Healthy Aging Impairs Photon Absorption Efficiency of Cones

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PURPOSE. Vision decline with healthy aging is a major public health concern with the unceasing growth of the aged population. In order to prevent or remedy the age-related visual loss, a better understanding of the underlying causes is needed. The current psychophysical study used a novel noise paradigm to investigate the causes of age-related contrast sensitivity loss by estimating the impact of optical factors, absorption rate of photon by photoreceptors, neural noise, and calculation efficiency on contrast sensitivity.

METHODS. The impact of these factors on contrast sensitivity was assessed by measuring contrast thresholds with and without external noise over a wide range of spatial frequencies (0.5–16 cycles per degree [cyc/deg]) and different luminance intensities for 20 young (mean = 26.5 years, SD = 3.79) and 20 older (mean = 75.9 years, SD = 4.30) adults, all having a good visual acuity (≥6/7.5).

RESULTS. The age-related contrast sensitivity losses were explained by older observers absorbing considerably fewer photons (4×), having more neural noise (1.9×), and a lower processing efficiency (1.4×). The aging effect on optical factors was not significant.

CONCLUSIONS. The age-related contrast sensitivity loss was mostly due to less efficient cones absorbing four times fewer photons than young adults. Thus, besides the ocular factors known to be considerably affected with aging, the decline of absorption efficiency of cones is also responsible for a considerable age-related visual decline, especially under dim light.

Keywords: contrast sensitivity, equivalent input noise, aging, photon absorption, neural noise, modulation transfer function

Vision decline with healthy aging is a major public health concern with the unceasing growth of the aged population.[1] To prevent or remedy this age-related vision loss, a better knowledge about the underlying causes is needed. A classical approach to quantify visual perception is to measure contrast sensitivity, which declines with healthy aging[2] due to optical factors such as pupillary miosis and yellowing of the lens, as well as neural factors such as an increase of neural spontaneous activity and lower neural efficiency.[3,4] Nevertheless, another factor that is neither optical nor neural is often overlooked: the absorption rate of photoreceptors. The current study aimed at quantifying the impact of healthy aging on absorption rate of photoreceptors and various neural factors.

Noise paradigms have been used to investigate the causes of age-related sensitivity losses by factorizing contrast sensitivity into equivalent input noise, which quantifies the sum impact of all internal noise sources, and calculation efficiency (also termed central efficiency[5]), which is equivalent to the signal-to-noise contrast ratio required to detect the signal.[6–8] The current study used an elaborated noise paradigm[9] to further decompose the equivalent input noise into the Modulation Transfer Function of the eye (MTF, which is accountable for the impact of most optical aberrations[10,11]), stochastic absorption rate of photons, and neural noise (see Fig. 1). The impacts of these components on contrast sensitivity can be disentangled because they vary differently as a function of the spatial frequency (SF) and because different sources of internal noise limit contrast sensitivity at different luminance intensi-

ties.[9,12–14] The current study therefore evaluated the impact of healthy aging on various factors (photon noise, neural noise, MTF, and calculation efficiency) by measuring contrast sensitivity at different luminance intensities, SFs, and with and without external noise for healthy young and older observers.

METHODS

Observers

Twenty young adults (mean age = 26.5 years, SD = 3.79; 12 females) and 20 older adults (mean age = 75.9 years, SD = 4.30; 11 females) from the Silversight cohort (Vision Institute, Paris, France) participated in the current study after giving their informed consent. All participants were screened and included only if they had no known visual, audiovestibular, sensorimotor, neuropsychological, or cognitive pathologies, and a good visual acuity (≥6/7.5) with their dominant eye (estimated by using the hole-in-card test). The screening of the participants was undertaken by an otorhinolaryngologist (audiometric and vestibular tests), a neuropsychologist (Mini Mental State Examination [MMSE], General Health Questionnaire [GHQ], medical history questionnaire), and an ophthalmologist (optical coherence tomography, fundus photography, visual acuity with an ETDRS chart viewed at 2 m, contrast sensitivity with a Pelli-Robson chart). No participants were under any medication known to alter visual perception, such as benzodiazepine.[15] Participants were wearing trial frames with trial lenses adjusted to their optimal correction according to each
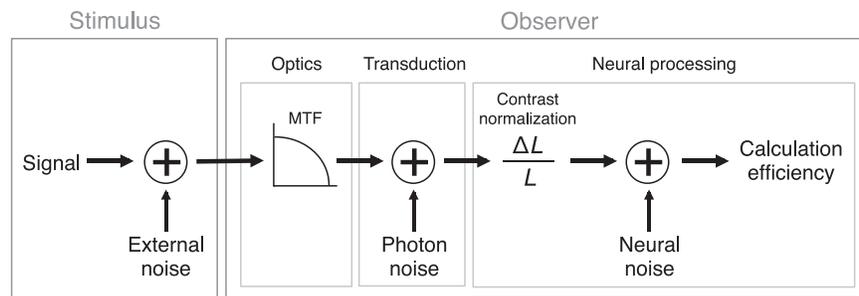
FIGURE 1. Observer model comprising the MTF, photon noise, neural noise, and calculation efficiency. The MTF models most of the optical factors; the photon noise represents the fluctuations of phototransduction, and the neural noise could represent, for instance, the spontaneous activity of neurons located after the contrast normalization.

