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# The effects of aging on orientation discrimination

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## Abstract

The current experiments measured orientation discrimination thresholds in younger (mean age ≈ 23 years) and older (mean age ≈ 66 years) subjects. In Experiment 1, the contrast needed to discriminate Gabor patterns (0.75, 1.5, and 3 c/deg) that differed in orientation by 12 deg was measured for different levels of external noise. At all three spatial frequencies, discrimination thresholds were significantly higher in older than younger subjects when external noise was low, but not when external noise was high. In Experiment 2, discrimination thresholds were measured as a function of stimulus contrast by varying orientation while contrast was fixed. The resulting threshold-vs-contrast curves had very similar shapes in the two age groups, although the curve obtained from older subjects was shifted to slightly higher contrasts. At contrasts greater than 0.05, thresholds in both older and younger subjects were approximately constant at 0.5 deg. The results from Experiments 1 and 2 suggest that age differences in orientation discrimination are due solely to differences in equivalent input noise. Using the same methods as Experiment 1, Experiment 3 measured thresholds in 6 younger observers as a function of external noise and retinal illuminance. Although reducing retinal illumination increased equivalent input noise, the effect was much smaller than the age difference found in Experiment 1. Therefore, it is unlikely that differences in orientation discrimination were due solely to differences in retinal illumination. Our findings are consistent with recent physiological experiments that have found elevated spontaneous activity and reduced orientation tuning on visual cortical neurons in senescent cats (Hua, T., Li, X., He, L., Zhou, Y., Wang, Y., Leventhal, A. G. (206). Functional degradation of visual cortical cells in old cats. *Neurobiology Aging, 27*(1), 155–162) and monkeys (Yu, S., Wang, Y., Li, X., Zhou, Y. & Leventhal, A. G. (2006). Functional degradation of visual cortex in senescent rhesus monkeys. *Neuroscience, 140*(3), 1023–1029; 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* (5620), 812–815).


*Keywords:* Aging; Orientation discrimination; Equivalent noise; Internal noise; Efficiency

## 1. Introduction

Many aspects of visual perception, including spatial and temporal contrast sensitivity, colour perception, symmetry perception, binocular vision, motion discrimination, and figure-ground segregation, decline with age (Faubert, 2002; Sekuler & Sekuler, 2000; Spear, 1993; Yu, Wang, Li, Zhou, & Leventhal, 2006). Some of the effects of age may be attributed to changes in the optical quality of the eye (Nguyen-Tri, Overbury, & Faubert, 2003; Shahidi & Yang, 2004; Weale, 1961; Weale, 1963; Weale, 1992; Winn, Whitaker, Elliott, & Phillips, 1994), but optical factors alone cannot account for all of the changes in vision that occur in old age (Ball & Sekuler, 1986; Bennett, Sekuler, & Ozin, 1999; Herbert, Overbury, Singh, & Faubert, 2002; Sekuler, Bennett, & Mamelak, 2000; Sekuler & Ball, 1986). Therefore, impaired visual performance in elderly human observers must be due, at least in part, to changes in the characteristics of visual neurons. Recent physiological findings are consistent with this idea: cortical visual cells in senescent monkeys (Leventhal, Wang, Pu, Zhou, & Ma, 2003; Yu et al., 2006) and cats (Hua et al., 2006) are less directionally selective, have higher rates of spontaneous

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activity, and have significantly broader orientation tuning than cortical cells in younger animals. Psychophysical evidence suggests that, at least in some conditions, motion perception is impaired in older human observers in a manner that is consistent with the physiological findings (Bennett, Sekuler, & Sekuler, 2007). In addition, Habak and Faubert (2000) found that age-related changes in grating detection thresholds were larger for second-order than first-order patterns, a result that is consistent with reports that the effects of aging are greater in extrastriate cortical visual areas (Yu et al., 2006). However, we know of no published findings on the effects of aging on the visual perception of orientation. The current paper therefore measured orientation discrimination thresholds in younger and older observers.

## 2. Experiment 1

In several experiments, we measured the amount of contrast needed to discriminate two Gabor patterns that differed slightly in orientation. The experiments used similar methods and analyses, and so they are presented here as three versions of Experiment 1.

Gabor patterns were embedded in static, two-dimensional visual noise. Many studies have demonstrated that thresholds for targets embedded in white noise follow the form

$$E = k(N + N_{eq}), \quad (1)$$

where $E$ is contrast energy, $N$ is the spectral density of the external noise, and $k$ and $N_{eq}$ are free parameters (Barlow, 1977; Kersten, Hess, & Plant, 1988; Legge, Kersten, & Burgess, 1987; Pelli, 1990). $N_{eq}$, the equivalent input noise, is defined as the spectral density of an external noise that raises threshold by a factor of two relative to a zero noise baseline. The parameter $k$ is a measure of the effective signal-to-noise ratio at threshold (Pelli & Farell, 1999), and is inversely related to indices of processing efficiency that have been referred to in the literature as sampling efficiency, calculation efficiency, and high-noise efficiency (Bennett et al., 1999; Gold, Sekuler, & Bennett, 2004; Legge et al., 1987; Pelli, 1990; Pelli & Farell, 1999). On logarithmic axes Eq. (1) defines a curvilinear relation between $E$ and $N$ in which $E$ is approximately constant at levels of external noise less than $N_{eq}$ and increases linearly with a slope of one at noises greater than $N_{eq}$ (Fig. 1, Observer A). $N_{eq}$ is therefore represented as the knee of the threshold-versus-noise function. Variations in $N_{eq}$ cause the knee of the threshold-versus-noise curve to shift along the abscissa but do not change the vertical position thresholds in high-noise conditions (Fig. 1, Observer B). Variations in $k$ cause the entire threshold-versus-noise curve to shift vertically (Fig. 1, Observer C).

The values of $N_{eq}$ and $k$ generally are thought to reflect the influence of different mechanisms on visual performance. For example, the effects of cataracts and corneal scarring on contrast sensitivity manifest themselves as increases in $N_{eq}$, whereas the effects of macular degeneration and optic neuritis manifest themselves as increases in $k$ (Kersten et al., 1988). Previous studies have shown that reduced contrast sensitivity in older observers for spatial frequencies of 1-6 c/deg is due to an increase in $k$ (i.e., reduced high-noise efficiency) rather than increased equivalent input noise (Bennett et al., 1999; Pardhan, Gilchrist, Elliott, & Beh, 1996). The main goal of Experiment 1 was to determine if there are age-related differences in orientation discrimination and, if such difference do exist, whether they are due to differences in $k$, $N_{eq}$, or both factors.

