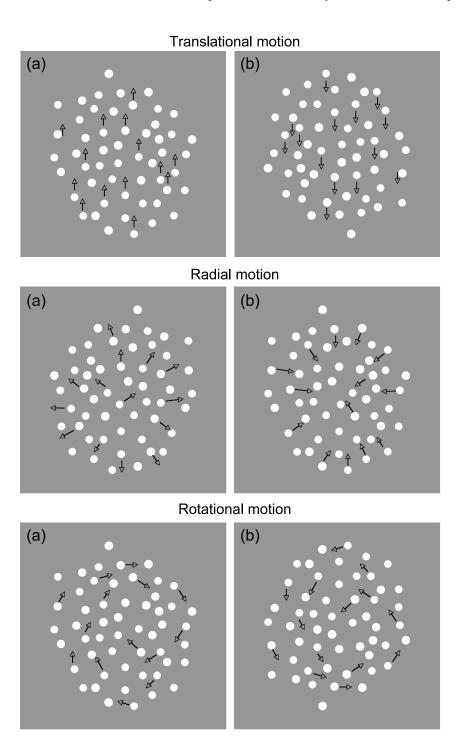


Figure 1. Illustrations of stimuli used in the experiments. Dots are illustrated at maximum contrast and their motion indicated by arrows on a subset of dots (arrows not shown in experiment). On each trial, participants indicated whether they saw the pattern indicated on the left or right.

contrast) could be varied in the range of 0.004–0.33 by increasing the luminance of the dots, with respect to the background, according to Equation 1:

Dot contrast =
$$(L_{dots} - L_{background})/(L_{dots} + L_{background}),$$
(1)

where L_{dots} and $L_{background}$ are the dot and background luminances, respectively. Each RDK was composed of a sequence of 8 images (each 53.3 ms), which produced continuous motion lasting 426.7 ms. Each image contained 50 non-overlapping dots (dot diameter 0.47°; density 0.44 dots/°2). At the beginning of each motion sequence, the position of each dot was randomly assigned. On subsequent frames, each dot was shifted by 0.3°, resulting in a speed of 5.6°/s. When a dot dropped off the edge of the circular display window, it was replotted in a random spatial position within the window.

This combination of dot density, dot diameter, and displacement magnitude was chosen on the basis of previous studies (e.g., Aaen-Stockdale, Ledgeway, & Hess, 2007a, 2007b; Aaen-Stockdale, Thompson, Huang, & Hess, 2009; Edwards & Badcock, 1994, 1995; Simmers, Ledgeway, Hess, & McGraw, 2003; Simmers, Ledgeway, Mansouri, Hutchinson, & Hess, 2006) to ensure that the individual dots were readily visible to the observers and there was a low probability of "false matches" occurring between different dots on successive displacements (Williams & Sekuler, 1984). The global coherence level of the stimulus was manipulated by constraining a fixed proportion of "signal" dots on each image update to move coherently along a trajectory. The remainder ("noise" dots) moved in random directions. In the case of translational motion, signal dot direction could be either upward or downward on each trial with equal probability. For radial motion, on each trial, signal dots were displaced along trajectories consistent with either expansion or contraction. For rotational motion, signal dots rotated either clockwise or anticlockwise. The magnitude of the dot displacement was always constant across space and did not vary with distance from the origin, as it would for strictly rigid global radial or rotational motion. This ensured that all stimuli were identical in terms of the speeds of the local dots (e.g., Burr & Santoro, 2001).

Procedure

Global motion thresholds were measured monocularly using a single-interval, two-alternative, forced-choice, direction discrimination procedure. Performance was measured separately for each of the motion types and the order of testing was randomized. For translational motion, the observers' task was to identify whether the motion was upward or downward. For radial motion, the task was to discriminate between expansion and contraction, and for rotational motion, the task was to discriminate between clockwise and anticlockwise rotations. Participants completed at least four 3-down, 1-up adaptive staircases (Edwards & Badcock, 1995) that varied the proportion of signal dots present on each trial, according to the observers' recent response history. The initial step size of the staircase was 8 signal dots and this was halved after each reversal. The staircase terminated after eight reversals and thresholds (79% correct performance) were taken as the mean of the last six reversals, for which the step size was one signal dot.

