

The effects of aging on motion detection and direction identification

Patrick J. Bennett^{a,b,*}, Robert Sekuler^c, Allison B. Sekuler^{a,b}

^a Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton Ont., Canada L8S 4K1

^b CIHR Research Group in Sensory & Cognitive Aging, Canada

^c Volen Center for Complex Systems, Brandeis University, Waltham, MA, USA

Received 9 June 2006; received in revised form 31 December 2006

Abstract

Random dot cinematograms were used to probe motion perception in human observers ranging from 23 to 81 years of age. Stimuli were either broadband directional *Noise*, which produces no experience of global motion flow, or a narrower band directional *Signal*, which tended to produce experiences of coherent, global direction flow. On each trial, subjects rated their certainty that a *Signal* had been presented, and used a computer mouse to indicate the direction of perceived global flow. At all ages, sensitivity to motion and accuracy of perceived direction improved significantly as stimulus duration increased from 75 to 470 ms. However, older subjects (>70 years of age) were significantly less sensitive to motion, and were significantly less accurate at identifying the direction of movement. A control experiment, which found that older subjects accurately perceived and remembered the orientation of a line, ruled out the possibility that the observed deficits in motion perception were due to an inability on the part of older subjects to manipulate the computer mouse. Those control results also showed that both younger and older observers maintained robust visual representations over durations ranging from .24 to 6.0 s. The motion detection and identification results obtained from subjects less than 70 years of age were well fit by a simple multichannel model of motion, although different levels of additive internal noise were needed to fit detection data and direction-identification data, suggesting that motion direction and identification are constrained by different mechanisms. To fit the data from the oldest subjects, however, the values of model parameters had to be significantly altered, either by increasing the level of additive internal noise substantially, or by a smaller increase in noise coupled with an increase in the bandwidth of the model's directionally selective channels. These results are qualitatively consistent with recent neurophysiological studies showing weaker directional selectivity and higher spontaneous noise in visual neurons of senescent monkeys and cats.

© 2007 Elsevier Ltd. All rights reserved.

Keywords: Motion; Direction selectivity; Modeling; Perceived direction; Detection; Orientation; Memory; Aging

1. Introduction

The population of the developed world is aging faster now than at any time in recorded history. This dramatic demographic shift is likely to amplify the personal and public health impacts of all age-related changes, including those that involve vision and neural processing. Some age-related changes in vision and neural processing, such as loss in acuity and contrast sensitivity, have been well

documented, and are fairly well understood; others, such as various aspects of visual motion processing, have not received the full attention they deserve (Sekuler & Sekuler, 2000). From motion on the retina, the human visual system extracts several distinct classes of behaviorally relevant, complex motion information. Some of these have been shown to deteriorate with normal aging. For example, older observers extract the direction of self-motion from optical flow less accurately than do younger observers (Warren, Blackwell, & Morris, 1989). Older subjects also are less efficient at using optical flow to detect and discriminate the curvature of smooth 3D surfaces (Anderson & Atchley, 1995; Norman, Dawson, & Butler, 2000), and to discrimi-

* Corresponding author.

E-mail addresses: bennett@mcmaster.ca (P.J. Bennett), sekuler@mcmaster.ca (R. Sekuler).

nate the shapes of two- (Wist, Schrauf, & Ehrenstein, 2000) and three-dimensional forms (Norman, Clayton, Shular, & Thompson, 2004).

To what extent are age-related deficits in complex motion perception related to lower level deficits (e.g., deficits in the detection and discrimination of direction)? In the primate brain, regions that extract motion signals are organized in a distributed, roughly hierarchical manner, with different areas specialized for extracting distinct aspects of the motion signal (Blake, Sekuler, & Grossman, 2003). The distributed character of this network opens the possibility that age-related changes in the brain could differentially impact distinct nodes in the brain's motion network, with resulting differential impact on performance on one motion-dependent task versus another. To explore this possibility, we carried out a cross-sectional study with human observers to determine age's impact on two behaviorally important tasks: detection of motion, and identification of motion's direction. We focused on these two tasks in part because earlier work, with young observers, showed that performance on the two tasks diverged under certain stimulus conditions (Ball, Sekuler, & Machamer, 1983). Such divergence is interesting theoretically because it may suggest the dependence on differential neural structures. By applying a computational model of both tasks to results from observers across the adult lifespan, we hoped to gain additional theoretical insight into the processes responsible for any observed age-related changes in performance on the two tasks.

Neurophysiological results show that aging increases the level of noise and decreases directional tuning of neurons in the primary visual cortex of cats (Hua et al., 2006) and macaque monkeys (Leventhal, Wang, Pu, Zhou, & Ma, 2003; Schmolesky, Wang, Pu, & Leventhal, 2000). Therefore, one might expect motion detection and discrimination thresholds in humans to increase with age. To date, only a few psychophysical studies have examined this issue, (e.g., Anderson & Atchley, 1995; Ball & Sekuler, 1986; Gilmore, Wenk, Naylor, & Stuve, 1992; Snowden & Kavanagh, 2006; Tran, Silverman, Zimmerman, & Feldon, 1998; Trick & Silverman, 1991). The results of these studies typically do show elevated thresholds (decreased performance) for detection and discrimination of motion, although the two performance measures usually were not examined concurrently, and so it is difficult to know the extent to which performance on the two tasks are linked.

In the current study, then, we simultaneously measured two distinct aspects of motion perception, namely sensitivity to coherent motion and the accuracy of the perceived direction of coherent flow, focusing on how they each change across the adult lifespan. To probe age-related changes in both of these aspects of motion perception we used a single, shared stimulus: a random dot cinematogram whose spatially intermingled, directionally diverse motion vectors give rise to a percept of unidirectional global flow (Williams & Sekuler, 1984). When a cinematogram's directional bandwidth is sufficiently narrow, the visual system

integrates the diverse directional information to generate a percept of global flow: The perceived direction of such flow varies over trials, but generally approximates the cinematogram's mean direction (Sekuler, Sekuler, & Penpeci, 1996).

Our use of the same stimulus for both tasks enhances the comparability of results from the tasks. Additionally, we chose to use cinematograms as stimuli because (i) with such stimuli, studies of motion perception yield quantitatively comparable results in both humans and monkeys (Britten, Shadlen, Newsome, & Movshon, 1992), which facilitates linkages between human psychophysics and single-cell physiology, (ii) there has been extensive modeling of subjects' ability to discriminate the perceived directions generated by pairs of cinematograms with different statistical properties, size, and duration (e.g., Watamaniuk & Sekuler, 1992), and (iii) previous research has demonstrated an age-related processing difference with related stimuli (e.g., Ball & Sekuler, 1986). As some age-related changes in perceptual responses have been attributed to a general slowing of processing (Salthouse, 1982; Kosnik, Winslow, Kline, Rasinski, & Sekuler, 1988; Porciatti, Fieorentini, Morrone, & Burr, 1999), we measured detection and identification of motion over a substantial range of stimulus durations. If age-differences in motion perception did result from slowed processing, additional viewing time should allow older subjects to compensate for any age-related decline in motion perception seen at short stimulus durations. We tested this hypothesis with stimuli presented for durations that span the range over which temporal integration has been demonstrated for cinematograms like ours (Watamaniuk & Sekuler, 1992).