testing distance, which varied across conditions. The visual correction of each subject was estimated before the experiment by an orthoptist. Ethical approval was obtained from the Comité de Protection des Personnes Ile de France V in agreement with the Declaration of Helsinki, and the clinical screening was carried out under medical supervision at the Clinical Investigation Center of the Quinze-Vingts Hospital, Paris.

Apparatus

All stimuli were generated by a homemade program and presented on a projector screen. The projector used was a LCD Panasonic PT-EW730Z (Kadoma, Osaka, Japan) with a refresh rate of 60 Hz and a resolution of 1280×800 pixels; it could project a luminance intensity up to 3700 cd/m^2. This projector was chosen for its brightness, which was essential to measure the impact of neural noise across a wide range of SFs (contrast sensitivity saturates at higher luminance intensities for higher SFs[9]). The projector was the only source of light in the room and was set behind the screen for a direct retroillumination. The output intensity of each color gun was carefully linearized using a Minolta spectroradiometer CS-1000 (Ramsey, NJ, USA). The Noisy-bit method[16] implemented independently to each color gun made the 8-bit display perceptually equivalent to an analog display having a continuous luminance resolution.

Stimuli and Procedure

An orientation discrimination task was carried out using a two-alternative forced-choice procedure (vertical or horizontal). To help the observer to stay focused and motivated, auditory feedback was given after each response made by pressing one of two keys. Note that such an orientation discrimination task using an external noise paradigm induces no considerable perceptual learning after two experimental sessions (as in the current study) even with feedback.[17]

The signal was a sinusoidal grating with a SF of 0.5, 1, 2, 4, 8, or 16 cycles per degree (cyc/deg), depending on the testing condition. The spatial window of the signal was a circular aperture with a diameter that depended on the SF of the signal and was set to eight visible cycles of the signal grating plus a half-cosine of half a cycle. To minimize spatial uncertainty, a black annulus centered on the stimulus and 2.5 times the size of the aperture was continuously displayed. Stimuli were presented for 500 ms plus an on and off half-cosine ramp of 250 ms each, resulting in a total presentation duration of 1 second. Stimuli were presented at the center of a gray square of 41×41 cm and were viewed monocularly through a 2.5-mm artificial pupil at a distance of 97, 194, and 388 cm from the screen depending on the SF of the stimulus (see Fig. 2 for a representation of the stimuli). For better comfort, participants monocularly viewed the stimuli with their dominant eye.

Given that calculation efficiency (i.e., contrast threshold in high noise) is independent of luminance intensity,[9,18,19] contrast thresholds in noise were measured only at the highest luminance intensity (i.e., 9145 trolands [Td]). The noise used was truncated-filtered noise[20] with a SF cutoff two octaves above the SF of the signal, temporally white (refreshed at 30 Hz), and its contrast was truncated at 1 standard deviation, which corresponded to 50%. The noise was spatiotemporally extended (i.e., full-screen and continuously displayed) to avoid triggering a shift in processing strategy.[21–23] For the highest SF of 16 cyc/deg, a pilot study revealed that this noise had little impact on contrast sensitivity of older adults, which compromised the estimation of the calculation efficiency at this SF. Therefore, to estimate the calculation efficiency at 16 cyc/deg, the calculation efficiencies measured for the other SFs (0.5–8 cyc/deg) were fitted with a quadratic function,[9] which was then used to extrapolate and estimate the calculation efficiency at 16 cyc/deg. The resulting noise energies were 1300, 324, 81, 20, and 5.1 µs.deg^2 for SF of 0.5 to 8 cyc/deg, respectively.

