Reduction in Direction Discrimination With Age and Slow Speed Is Due to Both Increased Internal Noise and Reduced Sampling Efficiency

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PURPOSE. Sensitivity to moving structure decreases with age and slow speeds may be selectively impaired. This loss could be caused by elevated internal noise in the responses of motion sensors or a reduction in the efficiency with which motion responses are integrated. We adapt an equivalent noise paradigm to analyze the perception of slow and fast speed motion as a function of normal aging.

METHODS. A total of 70 observers (20–89 years) identified the direction of global motion in a two-alternative forced choice task. In a central 8° aperture, 100 dots of 10% Michelson contrast were moving at 1.6 or 5.5°/s. The direction of each dot was drawn from a Gaussian distribution whose mean and SD were adaptively changed. Internal noise and sampling efficiency were estimated from direction discrimination thresholds as a function of external direction noise, speed, and age.

RESULTS. Direction sensitivity was significantly worse for slow speeds at all ages (paired *t*-test, $P < 0.05$) and decreased approximately 2% per year (linear regressions, $P < 0.01$). This aging deficit was due to significant changes in internal noise (5.5°/s) and sampling efficiency (1.6°/s) (linear regression, $P < 0.05$).

CONCLUSIONS. There is motion sensitivity loss with age that arises from an increase in internal noise in the responses of directional sensors and a decrease in responses that contribute to the global decision. Differences in the rates of progression at each speed indicate that motion is processed by independent systems tuned to different speeds, and that the channel for slow speed may be more vulnerable to normal age-related changes.

Keywords: direction discrimination, aging, internal noise, sampling efficiency

Generally, motion detection and discrimination deteriorate in healthy aging, depending on the level of contrast, speed, task, and type of stimuli.^{1–8} As our population ages, further understanding of the changes in the aging visual system is important, since impaired motion sensitivity is associated with age-related diseases including glaucoma⁸ and Alzheimer's disease,⁶ increases the risk of falling, and can result in serious injury in the elderly.^{9,10}

Safe navigation and mobility requires accurate perception of the relative movement between oneself and other objects in the environment. The visual system performs this task based on the responses of retinotopic motion sensors in primary visual cortex that are selective for the speed and direction of movement within a relatively small area of the visual field.¹¹ To estimate the movements over more global areas therefore requires integration of local estimates across space and time. Area V5/MT is identified as an area closely involved in this global motion processing.^{12–14}

Several studies have investigated the effects of aging on motion perception,^{1,3,6} although the studies are inconclusive as to what extent aging affects motion sensitivity, or what the underlying cause is. The lowest signal-to-noise dot ratio (motion

coherence threshold) in random dot kinematograms is often used to examine how aging affects motion sensitivity.^{2–4,15–17} Some studies report that motion coherence thresholds are impaired in older observers,^{1,3,6} whereas others have found no difference with age,^{2,5,18} or that the difference is manifest only at low stimulus contrast,¹ or depends on speed. At moderate speeds (4–8°/s), several groups have found a deficit in motion coherence sensitivity in older observers,^{1,3,6} although others have found no difference with age^{2,5,18} or the difference may be manifest only at low stimulus contrasts.¹ Sensitivity deficits in older observers have been reported at high (>16°/s) speeds^{3,18} and low (<1°/s) speeds,² whereas other groups have found no change as a function of age.⁵ In principle, any loss of motion sensitivity could be caused by at least two classes of underlying deficits: there could be increased uncertainty about the direction of individual dots; or there could be a reduction in the proportion of dots that are processed. It is possible that these two processes could change at different rates with speed and aging or that deficits in one process could be offset by improvements in another with age. Motion coherence paradigms are not able to identify how or which of these two parameters are affected. In the present study, we used an

FIGURE 1. Illustration of a single frame of the stimulus used in the experiments. On each trial, the observer fixated a *central colored point* and indicated whether the overall motion of the *black* and *white dots* moved clockwise or counterclockwise relative to upward.

equivalent noise (EN) paradigm to provide a direct estimate of these two factors.^{19,20} The essential difference between the direction threshold stimulus we used in this study and the motion coherence stimuli used in other studies, is that in the EN stimulus, all dots were signal elements, and gave information about the total direction.¹⁹ Many studies investigating motion sensitivity with age have used contrast noise in their stimuli.^{8,21–23} Stimuli with low contrast can be a disadvantage when testing the elderly since any loss in motion sensitivity may be due to age-related reduction in contrast sensitivity^{24,25} rather than an explicit motion processing deficit. To avoid problems with visibility of the stimuli, we use dots whose contrast was well above detection threshold and to examine speed-dependent effects, we examine motion perception at low and high speeds.