2. Methods

2.1. Observers

The 39 subjects ranged in age from 23 to 81 years and had normal or corrected-to-normal Snellen acuity (20/30 or better). Documentation from their eye-care providers certified that the older subjects were free of strabismus, amblyopia, macular degeneration, and cataracts; none was aphakic. Eight other potential subjects were excluded from the sample: four on the basis of the visual examination; two who could not reliably control the computer mouse, which was integral to the experimental task; and two who could not complete any of the test conditions. In addition, one subject's data for one condition were lost due to a computer malfunction; his remaining data were included in our analyses. Subjects were paid for their participation in the experiment.

2.2. Stimuli and apparatus

Stimuli were random dot cinematograms presented on a large computer monitor at a frame rate of 67 Hz (display resolution was 1152×870 pixels). Each cinematogram comprised 300 black dots on a white background; black and white corresponded to luminances of approximately 5 and 95 cd/m^2 , respectively. On each frame, every dot's direction was chosen randomly from a uniform distribution of directions. The direction in which any dot moved from one frame to the next was independent of both that dot's previous movements and the movements of other dots. The mean direction across all dots varied randomly from trial to trial. Dots moved at a fixed velocity of 6 °/s, with successive steps of 5.4 arcmin.

The entire computer display was white, but the array of moving dots was limited to a central, 6° circular aperture. A small cross in the middle of the aperture provided a fixation point.

Within blocks of 100 trials, two kinds of cinematograms, designated *Signal* and *Noise*, were randomly presented on different trials (see Williams & Sekuler, 1984; for a complete description of the stimulus class). In *Signal* cinematograms, the directions in which the spatially random dots moved between frames were drawn from a uniform distribution spanning 250 deg around some mean direction, producing a percept in young observers of coherent, global flow in a direction corresponding closely to the mean of the underlying distribution (Sekuler et al., 1996). In *Noise* cinematograms, the directions in which dots moved between frames were drawn from a uniform distribution spanning 360 deg, producing a percept of incoherent, random motions (similar to “snow” on a de-tuned television). Both *Signal* and *Noise* cinematograms were presented at stimulus durations of 75, 170, 255, and 470 ms, with duration blocked in groups of 100 trials, and the order of durations determined randomly for each subject.

2.3. Procedure

Subjects viewed the display binocularly through natural pupils from a distance of 114 cm. Head position was stabilized by a forehead/chin rest. On each trial, subjects made two judgments: the direction in which the cinematogram’s elements appeared to flow, and a confidence rating regarding whether a *Signal* cinematogram had been presented. Specifically, following each cinematogram, the subject indicated the direction of motion by using the computer’s mouse to move a cursor from the center of the screen to a position on a circle surrounding the area that had been occupied by the cinematogram. Subjects were told to make their best guess for the direction judgment even on trials for which they were confident that no signal had been presented. Once the cursor reached the desired location, a mouse click caused the computer to read and store that location. Immediately thereafter, subjects used a six-point rating scale to indicate whether they had perceived coherent motion (i.e., a *Signal*) or noise on the trial, and to express their confidence in that judgment. Confidence ratings were made by selecting one item from a six-item menu (Nachmias & Steinman, 1963): “Signal Definitely” (100% Sure), “Signal Probably” (80% Sure), “Signal Maybe” (60% Sure), “Noise Maybe” (60% Sure), “Noise Probably” (80% Sure), or “Noise Definitely” (100% Sure).

Subjects were informed at the beginning of the experiment that a *Signal* would be presented on half the trials. To start each trial, a participant used a computer mouse to click on the fixation point; this effectively deprived the participant of any external indication of the judgment made on the previous trial. Trials were separated by a minimum of two seconds. To minimize forgetting of the perceptual aspect that we thought might be more vulnerable to passage of time, direction judgments were always made first.

3. Results

We begin by presenting separate analyses of results on sensitivity to coherent motion, and then on accuracy of perceived direction of motion. All analyses were performed using the statistical computing environment, R (R Development Core Team, 2004). For purposes of analysis, subjects were divided into five age groups each containing 7–9 subjects (see Table 1). Following the initial analyses,

Table 1
Ages and number of subjects in each group

Group	Age range	Mean age (years)	<i>n</i>
1	20–29	25.1	8
2	30–39	33.9	8
3	40–59	49.6	7
4	60–69	65.1	7
5	70–81	74.9	9

we discuss the results of applying a standard computational model to the two aspects of motion perception.

3.1. Sensitivity to coherent motion

For each subject, confidence ratings were converted into ROC curves (Nachmias & Steinman, 1963), and sensitivity to motion was expressed as the area under the ROC curve (A_{roc}). Fig. 1a shows sensitivity for each age group plotted as a function of stimulus duration. An arcsine transform ($y = 2 \sin^{-1} \{\sqrt{A_{roc}}\}$) was used to normalize the distribution of sensitivity measures (Kirk, 1968). The inset of Fig. 1a shows the transformed sensitivity measures. Fig. 1a shows that sensitivity to motion increased with stimulus duration in all age groups, but that sensitivity in the oldest group was substantially lower than in the other groups.

The data were examined quantitatively by fitting with the following linear mixed-effects model:

$$y_{ijk} = \beta_0 + \beta_1 \log 10(d_k) + \beta_2 \{\log 10(d_k)\}^2 + \eta_j + b_i + e_{ijk} \tag{1}$$

where y_{ijk} is arcsine-transformed sensitivity for the i th subject in the j th age group with the k th stimulus duration; β_0 is the intercept; β_1 and β_2 are, respectively, the linear and quadratic fixed effects of log-transformed stimulus duration; η is the fixed effect of age group; and b and e are random effects distributed as independent, zero-mean Gaussian variables with variances σ^2 and δ_j^2 , respectively. Eq. (1) was fit to the data using the maximum likelihood estimation procedure in R’s *nlme* package (Pinheiro, Bates, DebRoy, & Sarkar, 2004).

The estimates of the fixed effects, age and stimulus duration, are shown in Table 2. Both the linear (β_1) and quadratic (β_2) effects of stimulus duration were statistically significant: sensitivity increased as a decelerating function of duration. It is likely that the significant quadratic component reflects, at least in part, the fact that sensitivity approached its maximum possible value at the longer stimulus durations. The effect of age group is represented in Table 2 by four independent parameters— η_1 through η_4 —showing how sensitivity in Groups 1–4 differed from that of the oldest subjects in Group 5 when all other factors are held constant: Sensitivity of all of the groups differed significantly from the oldest group. The overall effect of age was assessed by dropping the age group parameter, η , from Eq. (1), re-fitting the reduced model to the data, and then using a likelihood ratio test to compare the goodness-of-fit attained by the two models. The model that included the age group factor resulted in a significantly better fit (likelihood ratio = 23.6, $df = 4$, $p < 0.001$), hence the overall effect of age group was statistically significant. Finally, a series of Helmert contrasts was used to compare Group 2 to Group 1, Group 3 to the average of Groups 1 and 2, Group 4 to the average of Groups 1–3, and so forth. Only the comparison of Group 5, the oldest subjects, to the