Contrast thresholds in absence of external noise were measured at different luminance intensities. For the highest luminance intensity, at which neural noise was expected to limit contrast sensitivity, the retinal illuminance was 9145 Td and the whole range of SFs (0.5–16 cyc/deg) was tested. For the low luminance conditions, only the high SFs were tested (4–16 cyc/deg), at which photon noise was expected to limit contrast sensitivity. For 4 and 8 cyc/deg, the retinal illuminance was set to 9.1 Td, which was obtained by placing a neutral density filter with an optical density of 3 (which reduces luminance intensity by a factor of 1000) on the trial frames of the observer. For 16 cyc/deg, the retinal illuminance was set to 91 Td (trial frames with an optical density of 2), because contrast sensitivity was too low to be measured at 9.1 Td for the older adults.

Control conditions were designed to evaluate the age-related impact of the yellowing of the lens on contrast sensitivity by presenting stimuli on a red background. Long wavelengths (e.g., red) are little affected by the yellowing of
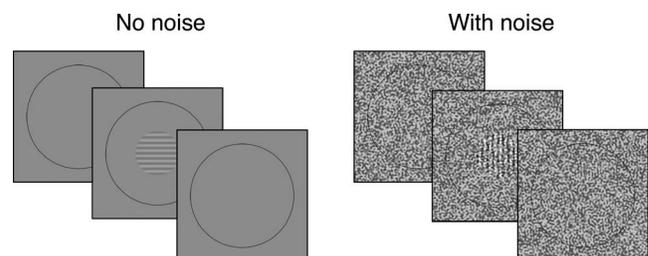
FIGURE 2. Stimuli samples without (*left*) and with (*right*) external noise. The stimulus was either vertical or horizontal and changed randomly at each trial.

the lens, which mainly blocks shorter wavelengths.[24] This control condition was done at high luminance intensity (1446 Td) with a SF of 0.5 cyc/deg, at which observers were expected to be limited by neural noise,[9] and at low luminance intensity (91 Td) with a SF of 16 cyc/deg, at which observers were expected to be limited by photon noise[9] obtained with a neutral density filter with an optical density of 1 and the red background (i.e., red color gun projecting wavelength longer than 580 nm) luminance fixed at 185 cd/m^{2}.

To evaluate the impact of age-related optical factors on contrast sensitivity, a control condition was conducted in which the impact of optical factors was neutralized using a 1-mm artificial pupil, which makes the impact of a small defocus negligible.[25] This control condition was conducted for the SF at which the optical factors had the greatest impact, that is, 16 cyc/deg. For comparative reasons, this control was conducted for a gray and a red background of 91 Td (by setting the luminance of the screen at 1170 and 370 cd/m^{2}, respectively, and adding a neutral density filter with an optical density of 1 and 0.5, respectively). Note that for all the experimental parameters (i.e., the different luminance intensities, SFs, and color of the background) the cones were mainly activated, because either the luminance intensity was too high for rods to be effective[26] (they were saturated) or the degree of visual angle of the observer was too small to activate photoreceptors outside of the fovea[26] (i.e., mostly cones).

Contrast detection thresholds were measured using a 3down1up staircase procedure[27] (the contrast of the stimulus decreases by one step after three consecutive correct answers and increases by one step after every wrong answer) with a step size of a factor of 1.25 and terminated after 14 reversals. Such a staircase converged to a criterion level of 79.4% correct response[27] corresponding to a d' of 1.16. For each staircase, the threshold was estimated as the geometric mean of the last 10 reversals. Two staircases were performed for each condition. The threshold for each condition was estimated as the geometric mean of the two estimated thresholds.