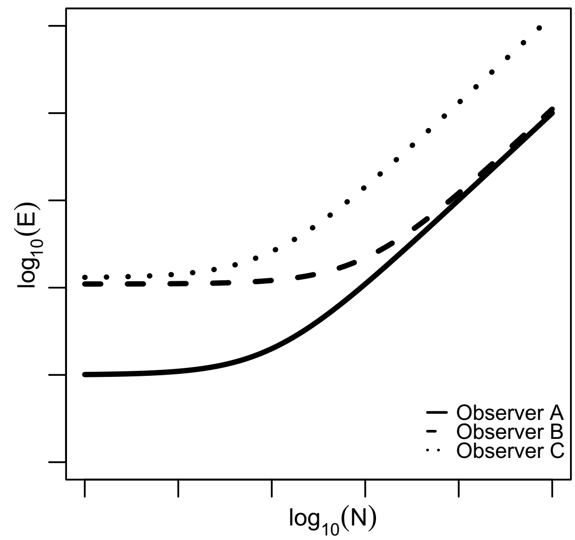


Fig. 1. Contrast energy thresholds are shown as a function of the amount of external noise for three hypothetical observers that differ in equivalent input noise ($N_{eq}$) and effective signal-to-noise ratio ($k$) (see Eq. (1)). Of the three hypothetical observers, A has the lowest values of $N_{eq}$ and $k$. Observer B has a higher value of $N_{eq}$ than Observer A, but the same value of $k$. Observer C has the same value of $N_{eq}$ as Observer A, but a higher value of $k$.

### 2.1. General methods

#### 2.1.1. Subjects

Community-dwelling adults 60 years of age and older were recruited from the Greater Hamilton Area through newspaper advertisements. Younger adults were recruited through the McMaster University participant pools. All subjects completed visual and general health questionnaires to screen for visual pathology, such as cataract, macular degeneration, amblyopia, etc. Prior to participation in the study, near and far decimal logMAR (logarithm of the minimum angle of resolution) acuities were measured for all subjects with CSV-1000EDTRS eye charts (Precision Vision, LaSalle, Illinois, USA). When measuring visual acuity, subjects wore their normal optical correction for each distance. We also measured visual acuity at the experimental viewing distance of 114 cm for subjects in Experiments 1b and 1c and found that it did not differ significantly from the near and far visual acuities. Older subjects completed the Mini-Mental State Examination, or MMSE (Folstein, Folstein, & McHugh, 1975; Folstein, Robins, & Helzer, 1983), to screen for age-related dementia. All of the older subjects included in the data analyses obtained MMSE scores equal to or greater than the normal lower quartile score for their individual age groups (Crum, Anthony, Bassett, & Folstein, 1993). The means and standard deviations of age, near and far acuities, and MMSE scores, for subjects who were included in the analyses are presented in Table 1. Separate groups of subjects participated in Experiments 1a, 1b, and 1c.

### *2.1.2. Apparatus*

Data were collected in two testing rooms that were essentially identical except for a slight difference between the mean luminance of the two displays (i.e., 41 $cd/m^2$ vs. 50 $cd/m^2$). Stimuli were presented on calibrated 20″ (51 cm) Sony Trinitron monitors with $1024 \times 768$ pixel resolution (pixel area $= 3.6 \times 10^{-4}$ $deg^2$) and 85 Hz frame rate (noninterlaced). The monitor calibration data were used to build a 1779-element look-up table (Tyler, Chan, Liu, McBride, & Kontsevich, 1992). Customized computer software constructed the stimuli on each trial by selecting the appropriate luminance values from the calibrated lookup table and storing them in the display's 8-bit lookup table. This procedure enabled us to manipulate contrast with high resolution: for example, pixel contrast could be varied from −0.2 to 0.2 in steps of 0.002.

The stimuli were generated and presented with a Macintosh G4 processor in the Matlab environment (v. 5.2) using the Psychophysics and Video Toolboxes (Brainard, 1997; Pelli, 1997). At the viewing distance of 114 cm, the display subtended approximately $18.3 \times 14.0$ deg of visual angle. Head position and viewing distance were stabilized with a chin/forehead rest. Behavioural responses were recorded on a standard Macintosh keyboard. The monitor was the sole light source in the room during testing.

### *2.1.3. Stimuli*

The stimuli were Gaussian-damped sine wave gratings (i.e., Gabors). One standard deviation of the Gaussian envelope subtended 0.65 deg of visual angle. On each trial, the phase of the sine wave relative to the center of the Gaussian envelope was randomized in the range of ±180 deg. Stimulus orientation was either horizontal or counterclockwise 12 deg from horizontal. Finally, the Gabor was embedded within a circular patch (diameter = 4.9°) of static, two-dimensional Gaussian noise centered in the monitor. A new patch of noise was generated on every interval of every trial, and the contrast variance of the noise varied across conditions. The circular patch of noise was surrounded by a thin, high-contrast, black circle (contour width = 1 pixel) that appeared exactly at the edge of the noise. The circle served to reduce uncertainty about stimulus position in conditions when noise contrast was very low.

### *2.1.4. Procedure*

Thresholds were measured using a two-interval forced-choice (2-IFC) procedure. Each trial began with the presentation of a small, high-contrast fixation point ($5 \times 5$ pixels) displayed in the middle of the display. The fixation point randomly changed from white to dark gray across trials to minimize adaptation. After the participant pressed the space bar on a computer keyboard, two stimuli were presented for 100 ms in succession with a 750 ms inter-stimulus interval. Subjects indicated which of the two intervals contained the horizontal Gabor by pressing a key on the keyboard. Auditory feedback informed the participant about the accuracy of the response, and then the fixation re-appeared to signal the beginning of the next trial.

Gabor contrast was adjusted with four independent, interleaved staircases. Two staircases followed a 2-down, 1-up rule and converged on the 71% correct point of the psychometric function; the other two staircases followed a 4-down, 1-up rule and converged on the 84% correct point. The staircase step size started at 0.16 log contrast units and, after four reversals, was reduced to 0.04 log units. At the end of testing, the data from all four staircases were combined and a single psychometric function was estimated by computing the best-fitting (maximum likelihood criterion) Weibull function. Discrimination threshold was defined as the contrast necessary to attain 77% correct performance ($d' = 1.05$). On rare occasions, the staircases did not converge to stable values, and the resulting estimate of threshold fell outside the range of stimulus contrasts that