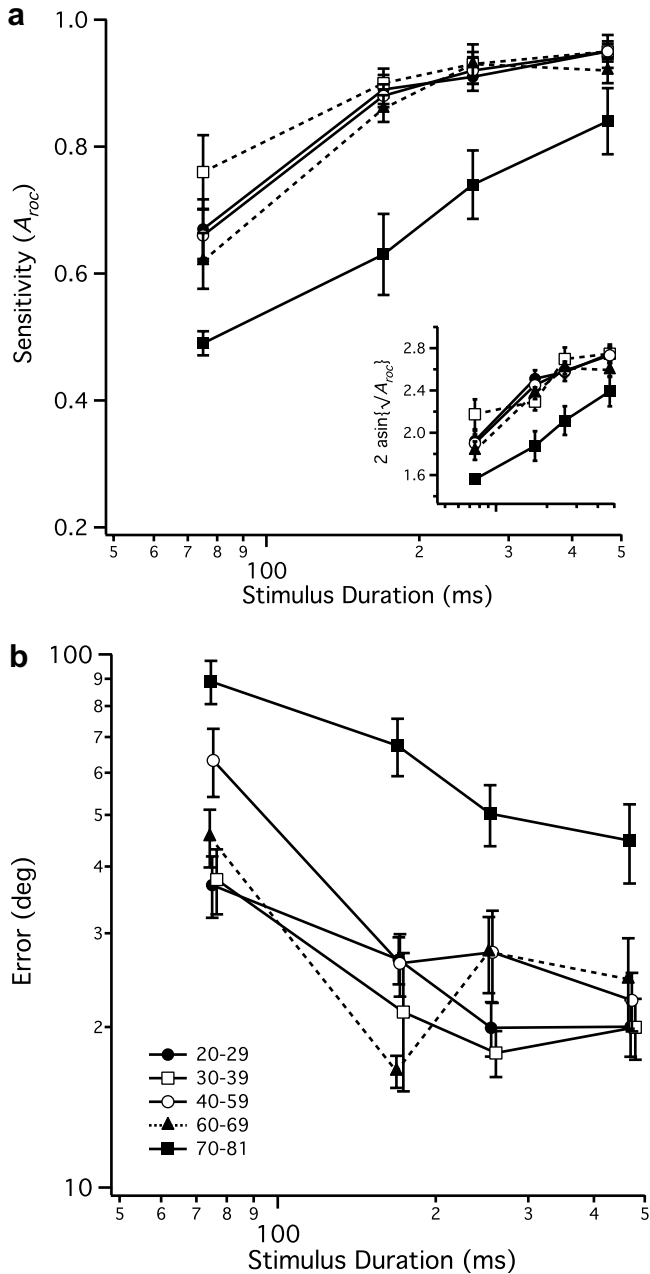


Fig. 1. (a) Sensitivity to motion, defined as the area under the ROC curve, plotted as a function of stimulus duration in milliseconds. Each point shows mean sensitivity averaged across subjects in a single age group; vertical bars represent ± 1 standard error. The inset shows the same sensitivity data after application of an arcsine transform. (b) Direction error (deg) associated with identifying the direction of motion on trials in which motion was detected (i.e., Hit trials). Each point shows the mean error averaged across subjects in a single age group; vertical bars represent ± 1 standard error.

average of Groups 1–4 was statistically significant ($t = 5.09$, $df = 34$, $p < 0.0001$).

To determine if the effect of age group varied with stimulus duration, terms representing the interactions between the age group and the linear and quadratic effects of duration were added to Eq. (1). The improvement in goodness-of-fit was not statistically significant (likelihood

Table 2
Estimates of fixed effects for Eq. (1)

Parameter	Value	Std. error	DF (error)	t (* $p < 0.001$)
β_0	-5.385	1.010	115	-5.33
β_1	5.575	0.899	115	6.19
β_2	-1.014	0.982	115	-5.11
η_1	0.453	0.11	34	4.22
η_2	0.553	0.11	34	5.06
η_3	0.431	0.11	34	3.92
η_4	0.367	0.11	34	3.28

ratio = 11.02, $df = 8$, $p = 0.20$). Therefore, it appears that the additive model in Eq. (1) provided an adequate fit to the data, and the effect of age did not vary significantly across stimulus duration.

3.2. Accuracy of perceived direction of motion

The error in perceived direction was defined as the absolute value of the angular difference between the direction of stimulus motion and the direction indicated by the subject. The direction error was calculated for every trial on which a subject correctly detected motion (i.e., on all Hit trials) and, for every subject, the median error was calculated for each confidence rating (i.e., 1, 2, or 3) and stimulus duration. One subject in the 30–39 years old group had errors of approximately 67 deg at the longest stimulus duration, and approximately 90 deg at the three shortest stimulus durations. These errors were more than two standard deviations away from the group means at all but the shortest stimulus duration, and so this subject was declared an outlier and removed from subsequent analyses. The median errors for each age group, after removing the outlier and averaging across confidence ratings, are plotted in Fig. 1b. Errors decreased with stimulus duration, but the oldest group exhibited larger errors at all durations.

The error data were analyzed with the following linear mixed-effects model:

$$\log_{10}(y_{ijk}) = \beta_0 + \beta_1 \log_{10}(d_k) + \beta_2 \{\log_{10}(d_k)\}^2 + \beta_3 + \beta_4 r + \eta_j + b_i + e_{ijk} \quad (2)$$

where y_{ijk} is the median direction error for the i th subject in the j th age group with the k th stimulus duration; β_0 is the intercept; β_1 and β_2 are, respectively, the linear and quadratic fixed effects of log-transformed stimulus duration, d_k ; β_3 is the fixed effect of sensitivity, s (i.e., $2 \sin^{-1}(\sqrt{A_{roc}})$); β_4 is the fixed effect of confidence rating, r ; η is the fixed effect of age group; and b and e are random effects distributed as independent, zero-mean Gaussian variables with variances σ^2 and δ_j^2 , respectively. The parameters of the model were estimated using the maximum likelihood procedure in R's *nlme* package (Pinheiro et al., 2004). The estimates of the fixed effects are shown in Table 3.

The effects of sensitivity (β_3) and response confidence (β_4) were significant, indicating that direction error

Table 3
Estimates of fixed effects for Eq. (2)

Parameter	Value	Std. error	DF (error)	<i>t</i> -value	<i>p</i> -value
β_0	3.360	0.817	398	4.11	0.000
β_1	−0.996	0.739	398	−1.35	0.179
β_2	0.221	0.160	398	1.38	0.168
β_3	−0.375	0.050	398	−7.55	0.000
β_4	−0.085	0.014	398	5.95	0.000
η_1	−0.166	0.051	33	−3.27	0.003
η_2	−0.246	0.061	33	−4.03	0.000
η_3	−0.103	0.054	33	−1.89	0.068
η_4	−0.192	0.053	33	−3.65	0.001

decreased as the motion stimulus became more detectable and as response confidence increased. The linear and quadratic effects of stimulus duration were not significant, which suggests that the low errors found at the longer stimulus durations (see Fig. 1b) can be accounted for by an increase in sensitivity and response confidence, rather than an increase in stimulus duration per se. The effect of age group is represented in Table 3 by four independent parameters— η_1 through η_4 —showing the log-difference between direction errors in Groups 1–4 and Group 5 when all other factors are held constant. Groups 1, 2, and 4 all had significantly lower errors than Group 5; the difference between Groups 4 and 5 was marginally significant ($p < 0.07$, two-tailed). The overall effect of age was assessed by dropping the age group parameter, η , from Eq. (2), re-fitting the reduced model to the data, and then using a likelihood ratio test to compare the goodness-of-fit attained by the two models. The model that included the age group factor resulted in a significantly better fit (likelihood ratio = 18.14, $df = 4$, $p < 0.01$), hence the overall effect of age group was statistically significant. To test the idea that only the oldest group differed from all the others, Eq. (2) was re-fit to the data after excluding Group 5. In this case, the effect of age group was no longer statistically significant.