Participants completed the experiment in two sessions lasting approximately 2 hours each, and many breaks were provided in each session in order to keep the participants motivated and alert. The first session covered the highest luminance intensity conditions, whereas the second session covered the lowest luminance intensities and controlled conditions, for which participants were light-adapted for 30 minutes by wearing on the trial frames neutral optical density filters of 3. For each session the order of the SFs was randomized, but to minimize the displacement between testing distances, the two staircases for each SF were blocked. For the first session at the highest luminance intensity, two contrast thresholds were measured for each SF to estimate the equivalent input noise and the calculation efficiency: one in absence of noise $c(0)$ and the other in high noise $c(N_{ext})$ (except at 16 cyc/deg, at which $c(N_{ext})$ could not be measured). The control condition with a red background corresponding to a retinal illumination of 1446 Td was also tested at the end of this session. For the second session, the participants were adapted to the lowest luminance intensity (9.1 Td), were tested at that luminance intensity, and then were tested at 91 Td, at which the remaining control conditions were also tested.

The energy threshold E (square of the stimulus' contrast function summed over space and time[28]) is known to be linearly related to the external noise energy N_{ext}.[28] When the phase of the signal is unknown, this linear function can be represented as[6]:

$$E(N_{ext}) = \frac{(d' + \sqrt{0.5})^2}{k}(N_{ext} + N_{eq}),\qquad(1)$$

where k represents the calculation efficiency. Thus, for each SF at which threshold in high noise was measured (0.5–8 cyc/deg), the calculation efficiency (k) in energy units was calculated based on the energy thresholds in absence of noise ($E(0)$) and in high noise ($E(N_{ext})$) at the highest luminance intensity of 9145 Td:

$$k = \frac{(d' + \sqrt{0.5})^2 N_{ext}}{E(N_{ext}) - E(0)}.\qquad(2)$$

The estimated calculation efficiencies as a function of the SF of each observer were fitted with quadratic functions[9] and these fits (i.e., k_{fit}) were then used to estimate the calculation efficiency at each relevant SF (0.5–16 cyc/deg) and estimate the equivalent input noise at the various luminance intensities. Based on Equation 1, equivalent input noise for each condition was estimated based on the energy threshold in absence of noise ($E(0)$) and the fit of the calculation efficiency (k_{fit}) estimated for the given SF:

$$N_{eq} = \frac{k_{fit}}{(d' + \sqrt{0.5})^2}E(0).\qquad(3)$$

Model

A model recently developed[9] was used to decompose the equivalent input noise into the MTF of the eye, photon noise, and neural noise. This model was applied on the estimated equivalent input noise of each subject and had four degrees of freedom; one for the optical aberrations (i.e., MTF modeled with a generalized Lorentzian function with a free exponent[29]), one for the photon noise (constant with respect to SF), and two for the neural noise (affine function in log-log units with respect to SF). In the current study, the model had only four degrees of freedom compared to six degrees of freedom in the original model[9] because the very low luminance intensities at which early noise (i.e., retinal neural noise occurring prior to the contrast normalization) dominates were not investigated. The spatial and luminance conditions were chosen with respect to a previous study,[9] in order to estimate the MTF, photon noise, and neural noise.

Data Statistics

The contrast thresholds, calculation efficiency, and equivalent input noise data were analyzed by means of 2-way repeated measures analysis of variance (ANOVA; age × SF), to take into account that a same participant was tested for the different SFs. The analysis was done for high and low luminance intensities conditions separately. The effect of SF on contrast thresholds and equivalent input noise, for the low luminance intensities conditions, was not reported because there were two different luminance intensities, making the data incomparable. The parameters of the model (MTF, photon noise, and neural noise) were analyzed with a 2-sample *t*-test.

The effect size for the 2-way ANOVAs was estimated with ω^2. A ω^2 near 0.01 is a small effect, near 0.06 is a medium effect, and near 0.14 is a large effect (ω^2 is between −1 and 1). The effect size for the *t*-tests were estimated with Hedges' *g* coefficient.[30,31] A *g* near 0.2 is a small effect, near 0.5 is a medium effect, and near 0.8 is a large effect.