Results: Experiment 1

Average global motion coherence thresholds (plotted as the mean number of signal dots required to accurately determine the direction of motion as a function of the dot contrast) are shown in Figure 2. Global motion coherence thresholds initially decreased as dot contrast increased, before asymptoting at moderate dot contrasts. At the lower dot contrasts tested, thresholds were lower for younger, compared to older, observers and differences in performance for the two groups were primarily characterized by a lateral shift of the threshold vs. contrast function along the horizontal axes (corresponding to a simple contrast rescaling). A 2 (age) \times 3 (motion type) \times 6 (shared contrast values) analysis of variance (ANOVA) was performed to compare coherence thresholds across the groups. There was no effect of motion type or interaction between motion type and age. Decreasing contrast increased coherence thresholds (F(5, 30) = 54.55, p <0.0005) and this interacted with motion type (F(10, 60) =4.19, p < 0.0005). Older adults had higher thresholds than younger adults (F(1, 6) = 9.74, p = 0.021). Age interacted with the effect of contrast (F(5,30) = 10.5, p < 0.0005). There was a (non-significant) trend toward a three-way interaction between motion type, age group, and contrast (F(10, 60) = 1.8, p = 0.077). These results illustrate that older adults require more signal dots to discriminate the direction of global motion and suggest that this might be modulated by contrast and motion type. This type of analysis, however, is limited as, of necessity, the two age groups were tested at different contrast ranges.

To better compare between the groups, we fitted a simple curve to the thresholds for each motion type and age group. In terms of quantifying the relationship between coherence thresholds and dot contrast, in all cases, the data were well described by

$$y = \left[\frac{(\text{sgn}(a-x)+1)\left(\frac{x}{a}\right)^c + \text{sgn}(x-a) + 1}{2}\right]b,$$
 (2)

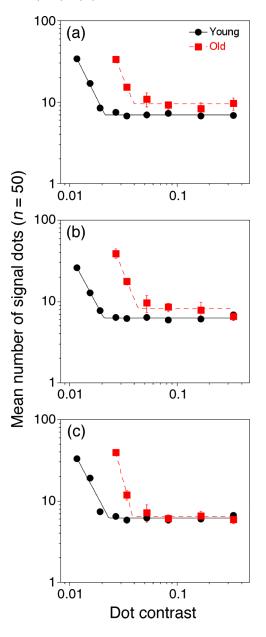


Figure 2. Average global motion coherence thresholds for determining the direction of (a) translational, (b) radial, and (c) rotational motions for older (squares; n = 10) and younger (circles; n = 10) observers. Error bars show ±1 standard error.

where x is the dot contrast and a, b, and c are constants. Parameter *a* is the knee point of the function and is an estimate of the critical dot contrast above which performance is no longer limited by contrast and asymptotes at the coherence threshold b, and c is the slope of the descending limb of the function (on log-log coordinates). Sgn(), or the signum function, is equal to either +1, 0, or -1 depending on whether the argument in parentheses is >0, 0, or <0, respectively. All curve fit values are given in Table 1. The curves were fitted to the data using KaleidaGraph 4.1, which implements a conventional leastsquares fitting procedure. This was done iteratively using the Levenberg-Marquardt algorithm, so the knee-point parameter (a) of Equation 2 was not chosen arbitrarily by eye but was determined automatically (directly) by the fitting procedure.

A 2 (age) \times 3 (motion type) ANOVA was performed for each of the parameters a, b, and c. For parameter a(knee point of the function), the main effect of age was significant (F(1, 18) = 112.98, p = 0.0005), confirming that older participants required about twice the dot contrast level to reach asymptotic performance as younger participants. Neither the main effect of motion type nor the interaction was significant. For parameter b (coherence threshold at asymptote), there was no significant main effect of age, but a significant main effect of motion type (F(2, 36) = 6.55, p = 0.004). Tukey pairwise comparisons revealed that thresholds for translational motion were significantly higher overall than those for the other types of motion (p < 0.01). More importantly, the interaction between age and motion type was significant (F(2, 36) =4.04, p = 0.026). To understand this interaction, separate 1-way ANOVAs were conducted for the older and younger participants. For younger participants, there were no significant effects. For older participants, coherence thresholds were different for the different motion types (F(2, 18) = 9.32, p = 0.002). Thresholds for translational motion were higher than those for radial motion (F(1, 9) =7.8, p = 0.021) and these were higher than for rotational motion in their turn (F(1, 9) = 10.15, p = 0.01; see Table 1). For parameter c neither the main effects nor the interaction reached significance, confirming that the slopes of the