Table 1
Means and standard deviations of age, acuity, and MMSE measures for subjects included in analyses

| Experiment | Number of subjects | Age ($\mu,\sigma$) | Near logMAR acuity ($\mu/\sigma$) | Far logMAR acuity ($\mu/\sigma$) | MMSE ($\mu,\sigma$) |
|---|---|---|---|---|---|
| Experiment 1a(3 c/deg) | 18 | 22.21 (0.79) | −0.01 (−0.08) | −0.02 (0.09) | |
| | 17 | 66.43 (1.07) | 0.12 (0.12) | 0.04 (0.10) | 28.68 (1.94) |
| Experiment 1b(1.5 c/deg) | 15 | 21.67 (2.09) | −0.08(0.09) | −0.06(0.09) | |
| | 12 | 66.13 (5.73) | 0.11(0.16) | 0.04 (0.12) | 28.8(1.68) |
| Experiment 1c(0.75 c/deg) | 23 | 22.74 (2.3) | −0.12 (0.10) | −0.11 (0.08) | |
| | 16 | 68.45 (6.83) | 0.03 (0.08) | 0.01 (0.08) | 28.70 (1.55) |
| Experiment 2(Δ orientation) | 19 | 24.9 (6.92) | −0.09 (0.10) | −0.05 (0.12) | |
| | 11 | 64.92 (2.75) | 0.04 (0.15) | −0.02 (0.10) | 28.92 (1.62) |
| Experiment 3(low luminance) | 6 | 22.85 (3.58) | −0.14 (0.07) | −0.14 (0.08) | |

were actually presented to the subject. Such thresholds were excluded from the statistical analyses.

Trials were blocked according to noise level, with 200 (Experiment 1a) or 150 (Experiments 1b and 1c) trials per block.

#### 2.1.5. Data analyses

Contrast thresholds were converted into units of contrast energy, $E$, using the formula

$$E = \sigma_G^2 n A_p, \quad (2)$$

where ${\sigma_G}^2$ is the contrast variance of the Gabor at discrimination threshold, $n$ is the number of pixels in the stimulus, and $A_p$ is the pixel area in $deg^2$. Likewise, noise contrast variances, ${\sigma_N}^2$, were converted into noise spectral density ($N$), in $deg^2$:

$$N = \sigma_N^2 A_p. \quad (3)$$

Repeated-measures ANOVAs were conducted on the log-transformed contrast energy thresholds to assess differences between groups and across the different noise levels. When necessary, the Huynh–Feldt estimate of epsilon, $\tilde{\varepsilon}$, was used to adjust the degrees of freedom to control the Type I error rate for tests of within-subject variables (Kirk, 1995).

#### 2.1.6. Experiment 1a: methods

Twenty-three older and 20 younger subjects participated in the Experiment 1a. One older observer was excluded due to age-related macular degeneration, and two additional older observers were excluded due to recently diagnosed cataracts. Two younger observers and three additional older observers were excluded from Experiment 1a because the staircases did not converge to a stable threshold value after 200 trials in at least one condition. Consequently, data from 17 older and 18 younger subjects were included in the final analysis.

The spatial frequency of the Gabor was 3 c/deg. The noise power spectral densities were $2.03 \times 10^{-6}$ $deg^2$ and $3.25 \times 10^{-5}$ $deg^2$ in the low and high noise conditions, respectively. Trials were blocked by noise condition, and the order of conditions was counterbalanced across subjects. The two blocks of trials were then repeated, in the same order, and the two thresholds in each condition were averaged.

### 2.2. Experiment 1b: methods

Sixteen older and 16 younger subjects participated in Experiment 1b. One older subject previously underwent cataract surgery, and was excluded from the experiment. In at least one condition, the staircases did not converge on a stable estimate of threshold after 150 trials for one younger and two older subjects, and so those subjects were excluded from further analyses. An additional older participant did not to complete the experiment, which left a final total of 15 younger and 12 older subjects.

The spatial frequency of the Gabor was 1.5 c/deg. Stimuli were embedded in external Gaussian noise with spectral densities of $2.03 \times 10^{-8}$ $deg^2$ (low noise), $2.03 \times 10^{-6}$ $deg^2$ (medium noise), and $3.25 \times 10^{-5}$ $deg^2$ (high noise). Testing occurred over two consecutive days, at approximately the same time each day. On each day, trials were blocked according to noise level, and the order of conditions was randomized for each subject. The three blocks were then repeated, in the same order, for a total of six thresholds per subject per day. The two thresholds from each noise condition were averaged into a single threshold estimate. The order of noise levels on the second day was identical to that presented on the first day.

### 2.3. Experiment 1c: methods

Twenty-three older and 23 younger subjects participated in Experiment 1c. One older participant scored below the normal lower quartile on the MMSE (<26 points for people 60–64 years; Crum et al., 1993), and so was excluded from the study. Three older subjects reported that they had cataracts in the visual health questionnaire, and were therefore excluded from the study. Finally, three additional older subjects were unable to perform the task even at the maximum displayable stimulus contrast, and were therefore excluded from the data analysis. Thus, the final sample of older subjects had 16 individuals.

The stimuli and procedure were identical to those used in Experiment 1b with two exceptions: first, the spatial frequency of the Gabor was 0.75 c/deg, and second, subjects participated in only a single day of testing.

### 2.4. Results

Preliminary analyses found no difference between thresholds obtained in the two testing rooms. All subsequent analyses therefore were performed on the pooled data.

#### 2.4.1. Discrimination thresholds

Thresholds from all three experiments are plotted as functions of external noise in Fig. 2. Similar results were obtained in all experiments. Orientation discrimination thresholds increased with increasing levels of external noise. In addition, thresholds were significantly higher in older subjects when the level of external noise was low, but not when external noise was high. The results of repeated-measures ANOVAs conducted on the log-transformed thresholds were consistent with these observations. In Experiment 1a, which used 3 c/deg stimuli, both the main effect of Noise ($F(1,33) = 533.3$; $p < .0001$) and the Age × Noise interaction ($F(1,33) = 11.1$; $p = .0021$) were significant (Fig. 2a). In Experiment 1b, which used 1.5 c/deg stimuli, the main effects of noise ($F(1.6, 40.2) = 637.51$, $p < .0001$, $\tilde{\varepsilon} = 0.804$), Age ($F(1,25) = 5.37$, $p = 0.029$), and the age × noise interaction ($F(1.6, 40.2) = 14.90$, $p < .0001$, $\tilde{\varepsilon} = .804$) were significant (Fig. 2b).