Pearson partial correlations were used to test if aging effects were due to potential confounding factors affecting contrast sensitivity. Partial correlations were evaluated between the dependent variables (MTF, photon noise, neural noise, and calculation efficiency) and age after controlling for the effects of sex (male or female), smoking (yes or no), education (score
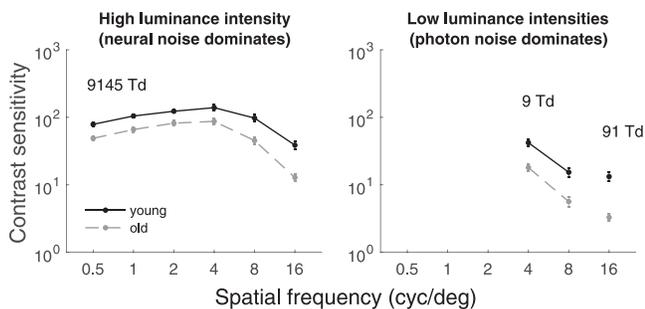
FIGURE 3. Contrast sensitivity of young and older adults. On the *left*, contrast sensitivity as a function of SF at 9145 Td is represented for the older adults (*gray dots* connected with *dashed lines*) and the young adults (*black dots* connected with *solid lines*). On the *right*, contrast sensitivity is represented for the older adults at 9 Td (*gray dots* connected with a *dashed line*) and at 91 Td (*gray dot*) and for the young adults at 9 Td (*black dots* connected with a *solid line*) and at 90 Td (*black dot*). The *error bars* represent the standard error of the mean (some of them are not visible, being smaller than the size of the marker).

from 0 to 5), cognitive impairments (score of MMSE), and depression (score of GHQ).

RESULTS

Contrast Sensitivity

Contrast sensitivity functions for young and older adults at high and low luminance intensities are represented in Figure 3. Older adults were less sensitive than young adults across the whole SF range for the high and low luminance conditions. Moreover, the contrast sensitivity functions were less band-pass (i.e., slope less steep at low SF) than what is typically observed in the literature,[32] which was expected[33,34] given that the stimulus had a fixed number of visible cycles causing the stimulus size to be greater at lower SFs.

A 2-way ANOVA (age × SF) of the contrast sensitivity at high luminance intensity showed a significant large effect of age ($F(1,38) = 33$, $P < 0.001$, $\omega^2 = 0.4$), a significant large effect of SF ($F(5,190) = 151$, $P < 0.001$, $\omega^2 = 0.8$), and a significant interaction between these factors ($F(5,190) = 8.3$, $P < 0.001$, $\omega^2 = 0.2$), which can be explained by the greater age-related sensitivity loss at high SFs.

A 2-way ANOVA (age × SF) of the contrast sensitivity at low luminance intensities also showed a significant large effect of age ($F(1,38) = 34$, $P < 0.001$, $\omega^2 = 0.5$) and a significant
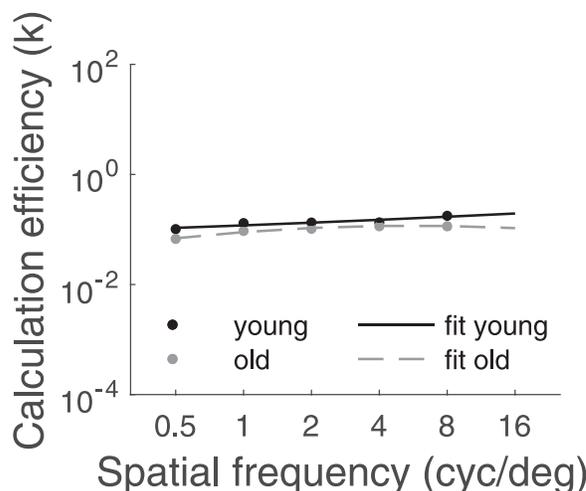

FIGURE 5. Calculation efficiency of young and older adults. Calculation efficiency (k, in energy units) as a function of SF at 9145 Td is represented for older adults (*gray dots*) fitted with our model with *dashed lines* (k_{fit}) and for young adults (*black dots*) fitted with our model with *solid lines*. The *error bars* represent the standard error of the mean (they are not visible, being smaller than the size of the marker). Note that at 16 cyc/deg the calculation efficiency could not be measured so only the fits are represented.

interaction between age and SF ($F(2,76) = 7.8$, $P < 0.001$, $\omega^2 = 0.2$), which can also be explained by the greater age-related sensitivity loss at higher SFs.