METHODS

Observers

A total of 70 observers aged 20 to 89 years, participated in the study. Subjects were binned into seven different groups per decade: 20 to 29 years ($n = 11$), 30 to 39 years ($n = 14$), 40 to 49 years ($n = 11$), 50 to 59 years ($n = 10$), 60 to 69 years ($n = 9$), 70 to 79 years ($n = 8$), and 80 to 89 years ($n = 7$). Most of the observers were recruited from the general population of Mosjøen, Norway, whereas some were recruited from the Institute of Optometry and Visual Science in Kongsberg, Norway. All were tested by an optometrist (L-GB) and were enrolled if they had normal or corrected-to-normal visual acuity (defined as better than 0.8 Snellen VA), and normal visual health. To compensate for the lack of accommodation in older

observers, additional lenses to correct for the testing distance were prescribed. Observers were excluded if they had a spherical equivalence of more than ± 4.00 diopters (D). All observers had no previous experience of psychophysical tasks. They all signed an informed consent and the tenets of the Declaration of Helsinki were followed. The study had an ethical approval from the Regional Ethical Committee of Norway.

Apparatus and Stimuli

Stimuli were written in a numerical computing environment (MatLab, version R2010a; The MathWorks, Natick, MA), generated using a MacBook Pro laptop (Apple Inc., Cupertino, CA), and presented on a 15-inch glossy widescreen liquid crystal display (refresh rate 75 Hz) with a mean luminance of 91 cd/m². The stimulus was presented in a circular aperture with a diameter of 5.8° and contained 100 black and white circular dots (Fig. 1); the dot diameter was 6 pixels (0.14°). The dot contrast (expressed as Michelson contrast) was 10%. Each dot had a limited lifetime of three frames to prevent observers tracking individual dots and was initialized with a random age to prevent simultaneous expiry of all dots. At the end of their lifetime, the dots were randomly repositioned in the display aperture. The movie duration was 0.5 seconds. Two different speeds were tested: 1.6 and 5.5°/s.

Procedure

The observers viewed the stimulus binocularly at 57 cm in a dark room, where the monitor was the only light source. The monitor was calibrated before each day of testing (using a Spyder 3 Elite; available in the public domain at <http://www>.

FIGURE 2. Direction discrimination threshold as a function of speed and age. (A, B) Individual data for 1.6°/s and 5.5°/s, including the fitted regression lines. (C, D) Mean data for participants binned according to age in decades. Error bars: $\pm 95\%$ confidence intervals. *Indicates a statistically significant difference between the oldest age groups and the youngest age group (ANOVA, $P < 0.05$).

datacolor.com/contact-us/; Datacolor, Lawrenceville, NJ). The program controlling the experiment incorporated elements of the PsychToolbox.^{26,27} The stimuli were presented in a single interval two-alternative forced choice manner. First, observers completed two runs for speed 5.5°/s, then two runs at speed 1.6°/s. This test sequence was chosen because speed 5.5°/s was easier in the pilot, and previous studies have found this helpful. The observer's task was to maintain fixation of a central colored fixation point and to indicate whether the overall direction of motion of the dots was clockwise or counterclockwise relative to straight up. Responses were collected by pressing a keypad and feedback was provided by changing the color of the fixation point. Some of the oldest observers were unable to press the keypad and reported verbally to the examiner who pressed the keypad for them without viewing the screen.