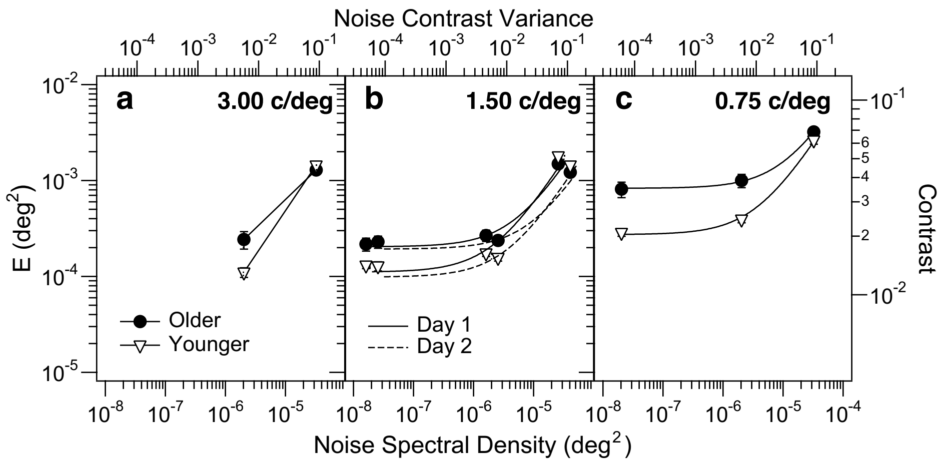


Fig. 2. Orientation discrimination thresholds, expressed as contrast energy ($E$), are shown as a function of external noise spectral density for (a) 3 c/deg stimuli (Experiment 1a), (b) 1.5 c/deg stimuli (Experiment 1b), and (c) 0.75 c/deg stimuli (Experiment 1c). Stimulus contrast and noise contrast variance are indicated by the right and top axes, respectively. Each symbol shows the average threshold; error bars represent ±1 standard error of the mean. The symbols representing thresholds on Days 1 and 2 have been displaced horizontally for clarity. Eq. (1) was used to create the smooth curves in panels b and c.

Finally, in Experiment 1c, which used 0.75 c/deg stimuli, the main effects of Noise ($F(1.8,67.1) = 535.30$, $p < .0001$, $\tilde{\varepsilon} = .907$) and age ($F(1,37) = 20.17$, $p < .0001$) and the Age × Noise interaction ($F(1.8,67.1) = 17.30$, $p < .0001$, $\tilde{\varepsilon} = .907$) were significant (Fig. 2c).

Careful inspection of Fig. 2b shows that, in Experiment 1b, thresholds in the medium and high noise conditions were slightly lower on Day 2 than on Day 1. These observations were verified in the ANOVA: the main effect of Day ($F(1,25) = 6.53$, $p = .017$) and the Day × Noise interaction ($F(1.94,48.47) = 4.81$, $p = .013$, $\tilde{\varepsilon} = .969$) were significant. A Day × Noise polynomial contrast revealed a strong linear component ($F(1,25) = 7.27$, $p = .012$), indicating that the effects of practice increased with increasing levels of external noise. Importantly, the effects of Day did not interact with age, so the effects of practice were similar in both age groups.

#### 2.4.2. Equivalent input noise & effective signal-to-noise ratio

Eq. (1) was fit to the log-transformed data. To simplify the curve fitting, the two thresholds measured at each level of external noise were averaged to yield a single value. The levels of external noise used in Experiment 1a were not low enough to provide stable estimates of $N_{eq}$. Therefore, Eq. ((1)) was used to estimate $N_{eq}$ and $k$ only from Experiments 1b and 1c.

Threshold-vs.-noise functions measured in Experiment 1b were well fit by Eq. (1), with $r^2$ ranging from 0.84 to 0.99. Equivalent input noise was higher in older than younger subjects on both days of testing: the mean difference was 0.34 log units (95% confidence interval = (0.12, 0.54)) on day one and 0.37 log units (95% confidence interval = (0.15, 0.58)) on day two (Fig. 3). An ANOVA on the log-transformed $N_{eq}$ measures revealed significant main effects of Age ($F(1,25) = 16.13$, $p = .0005$) and Day ($F(1,25) = 6.40$, $p = .018$), but the Age × Day interaction ($F(1,25) = .26$, $p = 0.616$) was not significant. The main effect of Day reflects the fact that the average $N_{eq}$ was higher on Day 1 than Day 2 by 0.11 and 0.07 log units in older and younger subjects, respectively. This result might seem to indicate that practice resulted in higher thresholds, but the increase in equivalent noise across days was counteracted by a decrease in the effective signal-to-noise ratio at threshold ($k$). Values of $k$ tended to be lower in older than younger subjects on both days of testing: the mean difference was −0.12 log units (95% confidence interval = (−0.24, 0.006)) on day one and −0.12 log units (95% confidence interval = (−0.24, −0.003)) on day two (Fig. 4). Furthermore, $k$ was 0.09 log units lower on day two than day one in both age groups. An ANOVA on the log-transformed $k$ values revealed significant main effects of age ($F(1,25) = 7.03$, $p = .014$) and Day ($F(1,25) = 13.41$, $p = .0012$), but the Age × Day interaction ($F(1,25) = 0.01$, $p = .92$) was not significant. In summary, $N_{eq}$ was higher in older than younger subjects.The effective signal-to-noise ratio at threshold, $k$, was lower in older subjects, which is equivalent to saying that older subjects exhibited *higher* high-noise efficiency than younger subjects (Pelli & Farell, 1999). These age differences did not vary significantly across days of testing. Finally, practice increased equivalent input noise and reduced the effective signal-to-noise ratio at threshold by similar amounts in both age groups.

Threshold-vs.-noise functions measured in Experiment 1c also were well fit by Eq. (1), with $r^2$ ranging from 0.85 to 0.99. Equivalent input noise was 0.39 log units higher in older than younger subjects (95% confidence interval = (0.19, 0.58); see Fig. 3). A two-sample $t$-test on the log-transformed $N_{eq}$ measures found a significant difference across groups ($t = -4.21$, $df = 20.09$, $p = .0004$). The distributions of $k$ were very similar in the two age groups (Fig. 4): The mean difference between groups was only 0.02 log units (95% confidence interval = (−0.13, 0.17)), and a $t$-test on the log-transformed data did not yield a

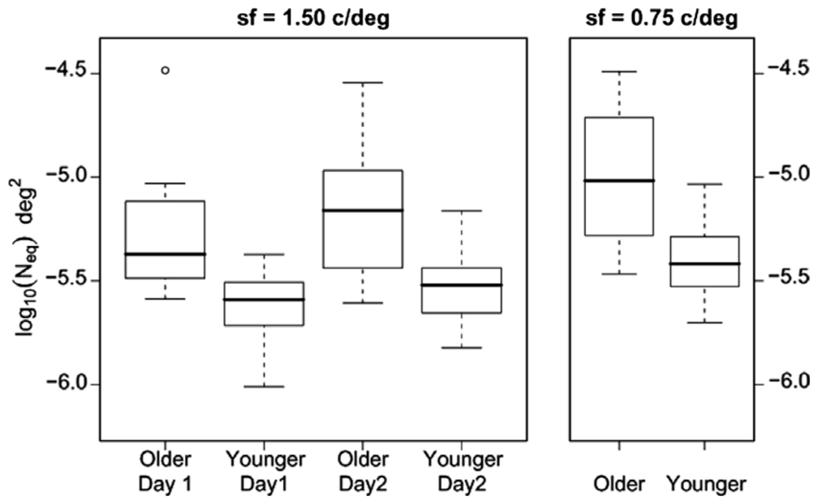


Fig. 3. Boxplots showing the distributions of equivalent input noise ($N_{eq}$) for older and younger subjects measured with a spatial frequency of 1.5 (Experiment 1b) and 0.75 (Experiment 1c). The lower and upper limbs of each box approximate the first and third quartiles, respectively; the horizontal line is the median. The whiskers extend to the farthest data points that are within ±1.5 times the inter-quartile range from the median. The unfilled circle represents an outlier.