To visualize the difference between contrast sensitivity at low and high luminance intensities, Figure 4 represents the data using Bland-Altman plots. A contrast sensitivity ratio higher than one indicates that the observer was more sensitive at high luminance intensity than at low luminance intensity. The fact that contrast sensitivity was always higher at high luminance intensity for all observers and all SFs is consistent with the expectation that at low luminance intensity the observers were limited by photon noise.

Calculation Efficiency

Calculation efficiencies measured at high luminance intensity for young and older adults varied little with SF (Fig. 5), which is expected when the number of visible cycles is constant.[34] A 2-way ANOVA (age × SF) showed a significant large effect of age ($F(1,38) = 14$, $P < 0.001$, $\omega^2 = .3$; older adults were less efficient than young adults by a factor of approximately 1.4 in
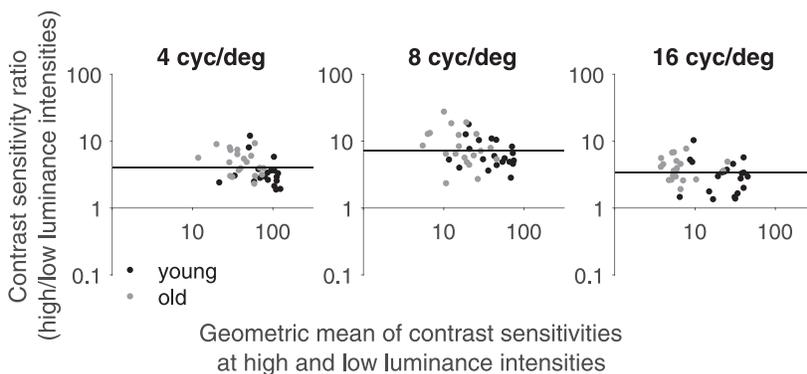
FIGURE 4. Bland-Altman plots. Comparison of contrast sensitivities at high and low luminance intensities for 4 cyc/deg (*left graph*), 8 cyc/deg (*middle graph*), and 16 cyc/deg (*right graph*). The older adults' data are represented by *gray dots* and the young adults' data by *black dots*. The *black lines* represent the geometric mean of the data.
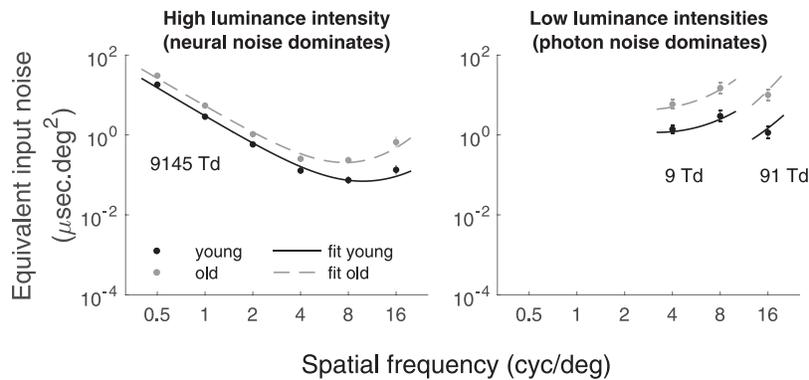
FIGURE 6. Equivalent input noise of young and older adults. On the *left*, equivalent input noise as a function of SF at 9145 Td is represented for the older adults (*gray dots* fitted with our model with *dashed lines*) and for the young adults (*black dots* fitted with our model with *solid lines*). On the *right*, equivalent input noise as a function of SF at 9 Td and 91 Td is represented for the older adults (*gray dots* fitted with our model with *dashed lines*) and for the young adults (*black dots* fitted with our model with *solid lines*). The *error bars* represent the standard error of the mean (most of them are not visible, being smaller than the size of the marker).

energy units), a significant large effect of SF ($F(4,152) = 15$, $P < 0.001$, $\omega^2 = 0.3$), which is consistent with previous findings,[9] and no interaction ($F(4,152) = 1.1$, $P = 0.36$).

Equivalent Input Noise

Equivalent input noises (Fig. 6) were estimated using Equation 3 based on the contrast sensitivities at various luminance intensities and SFs and on the calculation efficiency fits at various SFs (Fig. 5). The mean equivalent input noise of older observers was greater than the mean of young adults at all SFs and luminance intensities. For the high luminance conditions, a 2-way ANOVA (age × SF) showed a significant large effect of age ($F(1,38) = 20$, $P < 0.001$, $\omega^2 = 0.3$) and SF ($F(5,190) = 401$, $P < 0.001$, $\omega^2 = 0.9$), as well as an interaction between these factors ($F(5,190) = 4.4$, $P < 0.001$, $\omega^2 = 0.1$), which can be explained by the greater aging effect at high SFs.