Motion type	Group	a (knee)	b (asymp)	c (slope)	R^2
Translational	Young	0.0214 (0.0004)	7.0051 (0.1986)	-2.6177 (0.0843)	0.9989
	Old	0.0398 (0.0016)	9.457 (0.5214)	-3.1903 (0.3066)	0.9965
Radial	Young	0.0208 (0.0003)	6.2919 (0.1293)	-2.4605 (0.068)	0.9992
	Old	0.0434 (0.0022)	8.1465 (0.629)	-3.2604 (0.3209)	0.9969
Rotational	Young	0.0233 (0.0017)	6.1421 (0.5785)	-2.4528 (0.2077)	0.9913
	Old	0.0387 (0.0007)	6.4483 (0.2893)	-4.9466 (0.2098)	0.9994

Table 1. Mean (and standard deviation) of parameters from Equation 2 fitted to data in Figure 2. Parameter *a* corresponds to the knee point of the function (i.e., dot contrast at which coherence thresholds begin to rise), *b* is the asymptote, and *c* is the slope of the descending limb of the function. Ratios plotted in Figure 3 correspond to the ratios of old to young data of contrast (parameter *a*) and motion (parameter *b*) sensitivity. The last column contains the R^2 values for fitting the curve to the mean data.

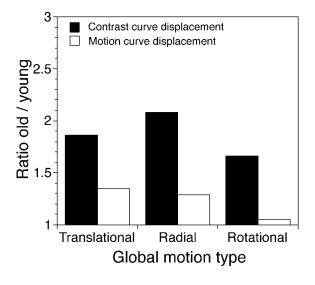


Figure 3. Ratio of old/young performance. Plot shows ratio of contrast and motion best fitting parameters, derived from Equation 2, for each motion type separately.

threshold vs. dot contrast functions were similar for both groups and types of global motion.

The ratios of the best fitting parameters from Equation 2 were used to calculate the extent of the contrast and motion deficits in older observers. Figure 3 shows the ratios (older/younger) of parameters a and b for each type of global motion. This suggests that the age-related deficits found for translational, radial, and rotational global motion patterns were driven primarily by contrast sensitivity impairment, characterized by an average contrast component shift of a factor of around 1.9 compared to an average motion component shift of a factor of around 1.2 (a value of 1 indicates equal values for both groups).

Since, even in healthy aging, the lens of the eye yellows and hardens and the pupil shrinks, it is possible that our findings may have arisen simply because of a reduction in the amount of light reaching the retina (e.g., Weale, 1975). To assess the possibility that our findings were due to degraded visual information being transmitted by an aging lens, motion coherence thresholds for translational motion were measured for four new younger observers with, and without, the addition of a 0.5 neutral density filter. Thresholds did not differ in the two conditions except slightly at the lowest dot visibilities tested (see Supplementary Figure 1).

Results: Experiment 2

Older adults were poor at discriminating the direction of low contrast global motion patterns. Older adults may also have worse temporal integration of information. It is possible that this will interact with contrast to decrease information quality for motion stimuli, perhaps more so for older adults. We investigated this possibility in a second experiment.

Methods

Methods were exactly as in the first experiment except: Two dot contrasts were tested (High: 0.34, Low: 0.05, except for one older adult who was tested at 0.034). The temporal sampling rate of the motion stimuli (rate at which the dot positions were updated) was manipulated, which influences the smoothness of the resulting motion. In the *standard* condition, motion was as in the main experiment except that the dots moved 0.28° every 53.3 ms. In the *smooth* condition, dot positions were updated every frame (13.3 ms) and moved 0.07° each time. Jump sizes were slightly changed from the first experiment to ensure that the resulting speed was identical in each case. There were 6 older (mean age = 73.5 years, SD = 3.02) and 6 younger participants (mean age = 25 years, SD = 2.19).