To determine if an additive model adequately fit the data, the statistical model was modified to include all possible two-way interactions between stimulus duration, sensitivity, response confidence, and age group. Adding the two-way interactions did not improve the goodness-of-fit significantly (likelihood ratio = 34.13, $df = 28$, $p = 0.2$). We also considered a model that included only the two-way interactions between age group and the other terms: Again, the more complex model did not provide a significantly better fit to the data (likelihood ratio = 16.68, $df = 15$, $p = 0.34$). Therefore, the additive model in Eq. (2) provided an adequate fit to the data, and the effect of age did not differ across levels of the other predictor variables. The lack of an interaction between the effects of age group and confidence was surprising because we expected there to be age-related differences in the ways different age groups judged their confidence, and we also expected the age difference in direction error to be reduced when subjects were highly confident that they detected

coherent motion. There were, in fact, differences between young and old subjects in the way they expressed confidence in their judgments of motion. At the three shortest stimulus durations, the subjects in Group 5 indicated that they were 100% confident of perceiving motion far more infrequently compared to Groups 1–4. Only with increased stimulus duration did the oldest subjects express confidence in their judgments similarly to the others. Such age-related differences in confidence ratings were not as apparent among the 80% and 60% confidence levels.

We therefore conducted an additional analysis to determine if there was a significant effect of age when the analysis was restricted only to trials on which subjects were most confident of their detection judgment. A comparison of two models that were fit to those “most confident” trials only—one that included the group factor, η , and one that did not—still found a significant effect of group (likelihood ratio = 11.25, $df = 4$, $p < 0.05$). So, the significant effect of age in the additive model was not the product of age-related differences in confidence.

In summary, errors in the perceived direction of motion were negatively correlated with sensitivity in the detection task, and with confidence in the detection judgment. Although direction errors decreased with increasing stimulus duration (Fig. 1b), the effect of duration was not significant when the effects of sensitivity and response confidence were taken into account. Most importantly, error in the perceived direction of motion varied significantly across age groups: errors made by the oldest subjects were significantly greater than errors made by subjects in all other groups, and this effect of age did not interact with other predictor variables.

3.3. Control experiment (memory for perceived orientation)

The literature contains numerous reports of age-related changes in the speed and precision of movements (reviewed in Ketcham & Stelmach, 2004). We wondered therefore whether the age-related increases in direction error that we observed might have arisen from age-related decreases in the speed and precision with which subjects controlled the computer cursor, rather than from a diminished ability to perceive motion direction accurately. To test this idea, we conducted a control experiment that required subjects to use a mouse to register the perceived orientation of a line in conditions that maximized the chances that stimulus orientation would be perceived accurately. In this control experiment, the stimulus display consisted of a single line (width = 1 arcmin) extending from the fixation point to a spot (diameter = 18 arcmin) that appeared at an eccentricity of 3 deg. The orientation of the line on each trial was selected from a uniform random distribution ranging from 0 to 359 deg in steps of 1 deg. The contrast of the line and spot were high ($\Delta L/L_{avg} = -0.91$), and stimulus duration was relatively long (i.e., 500 ms), and so it was anticipated that the orientation of the line would be perceived accurately. At the end of the stimulus presentation, the line,

spot, and fixation point disappeared, a cursor was presented at the location of the now-extinguished fixation point, and a circle (radius = 3 deg) was drawn, centered on the cursor. The subject used a computer mouse to move the cursor to click on the circle at a position corresponding to perceived orientation of the line.

Additionally, to determine whether potentially slower responses on the part of older observers could explain age-related changes in stimulus identification, we assessed the robustness of memory for orientation by randomly varying the delay between stimulus offset and the presentation of the computer cursor at the location of the fixation point among 7 different delays ranging from 0.024 to 6 s. Twenty-four responses were collected from each subject at each delay. Orientation error was defined as the median of the absolute value of the difference between stimulus orientation and perceived orientation. Fig. 2 shows orientation error at each delay averaged across 10 younger (mean age = 21.4 years; $SD = 4.4$) and 11 older (mean age = 71 years; $SD = 3.7$) subjects; none of subjects had participated in the main experiment. Performance in this task was quite good: the average error in the younger and older groups was 3.9 and 4.6 deg, respectively. Interestingly, for both age groups error was nearly constant across delays ranging from 24 ms to 1 s, and increased only slightly at longer delays.

The data were analyzed with the following linear mixed effects model:

$$y_{ijk} = \beta_0 + \beta_1 \log_{10}(d_k) + \beta_2 \log_{10}(d_k)^2 + \eta_j + b_i + e_{ijk}$$

where y_{ijk} is the orientation error for the i th subject in the j th age group with the k th stimulus duration; β_0 is the intercept; β_1 and β_2 are the linear and quadratic effects of log-transformed stimulus duration; η is the fixed effect of age group; and b and e are random effects distributed as independent, zero-mean Gaussian variables with variances σ^2 and δ^2 , respectively.

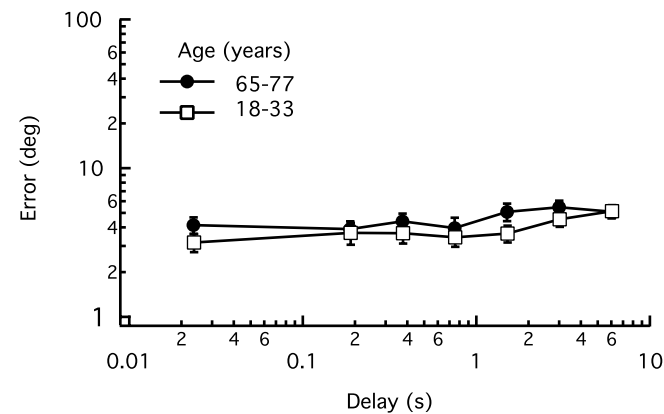


Fig. 2. Results of control experiment in which subjects identified the orientation of a high-contrast line. The orientation error (deg) is shown as a function of interval between the stimulus and the response. Mean errors are shown separately for younger and older subjects. Vertical bars are ± 1 standard error.