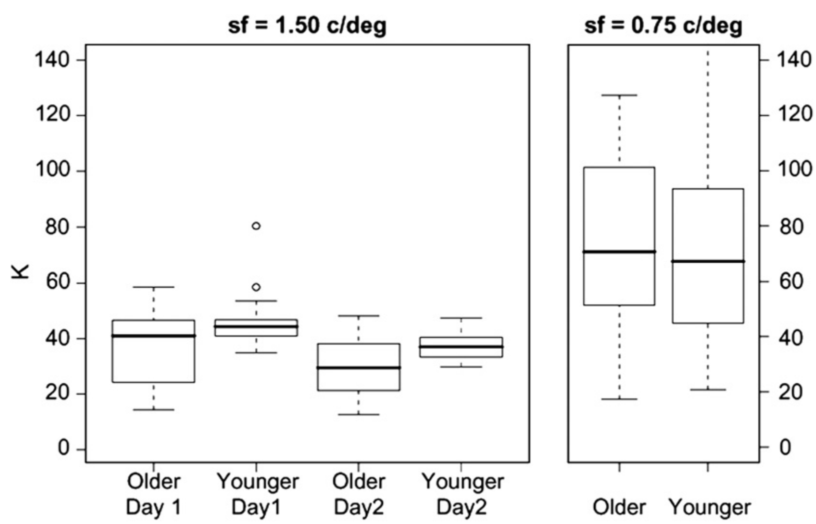


Fig. 4. Boxplots showing the distributions of effective signal-to-noise ratio at threshold ($k$) for older and younger subjects measured with a spatial frequency of 1.5 (Experiment 1b) and 0.75 (Experiment 1c). The lower and upper limbs of each box approximate the first and third quartiles, respectively; the horizontal line is the median. The whiskers extend to the farthest data points that are within ±1.5 times the inter-quartile range from the median. Unfilled circles represent outliers.

significant difference across groups ($t = -0.29$, $df = 31.74$, $p = 0.77$). In summary, equivalent input noise was higher in older than younger subjects, but the effective signal-to-noise ratio at threshold did not differ across groups. Therefore, unlike what was found in Experiment 1b, there was no evidence that high-noise efficiency was greater in older subjects.

### 2.5. Discussion

Experiments 1b and 1c found that equivalent input noise was higher in older subjects, but that the effective signal-to-noise ratio at threshold either did not differ across groups or was slightly lower in younger subjects. We were unable to fit Eq. (1) to the data from Experiment 1a because the levels of external noise used in that experiment were not low enough to provide stable estimates of $N_{eq}$. However, the significant age × noise interaction obtained in that experiment – which showed that age differences were greater in the low noise condition – is consistent with the claim that older subjects have higher equivalent input noise than younger subjects. The current results differ from previous studies of age differences in grating *detection* thresholds that found no age differences in equivalent input noise, at least for the range of spatial frequencies used in the current experiments (Bennett et al., 1999; Pardhan et al., 1996).

The linear model described by Eq. (1) has been used to characterize perceptual learning of faces and noise textures.

Gold and colleagues (Gold, Bennett, & Sekuler, 1999; Gold et al., 2004) showed that identification thresholds for faces and noise textures improved by similar amounts at all levels of external noise: within the context of Eq. (1), practice lowered $k$ but had no effect on $N_{eq}$. The current results differ from those findings: Experiment 1b showed that practice lowered orientation discrimination thresholds only in the high-noise condition. Instead, our results replicate the findings of Lu and Dosher (Lu & Dosher, 2004), who measured orientation discrimination thresholds in younger observers using stimuli and procedures that are similar to the ones used here. Lu and Dosher suggested that practice reduces the orientation bandwidths of the pattern-encoding mechanisms. This increased tuning, which they referred to as external noise exclusion, can account for the effects of practice provided that the source of performance-limiting internal noise is after the site of orientation filtering. Of critical importance to the current study, however, is the finding that the effects of practice were similar in both age groups.

## 3. Experiment 2

Studies that have measured orientation discrimination thresholds by fixing stimulus contrast and adjusting orientation have reported that thresholds are constant across a wide range of contrasts, and increase only as contrast is lowered to near-threshold levels (Skottun, Bradley, Sclar, Ohzawa, & Freeman, 1987; Webster, De Valois, & Switkes, 1990). For example, Skottun et al. (1987), using a 1 c/deg grating, found that discrimination thresholds were constant at approximately 0.5 deg until contrast was reduced below 0.03, at which point threshold increased significantly. The results of Experiment 1 are consistent with the hypothesis that effective stimulus contrast is slightly lower in older subjects, but that other aspects of orientation discrimination do not differ with age. This hypothesis predicts that threshold-vs-contrast functions, like the ones measured by Skottun et al. (1987), measured in older and younger subjects should have the same shape and reach the same lower limit at high contrast (i.e., the function for older subjects should be a rightward-shifted version of the function for younger subjects). Experiment 2 tested this prediction.

### 3.1. Method

#### 3.1.1. Subjects and equipments

Eleven older and 19 younger subjects participated in the experiment. The mean subject ages and logMAR decimal acuities are listed in Table 1. The experimental equipment was the same as Experiment 1.

### 3.2. Stimuli

The stimuli were 1.5 c/deg Gabor patches that were tilted clockwise or counterclockwise relative to the horizontal axis. The full-width (at half amplitude) of the Gaussian window was 2.3 deg. The phase of the sine wave grating relative to the center of the Gaussian was fixed at 90 deg. Mean luminance was 61.2 cd/m$^2$. Thresholds were obtained from older subjects at six stimulus contrasts ranging from 0.015 to 0.48. Thresholds were obtained from younger subjects at nine contrasts ranging from 0.005 to 0.8, although not all subjects were tested with every contrast. Stimulus contrast was blocked, and the order was randomized for each subject.