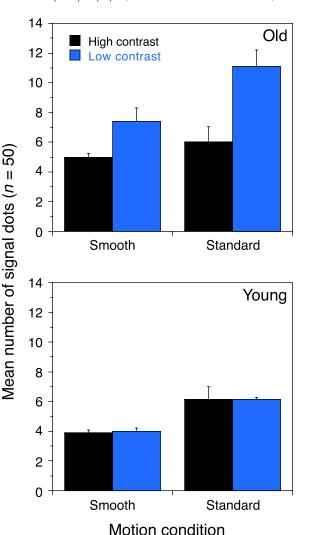
Results

Results, plotted in Figure 4, were analyzed by a 2 (age) \times 2 (motion smoothness) \times 2 (contrast) ANOVA on the coherence thresholds. The effects of motion smoothness and contrast were different for older and younger adults, as evidenced by a three-way interaction (F(1, 10) = 9.3), p = 0.012). There was also an overall main effect of motion smoothness (F(1, 10) = 67.4, p < 0.0005) and an interaction between contrast and motion smoothness (F(1, 10) = 7.5,p = 0.021). For younger participants (analyzed alone), only motion smoothness effected coherence thresholds (F(1, 5) = 21.5, p = 0.006). For older participants, however, the *smooth* condition decreased coherence thresholds (F(1, 5) = 67.6, p < 0.0005) relative to the *standard* condition, but this also interacted with the contrast of the stimulus (F(1, 5) = 15.6, p = 0.01). Thus, for older participants, but not younger, smoother motion ameliorated, to a degree, the effect of low contrast stimuli.

Discussion

We show that translational, radial, and rotational global motion perceptions are impaired in the elderly. The extent to which global motion was impaired was critically dependent on the contrast and temporal structure of the stimuli. Age-related global motion deficits appear to be driven primarily by deficits in low-level encoding, rather than by deficits in motion integration.

Replicating previous results, at high contrasts, we found some evidence of a relatively marginal, motion mechanismbased deficit for the older participants. Atchley and Andersen



Allen, Hutchinson, Ledgeway, & Gayle

Figure 4. Experiment 2. Coherence thresholds for older and younger adults for motion with two different update rates.

(1998) and Billino et al. (2008) found a 5–10% performance decline with age for translational, but not radial, motion (see also Bennett et al., 2007). On the other hand, Mapstone et al. (2008) reported a small age-related decline in performance for radial, but not translational, motion. We extend these findings to lower contrasts. When lower contrast patterns are used, performance is particularly degraded for older compared to younger participants. In addition, we find that this effect interacts with the smoothness of motion.

Before drawing conclusions, it is worth considering whether or not our results were specific to the set of stimulus parameters chosen. In our main experiment, the stimuli moved at 5.6°/s and had a diameter of 12°, which is comfortably within the range of speeds and stimulus sizes used in previous studies. Snowden and Kavanagh (2006) found no difference between older and younger adults' abilities to discriminate the direction of high contrast simple translational motion patterns at this speed but found greater differences between the groups at slower speeds (see also Bidwell, Holzman, & Chen, 2006). It is possible, therefore, that at very slow speeds, greater differences between the older and younger participants' performances might be found. With respect to stimulus size, Mapstone et al. (2008) found no difference in older adults' heading discrimination with stimuli of different sizes (unless a conflicting pattern was presented in the periphery). However, it should be noted that simply increasing the stimulus size, while maintaining dot density, also increases the number of moving dots (local motion samples) presented. Studies presenting fewer dots (e.g., Billino et al., 2008) have found qualitatively different results to those presenting greater numbers of dots (e.g., Mapstone et al., 2008). It is possible that stimulus size, when considered in terms of useable information content, affects older and younger adults differently. Some recent work has suggested, for example, that older adults have reduced surround suppression for moving patterns (Betts, Sekular, & Bennett, 2009; Betts, Taylor, Sekuler, & Bennett, 2005) although this may also be, in part, a function of contrast sensitivity (Aaen-Stockdale et al., 2009).