The linear ($F = 37.08$, $df = (1, 124)$, $p < 0.001$) and quadratic ($F = 11.44$, $df = (1, 124)$, $p < 0.001$) effects of stimulus duration were significant, but the effect of age group was not ($F = 1.01$, $df = (1, 19)$, $p = 0.33$). Of the 11 subjects in the older group, seven were 70 years old or older (i.e., the same range as Group 5 in the main experiment). An additional analysis that omitted the four older subjects who were less than 70 years of age yielded virtually identical results as the original analysis. Hence, the results of this control experiment show that the orientation of a high-contrast line can be perceived with approximately equal accuracy in younger and older adults. Most importantly, the findings demonstrate that older adults can use a computer mouse to record perceived orientation accurately, even when relatively long delays are required between stimulus presentation and response. Therefore, it is unlikely that the large age differences found in the motion perception experiment can be attributed to an inability on the part of older subjects to control the computer mouse or to increased response time among older subjects. The findings also are consistent with previous research on the long-lasting nature of visual memory for orientation in younger subjects (Magnussen, 2000), and extend previous demonstrations of preserved memory for simple visual attributes in older subjects (Bennett, Sekuler, McIntosh, & Della-Maggiore, 2001; Faubert, 2002; McIntosh et al., 1999; Sekuler, Kahana, McLaughlin, Golomb, & Wingfield, 2005). In both younger and older observers, we found remarkable preservation of visual information over a more than $2 \log_{10}$ unit increase in retention interval (with error rates increasing by only about 1.5 deg over the full range of retention intervals from 24 ms to 6 s).

3.4. Motion perception model

To understand the possible origin of the age-related changes we observed in motion sensitivity and in perceived direction, we exploited a previously developed quantitative model of motion perception. The model's basic elements were introduced by Williams, Tweten, and Sekuler (1991), and have been applied successfully to the perception of cinematograms with a wide range of directional bandwidths (Watamaniuk, 1993). The model's core is an ensemble of 12 evenly distributed, directionally selective mechanisms that span 2D directional space. The directional tuning of a single channel was defined by the function

$$t_{\theta}(d) = \frac{e^{-(d-\theta)^2/(2b^2)}}{b\sqrt{2\pi}}$$

where d is direction of motion, θ is the peak of the tuning function, and b is the bandwidth parameter, or standard deviation. A channel's response to a random dot stimulus was defined as

$$r_{\theta} = \sum_{n=1}^{\#dots} t_{\theta}(d_n) \cdot \gamma + \eta$$

where d_n is the direction of motion of dot n , γ is a Gaussian random variable with a mean of 1 and a standard deviation of ρ , η is a Gaussian random variable with a mean of zero and a standard deviation of σ . The resulting 12 scalar values (i.e., one from each channel) were half-wave rectified, raised to a power, p , and then combined using vector addition. The strength of the summed response was defined as $|r_{\text{total}}|^{1/p}$, where r_{total} is the resultant, and the direction of the summed response corresponded to the phase of r_{total} , or $\phi(r_{\text{total}})$. Response strength was used as the decision variable in the motion detection task: On each simulated trial the model was presented with Signal and Noise cinematograms, and the stimulus evoking the larger response strength was judged by the model to be the signal. Detection accuracy was compared to A_{roc} , which equals the proportion of correct responses in a 2-IFC task. The response variable in the direction identification task was the sum of response phase, $\phi(r_{\text{total}})$, and a Gaussian random variable ($\mu = 0$; $\sigma = 7.5$ deg), which was used to account for the small errors associated with moving the computer mouse. The median of the absolute values of this noise is approximately 5 deg, which is similar to the mean errors measured in the control experiment (Fig. 2). Direction errors on simulated trials in which the detection response was correct were compared to observed direction errors on Hit trials.

We did not do an extensive search of the model's parameter space to fit the data obtained from younger observers, opting instead for a parameter set that previously gave a good account of detection and identification of motion direction by a small set of young human observers tested with random dot cinematograms (Sekuler et al., 1996). Williams et al. (1991) showed that Gaussian tuning functions with standard deviations, b , of 30 deg gave a good account of psychophysical results in motion metamer experiments with young subjects, so we used that bandwidth to model the results obtained from Groups 1–4 in the current experiment. Sekuler et al. (1996) used multiplicative noise with a standard deviation, ρ , of 0.47 to fit young subjects' psychophysical responses to cinematograms similar to the ones we used here, and therefore we set ρ to that same value. Watamaniuk, Sekuler, and Williams (1989) found that setting the summation exponent, p , to 6 resulted in a good fit to motion discrimination data obtained with a brief cinematogram consisting of three frames, but that an exponent of 2 was better for data obtained with longer stimuli. We therefore used an exponent of 6 for our shortest stimulus duration and an exponent of 2 at all other durations. The final set of parameters determined the number of dots used to compute global direction. Watamaniuk and Sekuler (1992) showed that the spatial summation area for global direction is more than 65 deg², which is larger than area of our stimuli, and Watamaniuk et al. (1989) found that direction information for broad-band cinematograms, like the ones used here, was integrated across at least 25 stimulus frames spanning more than 1 s. Finally, Watamaniuk (1993) estimated that judgments of global direction are based on approximately 23% of the total number of stimu-

lus dots. Therefore, the current model assumed that direction information from 23% of the dots was combined across the entire stimulus area and across all stimulus frames. The model's single remaining free parameter, the standard deviation of additive noise (σ), was adjusted across simulations to maximally fit the detection and direction data.

For each condition of interest, we simulated 2500 psychophysical trials using a Matlab (The Mathworks; v 7.1) implementation of the model. From the simulated trials we derived two measures, the detectability of motion expressed as proportion correct in a two-alternative forced choice task, and the median absolute error of perceived direction (calculated on all Hit trials). The predictions of the model are shown in Fig. 3, along with the detection and direction error data averaged across Groups 1–4 and the data from Group 5 (i.e., the oldest subjects). A very good quantitative fit to the detection data from Groups 1–4 was obtained with an internal noise standard deviation of 0.56 (Fig. 3a). With this level of noise, the fit to the direction data from Groups 1–4 also was reasonably good, although the model slightly underestimated the direction errors by several degrees at all stimulus durations (Fig. 3b). Increasing the standard deviation of the additive noise to 0.8 or 1.12 resulted in a better fit to the direction error data from Groups 1–4, but at the cost of a slightly worse fit to the detection data (especially at the shortest stimulus duration).

Neurophysiological recordings have found broader directional tuning, and higher levels of spontaneous activity, in visual neurons of senescent cats (Hua et al., 2006) and senescent monkeys (Schmolesky et al., 2000). Based on these findings, we attempted to account for differences between younger and older subjects first by adjusting the level of model's additive internal noise, and then by adjusting channel bandwidth. Increasing the standard deviation of additive internal noise from 0.56 to 8 greatly reduced motion sensitivity (Fig. 3a); the loss of sensitivity was slightly greater at short stimulus durations, and consequently the shape of the curve relating proportion correct to log stimulus duration varied with internal noise. A noise standard deviation of approximately 2.5 yielded a good fit to the motion detection data from Group 5. However, with this level of internal noise the model gave a very poor fit to the direction judgments, underestimating errors at all stimulus durations by 22–30 deg (Fig. 3b). Only when the level of internal noise was very high ($\sigma = 8$) did the model provide a good fit to the direction judgment data obtained from the oldest subjects.