#### 3.2.1. Procedure

Viewing position was stabilized with a chin/head rest at a distance of 114 cm from the display. The monitor was the sole light source in the room during the testing period. Subjects were told that they would be shown a single stimulus on each trial, and that their task was to determine if it was rotated clockwise or counterclockwise from horizontal. After a minute of light adaptation, the subject completed 6 practice trials with patterns that were rotated ±32 deg, ±16 deg, and ±8 deg from horizontal, with two trials at each level, progressing from the largest rotations to the smallest. A dark fixation point appeared on the screen before the start of each trial. After the subject pressed the space bar on a computer keyboard, the fixation point flickered for 500 ms at a rate of 10 Hz to indicate the start of the trial and to attract attention to the center of the display. The fixation point was then erased and, after a delay of 250 ms, the Gabor was presented for 100 ms. The subject indicated the direction of rotation by pressing a button on the keyboard. Auditory feedback informed the participant about the accuracy of the response, and then the fixation re-appeared to signal the beginning of the next trial.

After the practice trials were completed, stimulus orientation was varied by two interleaved, 3-down/1-up staircases. One staircase converged on the orientation that yielded correct counterclockwise responses on 79% of the trials; the other staircase converged on the orientation yielding correct clockwise responses on 79% of the trials. In effect, this method estimated the 21% and 79% points on the psychometric function that related counterclockwise responses to stimulus orientation. Each staircase ended after eight reversals, and the average of the last six reversals were computed. Orientation discrimination threshold was defined as the absolute value of one-half of the difference between the orientations estimated by the two staircases.

### 3.3. Results and discussion

Median orientation discrimination thresholds for each age group are plotted as a function of stimulus contrast in Fig. 5. Smooth curves of the form $t = p_0 + (c/p_1)^{p_2}$, where $t$ is discrimination threshold, $c$ is stimulus contrast, and $p_0$, $p_1$, and $p_2$ are free parameters, were fit to 999 bootstrapped samples drawn from the data from each age group. The fits were then used to estimate the mean and

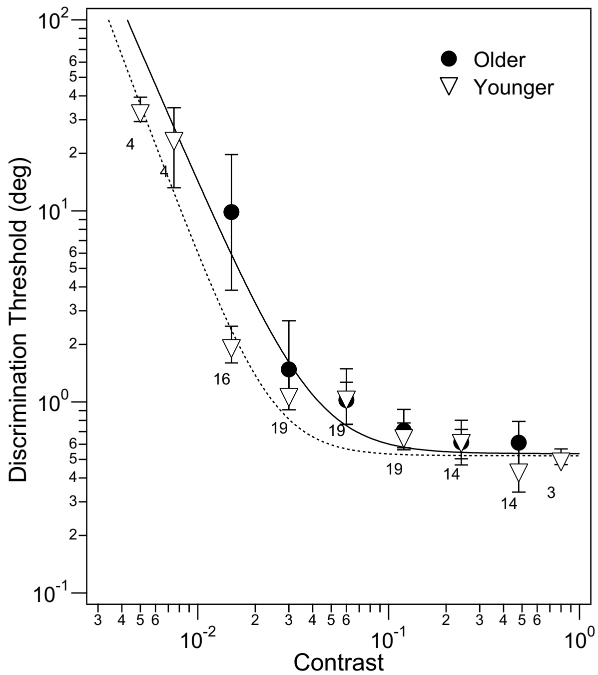


Fig. 5. The results of Experiment 2. Orientation discrimination thresholds are plotted as a function of stimulus contrast. Each symbol represents the median threshold; error bars represent 95% confidence intervals. The numbers next to the open symbols indicate the number of younger subjects tested in each condition. There were 11 older subjects in each condition. Smooth curves of the form $p_0 + (c/p_1)^{p_2}$ were fit to the data using the mean parameters listed in Table 2.

95% confidence interval for each parameter, which are shown in Table 2. The mean values of the parameters were used to create the smooth curves in Fig. 5. The value of $p_0$, which corresponds to the lower asymptote, did not differ across age groups: at high contrasts, thresholds were approximately 0.5 deg in both groups. Parameter $p_2$, which governs the log-log slope of the threshold-vs-contrast function at low contrasts, also did not differ significantly across groups. However, parameter $p_1$, which corresponds to the stimulus contrast at which discrimination threshold is 1 deg greater than the asymptotic value, was higher (by 0.012) in older subjects than younger subjects. These results indicate that older subjects needed slightly higher contrast to attain their lowest discrimination thresholds, but otherwise performed similarly to younger subjects.

Table 2
Means and 95% confidence intervals for best-fitting parameters for threshold-vs.-contrast curves measured in Experiment 2

| Group | Fitted parameter | Mean | Confidence intervals |
|---|---|---|---|
| Older Subjects | $p_0$ | 0.536 | (0.348,0.689) |
| | $p_1$ | 0.031 | (0.023, 0.043) |
| | $p_2$ | −2.320 | (−3.982, −1.261) |
| Younger Subjects | $p_0$ | 0.523 | (0.413, 0.623) |
| | $p_1$ | 0.019 | (0.017, 0.021) |
| | $p_2$ | −2.678 | (−2.915, −2.448) |

## 4. Experiment 3

Experiment 1 found that older subjects are less sensitive than younger subjects to small differences in grating orientation when the stimuli are embedded in low levels of external noise, but not when they are embedded in high levels of external noise. Experiment 2 found that orientation discrimination thresholds are higher in older subjects than in younger subjects when grating contrast is low, but not when grating contrast is high. In the framework of the linear model described by Eq. (1), the results of both experiments are consistent with the hypothesis that equivalent input noise is higher in older subjects. What might cause this age difference in equivalent input noise? In younger subjects, equivalent input noise measured in visual detection tasks increases as retinal illuminance decreases (Nagaraja, 1964; Pelli, 1990). In older subjects, changes in pupil size and lens opacity (Winn et al., 1994; Weale, 1961) combine to reduce retinal illuminance significantly, and so it is possible that reduced retinal illuminance contributed to the elevated $N_{eq}$ observed in older subjects in Experiment 1. The purpose of Experiment 3 was to evaluate the effects of reduced retinal illuminance on orientation discrimination thresholds.

### 4.1. Method

#### 4.1.1. Participants and apparatus

Seven young subjects were tested using the same experimental apparatus and stimuli that were used in Experiment 1c. One subject was unable to perform the task in the high noise condition and was excluded from the data analysis. Mean age and acuities are shown in Table 1. The subjects had not participated in Experiment 1.