Decreased inhibition or increased internal noise in older brains may offer a possible explanation for our results. Schmolesky, Wang, Pu, and Leventhal (2000) found decreased orientation and direction selectivity for drifting patterns as well as increased spontaneous activity (leading to lower signal-to-noise ratios) in early visual cortex of older, compared to younger, macaques. These results have been interpreted as being due to changes in acetylcholine regulation (Andersen & Ni, 2008) or reductions in GABA (Leventhal, Wang, Pu, Zhou, & Ma, 2003). Furthermore, application of GABA or GABA agonists has been shown to increase signal-to-noise ratios in macaque visual cortex (Leventhal et al., 2003). Behaviorally, these reductions in inhibitory processes have been linked to decreased direction selectivity and increased internal noise for motion mechanisms (Bennett et al., 2007). In the context of our study, if early, low-level, motion-sensitive mechanisms had increased internal noise, then this is likely to feed forward into later global motion processing mechanisms. This would reduce the fidelity of the input to these midlevel mechanisms, leading to worse performance (see also Edwards et al., 1996 for a related logic in young adults).

The results of our second experiment can also be explained in this context. Reducing the sampling rate effectively increases external temporal noise. This decreases performance for both older and younger adults with high contrast stimuli, as might be expected. For older adults, it is only when the motion signal is low contrast that this noise severely impairs performance (compared to smooth motion). At low contrasts, for older adults, the visual motion signal is attenuated, which increases the effect of the temporal noise. For younger adults, the signal is sufficient to overcome this noise at both contrasts tested. Older neurons are also proposed to behave in a more sluggish, sustained manner, perhaps because they lack the inhibitory component of the temporal response function (Blake et al., 2008; Shinomori & Werner, 2003). This might also be expected to influence the results of our Experiment 2. A slower temporal response, however, would predict the opposite of our results. Decreasing temporal sampling (as in our *standard* stimulus condition) will increase temporal noise; however, a more sustained or sluggish neural response would attenuate this noise and predict greater differences for younger, not older, participants.

We argue, therefore, that contrast sensitivity has a greater effect on motion perception than previously assumed. While replicating previous findings of minimal motion deficits with high contrast stimuli, our results offer a possible explanation for the performance of older adults on tasks such as heading detection (Falkenberg & Bex, 2007; Warren et al., 1989), collision detection (Anderson et al., 2000), and determining time to contact (Anderson & Enriquez, 2006). Although those studies used either real or simulated roadway stimuli, within these complex images it is likely that some image features are of low contrast and hence low visibility. Effectively, there could be less information in the displays for older adults. Consistent with this suggestion, older adults' performance improved when longer presentation durations were used, increasing the amount of available motion information (e.g., Anderson & Enriquez, 2006). Falkenberg and Bex (2007) found elevated contrast thresholds in older compared to younger adults, for detecting heading direction in noise. They attributed this to increased internal noise and decreased sampling efficiency in older adults.

In conclusion, we find an age-related deficit in the ability of adults to discriminate the direction of motion of translational, radial, and rotational motions. This deficit is most pronounced when the moving pattern is least visible. Older adults' deficits in motion processing are predominantly driven by deficits in contrast sensitivity that propagate through the visual pathways.

Acknowledgments

This work was funded by the ESRC and the University of Birmingham and previously presented at the Christmas 2008 Meeting of the AVA. We thank D. Apthorp and one anonymous reviewer for helpful suggestions.

Commercial relationships: none. Corresponding author: Harriet A. Allen. Email: h.a.allen@bham.ac.uk. Address: Edgbaston, Birmingham, B15 2TT, UK.

References

Aaen-Stockdale, C. R., Ledgeway, T., & Hess, R. F. (2007a). Second-order optic flow deficits in amblyopia.

Investigative Ophthalmology and Visual Science, 48, 5532–5538.