In further simulations we examined whether the effects of aging could be accounted for by increasing channel bandwidth. When the standard deviation of additive noise was fixed at 0.56, increasing channel bandwidth from 30 to 90 deg reduced motion sensitivity by approximately the same amount at all stimulus durations. In other words, increasing bandwidth simply shifted the curve relating proportion correct to stimulus duration downward, yielding

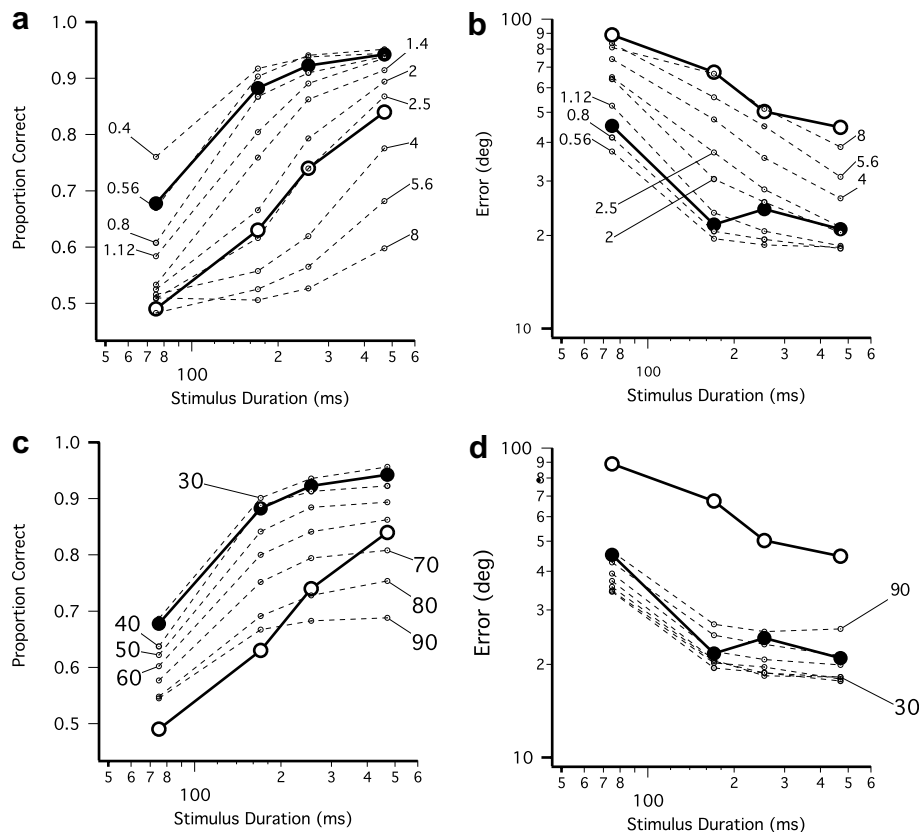


Fig. 3. Results of simulations. (a) Proportion correct in 2-AFC motion detection task is plotted as a function of stimulus duration. Results of simulations that used different levels of additive internal noise are shown by the dotted curves; the noise standard deviation is indicated by the labels in the figure. Channel bandwidth (i.e., standard deviation) was 30 deg. Sensitivity (i.e., area under the ROC curve) measured in real observers was converted to proportion correct. Data from Group 5 is shown by the filled circles; data from Groups 1–4 were averaged and are shown by the open symbols. (b) Direction error on Hit trials for models that differed in additive internal noise are shown by dotted lines. Noise standard deviation is indicated by the labels. For each subject, the median direction error was computed on all Hit trials irrespective of response confidence. The open symbols show direction errors averaged across subjects in Group 5; the filled symbols show errors averaged across Groups 1–4. (c) Same as (a), except the dotted lines show the predictions of models that differed in channel bandwidth. Channel bandwidth, in degrees, is indicated by the labels. Additive internal noise was fixed at 0.56. The open and filled symbols are the same as in (a). (d) Same as (b), except that the dotted lines show the direction errors for models that differ in channel bandwidth, which ranged from 30 to 90 deg in steps of 10 deg. For clarity, only the curves corresponding to bandwidths of 30 and 90 deg are labeled. Additive noise was fixed at 0.56. The open and filled symbols are the same as in (b).

curves that were shallower than the data from the oldest subjects (Fig. 3c). Surprisingly, direction errors were relatively insensitive to variations in channel bandwidth: Increasing bandwidth from 30 to 90 deg caused the direction errors to increase only by approximately 5 deg at each stimulus duration (Fig. 3d). These predictions obviously failed to fit the errors obtained from the oldest subjects. Hence, it was not possible to account for the differences between Groups 1–4 and Group 5 by varying channel bandwidth alone.

Finally, we note that for bandwidths up to about 55 deg it was possible to find some level of internal noise that adequately fit the detection and direction error data from Group 5. However, as was the case with a bandwidth of 30 deg, the standard deviation of the internal noise had to be increased roughly by a factor of three to fit the direction error data. As channel bandwidth increased beyond 55 deg it became increasingly difficult to fit the detection data from Group 5. In particular, the predicted curves relating percent correct detection to stimulus duration were

much shallower than the data obtained from the oldest subjects (see Fig. 3c).

In summary, the model adopted here provided a good quantitative account of the data obtained from observers ranging in age from 20 to 69 (Groups 1–4) using parameters derived from previous studies. However, those same parameters were not appropriate for modeling the results of the oldest subject group (Group 5). The differences between Groups 1–4 and Group 5 could be accounted for either by a substantial increase in additive internal noise, or by a combination of an increase in channel bandwidth and additive noise. Notably, an increase in channel bandwidth alone was not sufficient to explain the age-related change in motion perception. For both younger and older subjects, higher levels of internal noise were required to model the direction error data than the detection data. However, the difference in noise that was needed to model the detection and identification data was much greater in older subjects than in younger subjects.

4. Discussion

Our results reveal several previously unknown effects of aging upon motion perception. For example, compared to younger subjects, older subjects are less able to discriminate coherent global flow from random noise, and are also less accurate in identifying the direction of global flow. Moreover, we did not find evidence that these effects of aging emerge gradually across the lifespan. Instead, the age-related changes were apparent only in the oldest subjects that we tested (i.e., 70–81 years of age). Oldest observers viewing stimuli at the longer durations could perform similarly to younger observers viewing stimuli at shortest durations, but the older observers required considerably more time. Additionally, more time appeared to be required to obtain similar levels of performance for the direction identification task than for the motion detection task (see Figs. 1a and b). These effects of stimulus duration are qualitatively similar to the findings of Raghuram, Lakshminarayanan, and Khanna (2005), who reported that age differences in speed discrimination diminish as stimulus duration is increased from 500 ms to 1 s.

Overall, age-related changes in motion perception appeared to be much greater for direction identification than for coherent motion detection. Importantly, our statistical analyses demonstrate that age differences in direction errors persist even when differences in sensitivity to motion are taken into account. Furthermore, the oldest subjects exhibited greater direction errors even on trials on which they correctly responded with 100% confidence that they detected motion. Our results are consistent with previous findings that subjects can detect global flow despite being unable to render accurate judgments of the direction of motion (Ball et al., 1983; Sekuler et al., 1996), but this divergence between measures is even more dramatic in subjects over 70 years of age. The results of our control experiment show that such errors cannot be attributed to age-related changes in the ability to make accurate motor responses or to memory effects related to age-related increases in response time. Instead, the age-related effects for motion detection and identification seem to reveal changes in the fundamental mechanisms underlying motion perception.