Equivalent Noise Paradigm

To investigate the internal noise and reduced sampling efficiency for each observer, an equivalent noise (EN) paradigm¹⁹ was applied (Equation 1) to estimate internal noise σ_{int} and sampling efficiency N_{samp} for each observer. The EN paradigm exploits the additivity of the noise in the visual system and the stimuli, and performance is given by

$$\sigma_{obs} = \sqrt{\frac{\sigma_{int}^2 + \sigma_{ext}^2}{N_{samp}}}, \quad (1)$$

where σ_{obs} is the observed direction discrimination threshold, σ_{int} is internal noise (i.e., the direction uncertainty in the observer's visual system), σ_{ext} is external noise (i.e., the

variance of the direction distribution from which dot directions were drawn), and N_{samp} is the number of dots used by the observer to estimate the global direction of all dots. On this direction identification task, all dots are signal elements and performance improves with the precision of each dot's direction estimate and with the number of dots that can be integrated. At low levels of external directional noise, performance is limited by both internal noise and by pooling performance. At higher levels of external noise, the influence of local noise is relatively small compared with the high levels of noise in the stimulus; therefore, performance depends primarily on global extraction of information.¹⁹ Dakin and colleagues¹⁹ showed that the number of dots present in the EN stimuli limits both local noise and global sampling regardless of their density or size of field they occupy. A FAST²⁸ procedure was used to select the angular direction of motion and the SD of the direction distribution on each of 100 trials per test speed. This method selects the two test parameters (direction angle and SD) on each trial that maximizes information gain and provides significant increases in the efficiency of data collection.

Data Analysis

Linear regressions were used to investigate the effect of age for each speed separately and paired *t*-tests to compare individual performance for the two speeds. One-way ANOVA and post hoc Tukey tests were used to analyze differences between binned age groups. Statistical analysis was performed using a commercial analytical software program (SPSS 20.0.0; IBM Corp., New York, NY).

FIGURE 3. Internal noise as a function of speed and age for each observer. (A, B) Individual data for 1.6°/s and 5.5°/s, including the fitted regression lines. (C, D) Mean data for participants binned according to age in decades. Error bars: $\pm 95\%$ confidence intervals. *Indicates statistically significant difference between age groups ($P < 0.05$).

RESULTS

Figure 2 shows direction discrimination thresholds as a function of speed and age. Direction threshold is estimated from EN analysis as the angle required for correct direction detection on 75% trials when external direction variance is 0°. Figures 2A, 2B show the individual data for the two speeds. The slopes of the fitted regression lines indicate a progressive loss in direction sensitivity per year of 2.2% for speed 1.6°/s and 2.6% for speed 5.5°/s, respectively ($B_{1.6} = 0.2$, $t[68] = 3.7$, $P < 0.001$, $R^2 = 0.2$, $F_{1,68} = 13.56$, $P < 0.001$; $B_{5.5} = 0.11$, $t[68] = 3.9$, $P < 0.001$, $R^2 = 0.2$, $F_{1,68} = 15.91$, $P < 0.001$). There are large individual differences, but still a significant effect. It is also clear that direction discrimination thresholds were significantly higher at speed 1.6°/s than that at speed 5.5°/s for all observers (paired t -test: $t[69] = -6.8$, $P < 0.001$). Figure 2C shows data for speed 1.6°/s binned into decades. Direction discrimination thresholds were significantly higher for the oldest age group than the youngest age group (ANOVA, $F_{6,63} = 6.78$, $P < 0.01$; post hoc Tukey, $P < 0.01$). For speed 5.5°/s (Fig. 2D), the two oldest age groups were significantly worse than the youngest age group (ANOVA, $F_{6,63} = 3.48$, $P < 0.01$; post hoc Tukey, $P < 0.05$).