- Aaen-Stockdale, C. R., Ledgeway, T., & Hess, R. F. (2007b). Second-order optic flow processing. *Vision Research*, 47, 1798–1808.
- Aaen-Stockdale, C. R., Thompson, B., Huang, P., & Hess, R. F. (2009). Low-level mechanisms may contribute to paradoxical motion percepts. *Journal of Vision*, 9(5):9, 1–14, http://www.journalofvision.org/content/ 9/5/9, doi:10.1167/9.5.9. [PubMed] [Article]
- Andersen, G. J., & Ni, R. (2008). Aging and visual processing: Declines in spatial not temporal integration. *Vision Research*, 48, 109–118.
- Anderson, G. J., & Enriques, A.-J. (2006). Aging and the detection of observer and moving object collisions. *Psychology and Aging*, 21, 74–85.
- Anderson, N. D., Iidaka, T., Cabeza, R., Kapur, S., McIntosh, A. R., & Craik, F. I. M. (2000). The effects of divided attention on encoding- and retrieval-related brain activity: A PET study of younger and older adults. *Journal of Cognitive Neuroscience*, 12, 775–792.
- Atchley, P., & Andersen, G. J. (1998). The effect of age, retinal eccentricity, and speed on the detection of optic flow components. *Psychology and Aging*, 13, 297–308.
- Bennett, P. J., Sekuler, R., & Sekuler, A. B. (2007). The effects of aging on motion detection and direction identification. *Vision Research*, *47*, 799–809.
- Betts, L. R., Sekular, A. B., & Bennett, P. J. (2009). Spatial characteristics of center–surround antagonism in younger and older adults. *Journal of Vision*, 9(1):25, 1–15, http://www.journalofvision.org/content/9/1/25, doi:10.1167/9.1.25. [PubMed] [Article]
- Betts, L. R., Taylor, C. P., Sekuler, A. B., & Bennett, P. J. (2005). Aging reduces center–surround antagonism in visual motion processing. *Neuron*, *45*, 361–366.
- Bidwell, L. C., Holzman, P. S., & Chen, Y. (2006). Aging and visual motion discrimination in normal adults and schizophrenia patients. *Psychiatry Research*, 145, 1–8.
- Billino, J., Bremmer, F., & Gegenfurtner, K. R. (2008). Differential aging of motion processing mechanisms: Evidence against general perceptual decline. *Vision Research*, 48, 1254–1261.
- Blake, R., Rizzo, M., & McEvoy, S. (2008). Aging and perception of visual form from temporal structure. *Psychology and Aging*, *23*, 181–189.
- Burr, D. C., & Santoro, L. (2001). Temporal integration of optic flow measured by contrast and coherence thresholds. *Vision Research*, *41*, 1891–1899.
- Edwards, M., & Badcock, D. R. (1994). Global motion perception: Interaction of the ON and OFF pathways. *Vision Research*, *34*, 2849–2858.

- Edwards, M., & Badcock, D. R. (1995). Global motion perception: No interaction between the first- and secondorder pathways. *Vision Research*, *35*, 2589–2602.
- Edwards, M., Badcock, D. R., & Nishida, S. (1996). Contrast sensitivity of the motion system. *Vision Research*, *36*, 2411–2421.
- Elliott, D., Whitaker, D., & MacVeigh, D. (1990). Neural contribution of spatiotemporal contrast sensitivity decline in healthy aging eyes. *Vision Research*, *30*, 541–547.
- Falkenberg, H. K., & Bex, P. J. (2007). Sources of motion-sensitivity loss in glaucoma. *Investigative* Ophthalmology & Visual Science, 48, 2913–2921.
- Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). "Mini-mental state". A practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research*, 12, 189–198.
- Geesaman, B. J., & Andersen, R. A. (1996). The analysis of complex motion patterns by form/cue invariant MSTd neurons. *Journal of Neuroscience*, 16, 4716–4732.
- Gilmore, G. C., Wenk, H. E., Naylor, L. A., & Stuve, T. A. (1992). Motion perception and aging. *Psychology and Aging*, *7*, 654–660.
- Gurney, K., & Wright, M. J. (1996). Rotation and radial motion thresholds support a two stage model of differential-motion analysis. *Perception*, 25, 5–26.
- Humes, L. E., Busey, T., Craig, J. C., & Kewley-Port, D. (2009). The effects of age on sensory thresholds and temporal gap detection in hearing vision and touch. *Attention, Perception and Psychophysics*, 71, 860–871.
- Leventhal, A. G., Wang, Y. C., Pu, M. L., Zhou, Y. F., & Ma, Y. Y. (2003). GABA and its agonists improved visual cortical function in senescent monkeys. *Science*, 300, 812–815.
- Mapstone, M., Dickerson, K., & Duffy, C. J. (2008). Distinct mechanisms of impairment in cognitive ageing and Alzheimer's disease. *Brain*, 131, 1618–1629.
- Morrone, M. C., Burr, D. C., & Vaina, L. M. (1995). Two stages of visual processing for radial and circular motion. *Nature*, 376, 507–509.
- Morrone, M. C., Tosetti, M., Montanaro, D., Fiorentini, A., Cioni, G., & Burr, D. C. (2000). A cortical area that responds specifically to optic flow, revealed by fMRI. *Nature Neuroscience*, *3*, 1322–1328.
- O'Brien, H. L., Tetewsky, S. J., & Avery, L. M. (2001). Visual mechanisms of spatial disorientation in Alzheimer's disease. *Cerebral Cortex*, 11, 1083–1092.
- Pardhan, S. (2004). Contrast sensitivity loss with aging: Sampling efficiency and equivalent noise at different spatial frequencies. *Journal of the Optical Society of*