For the low luminance conditions, a 2-way ANOVA (age × SF) showed a significant large effect of age ($F(1,38) = 24$, $P < 0.001$, $\omega^2 = 0.4$; older adults had more equivalent input noise than young adults) and no interaction between SF and age ($F(2,76) = 2.2$, $P = 0.11$).

Internal Noise Sources and MTF

Using an elaborated noise model,[9] equivalent input noises were decomposed for each participant into the optical aberrations modeled by the MTF of the eye, photon noise caused by stochastic absorption of photons, and neural noise (Fig. 7). Optical factors (MTF) affected slightly more the older observers (up to a factor of 2.3 in energy units at 16 cyc/deg), but this effect was not statistically significant ($t(38) = -1.7$, $P = 0.10$). A significant aging effect on photon noise was found ($t(38) = -3.4$, $P < 0.01$, $g = 1$), suggesting that older adults had more photon noise than young adults by a factor of 4.0 in energy units. This greater amount of photon noise suggests that photoreceptors of the older adults absorbed approximately 4.0 times fewer photons than the young adults. No significant aging effect was found on the slope of the affine function fitting neural noise ($t(38) = -0.4$, $P = 0.71$), but a significant aging effect was found on the neural noise's mean across the SFs ($t(38) = -2.5$, $P < 0.05$, $g = 0.8$), which suggests that the older adults had 1.9 times more neural noise than the young adults.

The age-related effects described above on the photon noise, neural noise, and calculation efficiency show significant differences between young and older groups. These effects could be due to age or some other confounding factor differing between the two groups such as education, sex, smoking, cognitive impairments, and depression, which can affect contrast sensitivity.[35–37] Partial correlations between each dependent variable and age were evaluated while controlling for the effects of sex (male or female), smoking (yes or no), education (score from 0 to 5), cognitive impairments (score of MMSE), and depression (score of GHQ). The aging effects on photon noise, neural noise, and calculation efficiency all remained significant after controlling for these factors ($r = 0.38$, $P < 0.05$; $r = 0.36$, $P < 0.05$; $r = -0.62$, $P < 0.001$, respectively), which shows that the observed aging effects cannot be explained by these factors (sex, smoking, education, cognitive impairments, and depression).

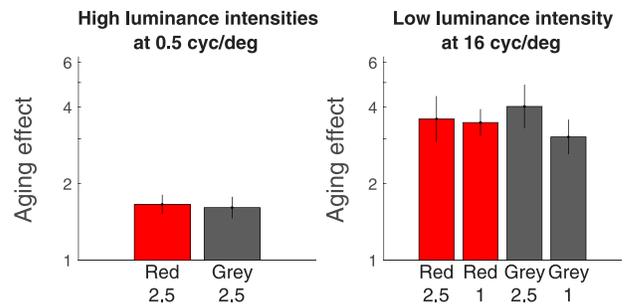## Yellowing of the Lens and MTF Controls

All the controlled conditions for the yellowing of the lens showed a similar age-related sensitivity loss (i.e., aging effect) using a gray or red background (Fig. 8), which suggests that the older adults did not have a yellowing of their lens considerably affecting contrast sensitivity. Moreover, the similar age-related sensitivity losses observed with a 2.5- and a 1-mm artificial pupil (right graph in Fig. 8) suggest that there was no considerable aging effect on optical aberrations, which is consistent with the nonsignificant aging effect found on the MTF of our model (see first graph of Fig. 7).