Random dot cinematograms can elicit eye movements even when the motion signal is near threshold (Kosnik, Fikre, & Sekuler, 1985; Watamaniuk & Heinen, 1999). If these eye movements affect psychophysical judgments in our task, and if such movements differed in younger and older subjects, then the current results might reflect age differences in eye movements rather than motion perception per se. Several lines of evidence argue against this hypothesis. First, although studies have shown that latency of saccades (Munoz, Broughton, Goldring, & Armstrong, 1998) and smooth pursuit (Knox, Davidson, & Anderson, 2005) increases with age, the evidence that accuracy of eye movements declines with age is mixed. For example, some studies (e.g., Sharpe & Zackon, 1987) report that the accuracy

of saccades, as indexed by the ratio of the amplitude of a saccade and the target's eccentricity, declines with age whereas other studies (e.g., Munoz et al. 1987; Yang & Kapula, 2006) find no effect of age. Also, although the gain of smooth pursuit eye movements is lower in older than younger subjects, the age difference is small (i.e., less than 10%) for target speeds similar to the one used in the current experiment (Sharpe & Sylvester, 1978). Second, previous studies have shown that directional judgments by younger observers about random dot cinematograms are not related to eye movements. For example, Kosnik et al. (1985) found that improvements in direction discrimination that occur with practice were not accompanied by changes in eye movements, and Watamaniuk and Heinen (1999) reported that psychophysical direction discrimination thresholds for random dot cinematograms were 2–3 lower than thresholds estimated from the direction of smooth pursuit eye movements. Both findings are inconsistent with the idea that, in our study, younger observers somehow were able to use directional eye movements to improve sensitivity to motion or to encode direction more accurately. Hence, there is no compelling evidence that the accuracy of eye movements differ significantly across age, or that eye movements contribute significantly to psychophysical judgments of the direction of global flow in the near-threshold conditions of the current experiments. Therefore, we tentatively suggest that the age differences observed in the current study are caused by age differences in motion perception, rather than differences in eye movements.

In the context of our model, which previously has been used successfully to account for younger subjects' performance in several studies (Sekuler et al., 1996; Watamaniuk, 1993; Williams et al., 1991), we were not able to account for the age-related declines in motion perception by simply increasing the bandwidth of directionally tuned mechanisms. However, it was possible to account for the age differences in motion detection by assuming that either (1) older subjects have much greater additive internal noise, or (2) older subjects have increased channel bandwidth paired with increased internal noise. These modeling results are consistent with recent neurophysiological studies that have found weaker directional selectivity and higher spontaneous activity in primary visual cortical neurons in senescent monkeys (Schmolesky et al., 2000; Wang, Zhou, Ma, & Leventhal, 2005) and cats (Hua et al., 2006).

Interestingly, we were not able to simultaneously account for age-related changes in the pattern of motion detection and direction identification with a single set of model parameters. Specifically, a higher level of additive internal noise was needed to fit the direction identification errors. This failure to account simultaneously for both sets of data suggests the detection and identification judgments are constrained by distinct mechanisms, as suggested by Ball et al. (1983). Additional support for this idea comes from a recent study by Vaina, Cowey, Jakab, and Kikinis (2005), in which patients with damage to different extrastriate motion processing areas revealed considerably different

patterns of performance on a range of motion processing tasks (including some linked more closely to motion detection, and others to direction discrimination). Our results are consistent with the idea that aging exerts different effects on the various parts of the brain that contribute to motion perception. The conditions under which one sees larger effects of aging may be linked to the complexity of the stimulus and/or task (Faubert, 2002), an idea consistent with the notion that functional reorganization of the aged brain (Bennett et al., 2001; Della-Maggiore et al., 2000; McIntosh et al., 1999) provides only limited compensation for age-related declines in neural processing.

We think it is especially noteworthy that our modeling identified variation in noise as a key source of the age-related changes seen in both dependent measures: sensitivity and accuracy of direction perception. For more than two decades, the literature on aging has included reports in which age-related changes in cognitive function have been attributed to older adults' relatively higher levels of neural noise (for example, Welford, 1984). However, such conjectures have rarely been quantified. Such an approach is now possible, as researchers and modelers have developed powerful computational methods for testing detailed descriptions of noise's role in cognitive functions, distinguishing between different sources of noise, such as internal vs. external noise, and different forms of noise, such as multiplicative vs. additive noise (e.g., Bennett, Sekuler, & Ozin, 1999; Gold, Bennett, & Sekuler, 1999). The application of such techniques to results from adults across the lifespan could provide extremely useful information about the nature and extent of variations in neural noise as a function of age.

Acknowledgments

We thank the subjects who patiently participated in this study, and Carol Dengis for collecting the data reported here. The work was supported by CIHR Grant 38059; NIH Grant MH068404; and the Canada Research Chair Program (ABS & PJB). Address correspondence to Dr. P. J. Bennett or Dr. A. B. Sekuler, Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton, ON, Canada L8S 4K1.