Estimated internal noise is shown in Figure 3 as a function of age for two speeds. Figures 3A, 3B show individual data for the two speeds with the fitted linear regression lines. It can be seen that internal noise increases gradually with age. For speed 5.5°/s (Fig. 3B), the increase is 2.3% per year ($B_{5.5} = 0.2$, $t[68] = 3.9$, $P < 0.001$, $R^2 = 0.2$, $F_{1,68} = 15.73$, $P < 0.001$). Figure 3D shows that the internal noise was significantly higher for the oldest age group than that for the youngest (ANOVA, $F_{6,3} = 3.140$, $P < 0.01$; post hoc Tukey, $P < 0.01$). Figure 3 also shows

that internal noise was significantly higher for all observers at speed 1.6°/s compared with speed 5.5°/s (paired t -test: $t[69] = -3.63$, $P < 0.01$). For speed 1.6°/s there was no significant difference with age (Figs. 3A, 3C), ($B_{1.6} = 0.05$, $t[68] = 1.4$, $P = 0.178$, $R^2 = 0.03$, $F_{1,68} = 1.85$, $P = 0.178$). (Without the two 89 year olds, there is an age-effect. Linear regression; $P < 0.05$.)

Figure 4 shows sampling efficiency as a function of age for 1.6°/s and 5.5°/s. Figures 4A, 4B show individual data for the two speeds with fitted linear regression lines. For speed 1.6°/s, there is a progressive loss in sampling efficiency of 1.0% per year ($B_{1.6} = -0.03$, $t[68] = -2.4$, $P < 0.05$, $R^2 = 0.07$, $F_{1,68} = 5.57$, $P < 0.05$). Figure 4C shows that the oldest age group is significantly lower than the youngest. A post hoc subject t -test between the youngest and the oldest age group was performed according to a Levenes's test of equal variance. Variances for these two groups were not equal and so we therefore used a corrected independent samples t -test, whereas equal variances were not assumed, this t -test revealed a significant difference ($t[16] = 2.769$, $P = 0.02$). A paired t -test showed that sampling efficiency was significantly lower at speeds, 1.6°/s compared with speed 5.5°/s (paired t -test: $t[69] = 4.59$, $P < 0.01$). For speed 5.5°/s there was no statistical difference with age ($B_{5.5} = -0.024$, $t[68] = -0.87$, $P = 0.38$, $R^2 = 0.01$, $F_{1,68} = 0.75$, $P = 0.38$).

DISCUSSION

The results show that the ability to discriminate the direction of motion gradually declines in normal aging. This is in agreement with other studies using random dots and gratings.^{1,2,4,18,29-31} In addition, all observers need a signifi-

FIGURE 4. Sampling efficiency as a function of speed and age for each observer. (A, B) Individual data for 1.6°/s and 5.5°/s, including the fitted regression lines. (C, D) Mean data for participants binned according to age in decades. Error bars: $\pm 95\%$ confidence intervals. *Indicates statistically significant difference between the oldest age group and the youngest ($P < 0.05$).

cantly larger angle to discriminate the direction when the dot stimuli were moving at speed 1.6°/s compared with speed 5.5°/s. This age-related sensitivity loss can be caused by judging the overall direction based on a smaller dot sample (reduced sampling efficiency), or with more noisy estimates in the direction of each dot (increased internal noise). However, previous studies were not able to separate these two limiting factors. In this study, we use an EN paradigm to separate the influences of internal noise and sampling efficiency, and show that the decline with age is due to increased levels of internal noise (speed 5.5°/s) and reduced sampling efficiency (speed 1.6°/s). The gradual decline that we report is in good agreement with other studies of global motion processing over a lifespan.^{3,6,32,33} Our results also show that at all ages, the increased direction discrimination threshold for speed 1.6°/s is due to both a lower sampling efficiency and increased internal noise.

We find that internal noise gradually increases with age. Although there is an age effect at both speeds, this failed to reach significance at speed 1.6°/s. An increase in internal noise suggests that older observers are more uncertain about the direction of individual dots. This result is consistent with Bennett and colleagues,⁴ who reported a similar loss in direction sensitivity for their older subject (>70 years). They fit their data with a multichannel direction model with either an increase in additive internal direction noise, or an increase in directional bandwidth for older observers. This explanation is further supported by electrophysiological recordings from primary visual cortex of rhesus monkeys, which show a loss of directional selectivity with age.^{4,30}