#### 4.1.2. Procedure

Subjects performed the orientation discrimination task across four days at four different mean luminances: 61.2, 26.3, 11.3, and 4.9 cd/m$^2$. The order of luminance conditions was randomized for each individual subject. Mean luminance was manipulated by placing neutral density filters across the stimulus display. Gabor spatial frequency was 0.75 c/deg, as in Experiment 1c. On each day, two thresholds were measured at each level of external noise, and the two thresholds were averaged to obtain one estimate per noise level. Pupil sizes were measured in each luminance condition. Subjects wore an Eyelink II headset while viewing a uniform field with a millimeter scale placed below each eye. The Eyelink system illuminated the pupils using infrared sources, and images of the eyes were recorded by cameras placed just in front of, and below, each eye. Several images of the left and right eyes were digitized and saved for later analysis. The horizontal diameter of each pupil was measured using the Carnoy 2.0 software package (Lab of Plant Systematics, K. U. Leuven, Flanders, Belgium). The maximum diameter for each eye was recorded, and then averaged to calculate a single pupil measurement for each subject. The retinal illuminance, in Trolands, was then calculated for each subject by multiplying the pupil area, in $mm^2$, by the monitor luminance, in $cd/m^2$.

### 4.2. Results

Mean pupil diameters ranged from 3.49 mm (SEM = 0.275) at the highest display luminance to 4.61 mm (SEM = 0.444) at the lowest luminance. Although these diameters are smaller than those reported by Winn et al. (1994), the exponent of the best-fitting power function relating pupil diameter to luminance (exponent = −0.106) was very similar to the exponent derived from the Winn et al. data (exponent = −0.107). Based on our pupil measurements, the relation between retinal illuminance and display luminance was well-described by a power function with an exponent of 0.76 (Fig. 6a), a value that is consistent with previous reports (LeGrand, 1957; Winn et al., 1994). The close correspondence between current and previous measures suggests that our estimate of how retinal illuminance varied across conditions was accurate.

Discrimination thresholds, expressed in terms of contrast energy, are plotted as a function of external noise in all four luminance conditions in Fig. 6b. Three trends are clearly evident: (1) at each luminance, thresholds increased with increasing levels of noise; (2) at each level of noise, thresholds generally were higher at lower luminances; and (3) the effect of luminance on threshold was much greater at the two lowest levels of external noise. These observations were confirmed by a repeated-measures ANOVA performed on the log-transformed thresholds, which found significant main effects of noise ($F(2,10) = 350.93$, $p < .0001$, $\tilde{\varepsilon} = 1$) and luminance ($F(3,15) = 16.53$, $p = .0001$, $\tilde{\varepsilon} = 1$), and a significant luminance × noise interaction ($F(5.5, 27.5) = 5.74$, $p = .0007$, $\tilde{\varepsilon} = 0.92$).

Eq. (1) was fit to log-transformed thresholds (mean $r^2 = .98$) from each subject to estimate $N_{eq}$ and $k$ at each

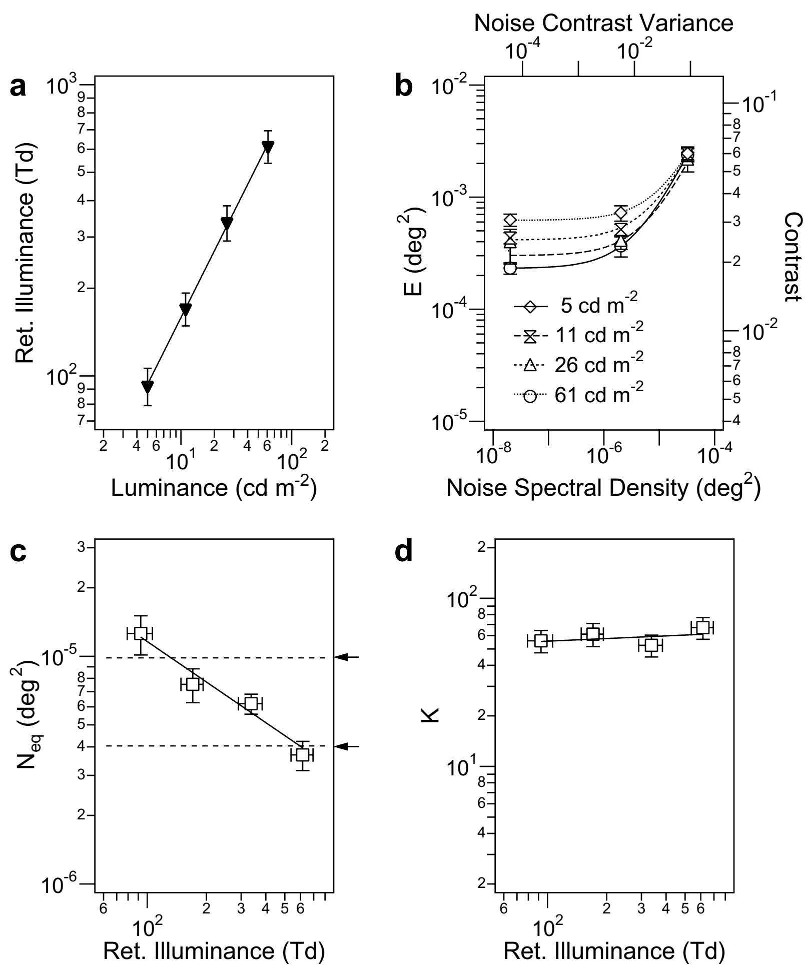


Fig. 6. The results of Experiment 3. Each symbol represents the mean of six younger subjects; error bars represent ±1 standard error. (a) Retinal illuminance, in Trolands, is plotted as a function of display luminance. The solid line is a power function that was fit to the data: the log-log slope is 0.76. (b) Discrimination thresholds are plotted as a function of external noise spectral density. The smooth curves are the best-fitting versions of Eq. (1). (c) Equivalent input noise plotted as a function of retinal illuminance. The solid line represents the best-fitting power function; the log-log slope is −0.6. The upper and lower arrows indicate, respectively, the average equivalent input noise in older and younger subjects in Experiment 1c. (d) Effective signal-to-noise ratio plotted as a function of retinal illuminance. The solid line represents the best-fitting power function; the log-log slope is 0.05.

luminance. $N_{eq}$ fell significantly with increasing retinal illuminance (Fig. 6C). The exponent of the best-fitting power function was −0.59, and an ANOVA on the log-transformed $N_{eq}$ measures revealed a significant effect of luminance ($F(2.31,11.56) = 11.36$, $p = .0014$, $\tilde{\varepsilon} = 0.77$). The effect of luminance on $k$ was much smaller (Fig. 6D). The exponent of the best-fitting power function relating $k$ to retinal illuminance was only 0.05, and an ANOVA failed to obtain a significant effect of Luminance ($F(1.43,7.17) = 1.90$, $p = .21$, $\tilde{\varepsilon} = 0.48$).