References

- Anderson, G. J., & Atchley, P. (1995). Age-related differences in the detection of three-dimensional surfaces from optic flow. *Psychology and Aging, 10*, 650–658.
- Ball, K., & Sekuler, R. (1986). Improving visual perception in older observers. *Journal of Gerontology, 41*, 176–182.
- Ball, K., Sekuler, R., & Machamer, J. (1983). Detection and identification of moving targets. *Vision Research, 23*, 229–238.
- Bennett, P. J., Sekuler, A. B., McIntosh, A. R., & Della-Maggiore, V. (2001). The effects of aging on visual memory: evidence for functional reorganization of cortical networks. *Acta Psychologica (Amsterdam), 107*, 249–273.
- Bennett, P. J., Sekuler, A. B., & Ozin, L. (1999). Effects of aging on calculation efficiency and equivalent noise. *Journal of the Optical Society of America A, 16*, 654–668.
- Blake, R., Sekuler, R., & Grossman, E. (2003). Motion processing in human visual cortex. In J. H. Kaas & C. E. Collins (Eds.), *The primate visual system*. Boca Raton: CRC Press.
- Britten, K. H., Shadlen, M. N., Newsome, W. T., & Movshon, J. A. (1992). The analysis of visual motion: a comparison on neuronal and psychophysical performance. *Journal of Neuroscience, 12*, 4745–4765.
- Della-Maggiore, V., Sekuler, A. B., Grady, C. L., Bennett, P. J., Sekuler, R., & McIntosh, A. R. (2000). Corticolimbic interactions associated with performance on a short-term memory task are modified by age. *Journal of Neuroscience, 20*, 8410–8416.
- Faubert, J. (2002). Visual perception and aging. *Canadian Journal of Experimental Psychology, 56*, 164–176.
- Gilmore, G. C., Wenk, H. E., Naylor, L. A., & Stuve, T. A. (1992). Motion perception and aging. *Psychology and Aging, 7*, 654–660.
- Gold, J., Bennett, P. J., & Sekuler, A. B. (1999). Signal but not noise changes with perceptual learning. *Nature, 402*, 176–178.
- Hua, T., Li, X., He, L., Zhou, Y., Wang, Y., & Leventhal, A. G. (2006). Functional degradation of visual cortical cells in old cats. *Neurobiology of Aging, 27*, 155–162.
- Ketcham, C. J., & Stelmach, G. E. (2004). Movement control in the older adult. In R. W. Pew & S. B. van Hemel (Eds.), *Technology for adaptive aging*. Washington, DC: The National Academies Press.
- Kirk, R. E. (1968). *Experimental design: Procedures for the behavioral sciences*. Belmont, CA: Brooks/Cole Publishing Company.
- Kosnik, W., Fikre, J., & Sekuler, R. (1985). Improvement in direction discrimination: no role for eye movements. *Perception and Psychophysics, 38*, 554–558.
- Kosnik, W., Winslow, L., Kline, D., Rasinski, K., & Sekuler, R. (1988). Visual changes in daily life throughout adulthood. *Journals of Gerontology, 43*, P63–P70.
- Knox, P. C., Davidson, J. H., & Anderson, D. (2005). Age-related changes in smooth pursuit initiation. *Experimental Brain Research, 165*, 1–7.
- Leventhal, A. G., Wang, Y., Pu, M., Zhou, Y., & Ma, Y. (2003). GABA and its agonists improved visual cortical function in senescent monkeys. *Science, 300*, 812–815.
- McIntosh, A. R., Sekuler, A. B., Penpeci, C., Rajah, M. N., Grady, C. L., Sekuler, R., et al. (1999). Recruitment of unique neural systems to support visual memory in normal aging. *Current Biology, 7*, 523–528.
- Magnussen, S. (2000). Low-level memory processes in vision. *Trends in Neuroscience, 23*, 247–251.
- Munoz, D. P., Broughton, J. R., Goldring, J. E., & Armstrong, I. T. (1998). Age-related performance of human subjects on saccadic eye movement tasks. *Experimental Brain Research, 121*, 391–400.
- Nachmias, J., & Steinman, R. M. (1963). Study of absolute visual detection by the rating-scale method. *Journal of the Optical Society of America, 53*, 1206–1213.
- Norman, J. F., Clayton, A. M., Shular, C. F., & Thompson, S. R. (2004). Aging and the perception of depth and 3-D shape from motion parallax. *Psychology and Aging, 19*, 506–514.
- Norman, J. F., Dawson, T. E., & Butler, A. K. (2000). The effects of age upon the perception of depth and 3-D shape from differential motion and binocular disparity. *Perception, 29*, 1335–1359.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. (2004). nlme: Linear and nonlinear mixed effects models. R package version 3.1-53.
- Porciatti, V., Fieorentini, A., Morrone, M. C., & Burr, D. C. (1999). The effects of ageing on reaction times to motion onset. *Vision Research, 39*, 2157–2164.
- R Development Core Team (2004). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>.
- Raghuram, A., Lakshminarayanan, V., & Khanna, R. (2005). Psychophysical estimation of speed discrimination. II. Aging effects. *Journal of the Optical Society of America A, 22*, 2269–2280.
- Salthouse, T. A. (1982). *Adult cognition: An experimental psychology of human aging*. New York: Springer-Verlag.
- Schmoleksy, M. T., Wang, Y., Pu, M., & Leventhal, A. G. (2000). Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. *Nature Neuroscience, 3*, 384–390.

- Sekuler, A. B., Sekuler, R., & Penpeci, C. (1996). Perceived direction of motion vs detection of global flow in random dot cinematograms. *Investigative Ophthalmology and Visual Science*, (Suppl.), 37, S515.
- Sekuler, R., Kahana, M. J., McLaughlin, C., Golomb, J., & Wingfield, A. (2005). Preservation of episodic visual memory in aging. *Experimental Aging Research*, 31, 1–13.
- Sekuler, R., & Sekuler, A. B. (2000). Visual perception and cognition. In J. G. Evans, T. F. Williams, B. L. Beattie, J. P. Michel, & G. K. Wilcock (Eds.), *Oxford textbook of geriatric medicine* (pp. 874–880). New York: Oxford University Press.
- Sharpe, J. A., & Sylvester, T. O. (1978). Effect of aging on horizontal smooth pursuit. *Investigative Ophthalmology and Visual Science*, 17, 465–468.
- Sharpe, J. A., & Zackon, D. H. (1987). Senescent saccades. Effects of aging on their accuracy, latency and velocity. *Acta Oto-Laryngologica*, 105, 422–428.
- Snowden, R. J., & Kavanagh, E. (2006). Motion perception in the ageing visual system: minimum motion, motion coherence, and speed discrimination thresholds. *Perception*, 35, 9–24.
- 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.
- Trick, G. L., & Silverman, S. E. (1991). Visual sensitivity to motion: age-related changes and deficits in senile dementia of the Alzheimer type. *Neurology*, 41, 1437–1440.
- Vaina, L. M., Cowey, A., Jakab, M., & Kikinis, R. (2005). Deficits of motion integration and segregation in patients with unilateral extrastriate lesions. *Brain*, 128, 2134–2145.
- Wang, Y., Zhou, Y., Ma, Y., & Leventhal, A. G. (2005). Degradation of signal timing in cortical areas V1 and V2 of senescent monkeys. *Cerebral Cortex*, 15(4), 403–408.
- Warren, W. H., Jr., Blackwell, A. W., & Morris, M. W. (1989). Age differences in perceiving the direction of self-motion from optical flow. *Journal of Gerontology: Psychological Sciences*, 44, 147–153.
- Watamaniuk, S. N. J. (1993). Ideal observer for discrimination of the global direction of dynamic random-dot stimuli. *Journal of the Optical Society of America A*, 10, 16–28.
- Watamaniuk, S. N. J., & Heinen, S. J. (1999). Human smooth pursuit direction discrimination. *Vision Research*, 39, 59–70.
- Watamaniuk, S. N. J., & Sekuler, R. (1992). Temporal and spatial integration in dynamic random-dot stimuli. *Vision Research*, 32, 2341–2347.
- Watamaniuk, S. N. J., Sekuler, R., & Williams, D. W. (1989). Direction perception in complex dynamic displays: the integration of direction information. *Vision Research*, 29, 47–59.
- Welford, A. T. (1984). Between bodily changes and performance: some possible reasons for slowing with age. *Experimental Aging Research*, 102, 73–88.
- Williams, D. W., & Sekuler, R. (1984). Coherent global motion percepts from stochastic local motions. *Vision Research*, 24, 55–62.
- Williams, D. W., Tweten, S. D., & Sekuler, R. (1991). Using metamers to explore motion perception. *Vision Research*, 31, 275–286.
- Wist, E. R., Schrauf, M., & Ehrenstein, W. H. (2000). Dynamic vision based on motion-contrast: changes with age in adults. *Experimental Brain Research*, 134, 295–300.
- Yang, Q., & Kapula, Z. (2006). Aging does not affect the accuracy of vertical saccades nor the quality of binocular coordination. A study of special elderly group. *Neurobiology of Aging*, doi:10.1016/j.neurobiolaging.2006.11.007.