Age-related anterior eye changes such as increased light scatter by lens opacities, senile miosis, and pupil-based

reduced retinal luminance have been shown to have relatively little effect on the motion sensitivity decline such as motion coherence thresholds.^{7,34,35} Similarly, although unstable eyes can lead to a decrease in motion sensitivity,³⁶ fixation is approximately invariant of aging up to at least 70 years.³⁷ These findings indicate that neural degeneration in the visual pathway is an essential reason for the decline.^{8,38,39} Such neural effects may be mediated by reduced surround inhibition^{40,41} or suppression.^{40,42} This study shows that sampling efficiency is significantly lower for the older observers at speed 1.6°/s. This means that older observers effectively integrate fewer elements and, consequently, need a larger angle to discriminate the direction of motion at speed 1.6°/s. For the detection of static targets in noise, several authors have demonstrated that an age-related loss in contrast sensitivity was associated with a decrease in sampling efficiency.^{21,22} Allen and colleagues¹ argued that optical changes and loss in contrast sensitivity may be the leading factors to motion sensitivity loss. However, they were unable to investigate the factors of sampling efficiency since they measured motion coherence thresholds, which do not separate out sampling efficiency and internal noise. Ball and Sekuler³⁴ also found that motion perception was not affected by induced blur. In the present study, all observers were fully corrected for the test distance, had good visual acuity, and contrast sensitivity, so we are certain this is not the cause of reduced sampling efficiency.

Sampling efficiency describes how well the observer uses all the information that is given in the stimulus, and gives an indication as to how well the available stimulus information is received by the visual system.⁴³ The reduced sampling efficiency with age may be caused by retinal ganglion cell death, cell loss in the visual pathway, reduced/lack of attention,

or neural dysfunction.^{20,43} Other explanations of reduction of sampling efficiency may be a mismatch of template matching,^{21–23} or pooling additional noise over an inefficiently large receptive field.⁴⁴ Falkenberg and Bex⁸ found a decrease in sampling efficiency in an older control group and in a glaucoma group, and explained the decrease by age-related retinal ganglion cell loss across the retina. Impairments in motion processing efficiency may be due to neural cell loss, neurotransmitter changes, lipofuscin accumulation, and degeneration of myelin and cells.^{39,45,46}

Several studies suggest that multiple speed-tuned global-motion systems process motion at different speeds,^{16,47,48} and the present study also supports this finding. Almost all MT neurons are selective for a limited speed range.^{49,50} In single-unit electrophysiological recordings from primate brains, MT neurons gave optimal functional MRI responses for speeds between 4 and 16°/s,^{51,52} whereas the peak response was to 4–8°/s in studies of human brains.⁵³ It was suggested by Edwards and colleagues¹⁶ that global motion extraction depends on at least two independent speed-tuned systems, one tuned to slower speeds, 1.2°/s, and the other specializing for faster speeds, 4.8°/s. This is similar to the speed used in this study.

There was reduced performance at speed 1.6°/s for all observers: direction discrimination thresholds were elevated, and the effect was associated with increased internal noise and decreased sampling efficiency. This observation may be a result of the dot displacement size in the stimulus. The lifetime of each dot was fixed at three video frames, thus slower moving dots traveled a shorter overall distance than faster moving dots. This means that the direction vector has higher uncertainty in the slow compared with the moderate speed condition. Higher uncertainty of each dot's direction would cause an increase in internal noise, consistent with our results. To equate the direction vector, the duration of the slower moving dot would have to increase, and that is known to affect motion sensitivity.⁵⁴

In conclusion, motion sensitivity decreases by approximately 2% per year in normal ageing. This progressive loss arises from a gradual increase in the levels of internal noise in the responses of directional sensors, causing older observers to be more uncertain of the direction of each element. In addition, the reduction in sampling efficiency suggests that observers use fewer samples as they get older and there is a gradual decrease in the number of responses that contribute to the global decision. Differences in the rates of progression at each speed indicate motion is processed by at least two independent systems tuned to different speeds. This suggests that the channel for slow speed is the most vulnerable to optical and neural age changes. Our findings also suggest that speed-tuning changes with age and optimal sensitivity becomes restricted to a much narrower range of speeds in the aging visual system.

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