### 4.3. Discussion

Consistent with previous reports (Nagaraja, 1964; Pelli, 1990; Raghavan, 1995; Rovamo, Kukkonen, Tiippana, & Nasanen, 1993), we found that reducing display luminance increased thresholds primarily in low-noise conditions. In the context of the linear model (Eq. (1)), lowering retinal illuminance raised equivalent input noise ($N_{eq}$), but did not alter the effective signal-to-noise ratio at threshold ($k$). Although these effects are qualitatively similar to the results obtained in Experiment 1c, which also used a spatial frequency of 0.75 c/deg, they are much smaller than the age differences found in that experiment. Winn et al. (1994) reported that changes in pupil area reduced retinal illuminance by about 0.25 log units between the ages of 25 and 65 years when subjects viewed a uniform field of 44 cd/m$^2$, which is similar to the luminance used in Experiment 1c. (Our own measurements of pupil area taken on two samples of younger ($n = 42$, age = 18–32) and older ($n = 30$, age = 60–72) yielded similar estimates of the reduction in retinal illuminance (0.2 log units) in similar viewing conditions). In the current study, decreasing retinal illuminance by 0.25 log units in younger subjects increased equivalent input noise on average by 0.15 log units, but this effect on $N_{eq}$ was much smaller than the 0.39 log unit difference between older and younger subjects found in Experiment 1c (see Fig. 6C). Therefore, it seems that age differences in $N_{eq}$ are greater than what one would predict based on age-related changes in pupil size alone.

Of course, other factors may further reduce illuminance in senescent eyes. Weale (1961, 1963, 1992) suggested that the effects of decreased pupil size and increased optical density of the ocular media combine to reduce retinal illuminance by 0.3–0.5 log units between the age of 20 and 65 years. However, even this larger reduction is not sufficient to account for age differences in equivalent input noise: in the current experiment, retinal illuminance in younger subjects needed to be reduced by 0.65 log units to increase equivalent input noise to the level measured in our older subjects. It seems unlikely, therefore, that reductions in retinal illuminance are sufficient to account for the age differences found in Experiment 1.

We found that $N_{eq}$ was related to retinal illuminance by a power function with an exponent of −0.6. This result differs from the findings of Pelli (1990), who re-analyzed several studies that measured detection thresholds as functions of retinal illumination and external noise and found that equivalent input noise was inversely proportional to retinal illuminance. Pelli (1990) argued that this inverse relation between $N_{eq}$ and retinal illuminance was strong evidence that equivalent input noise was closely linked to photon noise. However, Raghavan (1995) found that the relation between $N_{eq}$ and retinal illuminance in a letter identification task depended strongly on the spatial characteristics of the stimulus. For small letters, $N_{eq}$ was inversely proportional to retinal illuminance, but for large letters $N_{eq}$ was inversely proportional to the square root of retinal illuminance. Raghavan (1995) claimed that the square-root relation, which is similar to the one found in the current experiment, was inconsistent with the idea that equivalent input noise was yoked to photon noise, and presented evidence that a central source of noise that arises after binocular integration constrained performance with large letters (also see Pelli & Farell, 1999). Our findings raise the possibility that the performance-limiting noise in the orientation discrimination task used in the current experiment also has a central origin.

## 5. General discussion

Experiment 1 found that older subjects had higher orientation discrimination thresholds than younger subjects when stimuli were embedded in low levels of external noise, but that thresholds were similar in both age groups at high levels of external noise. The threshold vs. noise functions obtained in both age groups were well-fit by Eq. (1), in which performance is constrained jointly by equivalent input noise and the effective signal-to-noise ratio at threshold. In the framework of that model, age differences in orientation discrimination were attributed to higher equivalent input noise in older subjects (see Fig. 3). Equivalent input noise can be thought of as an internal noise which adds to the display noise (Pelli & Farell, 1999). Alternatively, it can be characterized as an attenuation of the signal that occurs prior to the addition of internal noise (Kersten et al., 1988; Raghavan, 1995). In both cases, the result is an increase in threshold when the external noise is low, but not when it is high. The results of Experiment 2 also are consistent with the claim that age differences in orientation discrimination reflect differences in equivalent input noise.

Experiment 3 examined the hypothesis that age differences in equivalent input noise were linked to differences in retinal illumination. Although reducing retinal illumination in younger subjects did increase equivalent input noise, the effects were too small to account for the age differences in equivalent input noise that were observed in Experiment 1.

What other factors might contribute to differences in $N_{eq}$? One possibility is that differences in equivalent input noise are produced by differences in optics. Substantial differences between the lens modulation transfer functions (MTFs) in old and young eyes exist at spatial frequencies as low as 2 c/deg (Artal, Ferro, Miranda, & Navarro, 1993). Increased blur reduces the signal-to-noise ratio in conditions using low external noise and therefore increases $N_{eq}$ but does not affect $k$ (Kersten et al., 1988; Raghavan, 1995). One argument against the idea that the differences in $N_{eq}$ that we observed are due to differences in blur is that similar age differences were found with 0.75, 1.5, and 3 c/deg stimuli. Age differences in blur vary greatly over this range of spatial frequencies (Artal et al., 1993), and so blur-induced differences in $N_{eq}$ ought to change, too. Another factor contributing to age differences in $N_{eq}$ might be intraocular scatter, which increases significantly with age (Shahidi & Yang, 2004). Unlike blur, scatter reduces retinal contrast at even very low spatial frequencies, and therefore could account for the finding that differences in $N_{eq}$ were relatively constant across spatial frequency. However, this explanation fails to account for previous reports that $N_{eq}$ does *not* differ in older and younger subjects in grating detection tasks (Bennett et al., 1999; Pardhan et al., 1996).

Another possible explanation of age differences in $N_{eq}$ is that neural noise within the visual pathway increases with age. Several studies have reported elevated spontaneous firing rates in LGN and V1 neurons in senescent monkeys and cats (Hua et al., 2006; Leventhal et al., 2003; Schmolesky, Wang, Pu, & Leventhal, 2000; Spear, Moore, Kim, Xue, & Tumosa, 1994; Wang, Zhou, Ma, & Leventhal, 2005; Yu et al., 2006). This increase in spontaneous activity could manifest itself as an increase in equivalent input noise if it were contrast-invariant and if signals from such neurons influence perceptual decisions in orientation discrimination tasks. To account for the previous findings that $N_{eq}$ in grating detection tasks does not differ across age, at least over the range of spatial frequencies tested in the current experiments (Bennett et al., 1999; Pardhan et al., 1996), it would be necessary to assume that the increased neural noise has a greater effect in discrimination tasks such as the ones used in the current experiments. In this regard, it is interesting to note that the relation between $N_{eq}$ and retinal illuminance found in Experiment 3 differs considerably from the relation found in many detection tasks (Pelli, 1990), but is similar to the one found for a letter identification task that is constrained by noise that arises at some point after binocular integration (Raghavan, 1995). Thus, it is plausible to suggest that the increased equivalent input noise found in older subjects is linked to changes in the variability of the responses of visual cortical neurons.

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