America A, Optics, Image Science, and Vision, 21, 169–175.

- Perrone, J. A., & Stone, L. S. (1998). Emulating the visual receptive field properties of MST neurones with a template model of heading estimation. *Journal of Neuroscience*, 18, 5958–5975.
- Ross, J. E., Clarke, D. D., & Brown, A. J. (1985). The effect of age on contrast sensitivity function: Uniocular and binocular findings. *British Journal of Ophthalmology*, 69, 51–56.
- Schmolesky, M. T., Wang, Y. C., Pu, M. L., & Leventhal, A. G. (2000). Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. *Nature Neuroscience*, 3, 384–390.
- Scialfa, C. T., Kline, D. W., & Lyman, B. J. (1987). Agedifferences in target identification as a function of retinal location and noise-level—Examination of the useful field of view. *Psychology and Aging*, 2, 14–19.
- Shinomori, K., & Werner, J. S. (2003). Senescence of the temporal impulse response to a luminous pulse. *Vision Research*, *42*, 617–627.
- Simmers, A. J., Ledgeway, T., Hess, R. F., & McGraw, P. V. (2003). Deficits to global motion processing in human Amblyopia. *Vision Research*, 43, 729–738.
- Simmers, A. J., Ledgeway, T., Mansouri, B., Hutchinson, C. V., & Hess, R. F. (2006). The extent of the dorsal extra-striate deficit in amblyopia. *Vision Research*, 46, 2571–2580.
- Snowden, R. J., & Kavanagh, E. (2006). Motion perception in the aging visual system: Minimum motion, motion coherence and speed discrimination thresholds. *Perception*, 35, 9–24.
- Tanaka, K., & Saito, H. (1989). Analysis of motion of the visual field by direction, expansion/contraction and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology*, 62, 626–641.
- Tran, D. B., Silverman, S. E., Zimmerman, K., & Feldon, S. E. (1998). Age-related deterioration of motion perception and detection. *Graefes Archive for Clinical and Experimental Ophthalmology*, 236, 269–273.
- Warren, W. H., Blackwell, A. W., & Morris, M. W. (1989). Age differences in perceiving the direction of self motion from optical flow. *Journal of Gerontol*ogy, 44, 147–153.
- Weale, R. A. (1975). Senile changes in visual acuity. *Transactions of the Ophthalmological Society*, UK, 95, 36–38.
- Williams, D. W., & Sekuler, R. (1984). Coherent global motion percepts from stochastic local motions. *Vision Research*, 24, 55–62.

- Wood, J. M., & Bullmore, M. A. (1995). Changes in the lower displacement limit for motion with age. *Ophthalmic and Physiological Optics*, 15, 36.
- Wright, C. E., & Drasdo, N. (1985). The influence of age on the spatial and temporal contrast sensitivity function. *Documenta Ophthalmologica*, 59, 385–395.