DISCUSSION

Healthy aging was found to affect contrast sensitivity across a wide range of SFs at high and at low luminance intensities. By measuring contrast thresholds in high noise and using an elaborated noise model, contrast sensitivity was decomposed into various factors: the MTF of the eye, photon noise (caused by probabilistic absorption), neural noise, and calculation efficiency. The age-related impacts of these internal factors on sensitivity (in energy units) are summarized in Figure 9. Calculation efficiency (CE) dropped by a factor of approximately 1.4 (averaged across SFs). Though the impact of optical aberrations on sensitivity (i.e., MTF) at high SFs was greater for older adults (2.3× at 16 cyc/deg), this effect was not statistically significant. Neural noise, which affected sensitivity at the high luminance intensity (left graph), was affected by a factor of approximately 1.9 (averaged across SFs), whereas

MTF

$e_Y = 0.95$

$e_A = 1.2$

Photon noise

Neural noise

$s_Y = -2.4$

$s_A = -2.3$

Spatial frequency (cyc/deg)
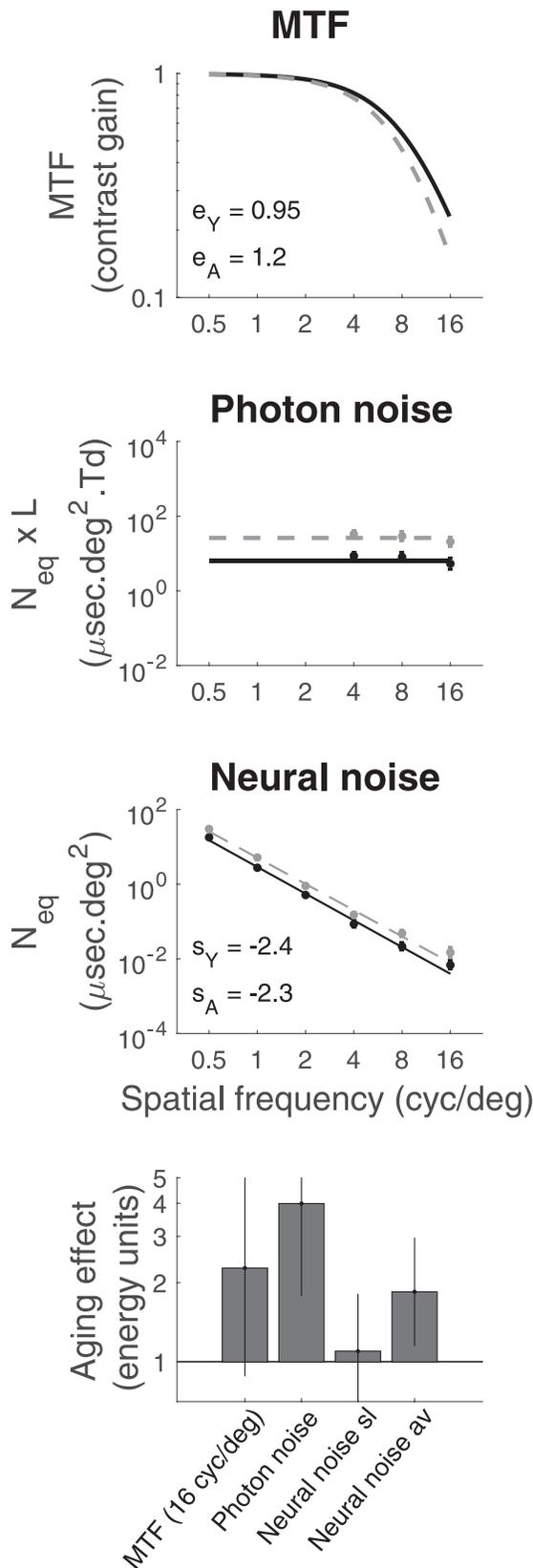
FIGURE 7. Internal noise sources. The *top graph* represents the MTF of the eye as a function of SF for the older (*dashed line*) and the young adults (*solid line*). The exponent of the generalized Lorentzian function is represented by e_A for the older adults and by e_Y for the young adults. The *second graph* represents equivalent input noise of the low luminance conditions multiplied by luminance intensity ($N_{eq} \times$


FIGURE 8. Experimental controls. The first graph on the *left* represents the aging effect of the experiment controlling for the effect of the yellowing of the lens at high luminance intensities and at 0.5 cyc/deg, at which neural noise is the dominating source of noise (gray background at 9145 Td versus red background at 1446 Td). The second graph on the *right* represents the aging effect of the experiment controlling for the effect of the yellowing of the lens at low luminance intensity (91 Td) and at 16 cyc/deg, at which the photon noise is the dominating noise source (gray background versus red background for a 2.5- and a 1-mm pupil). The *error bars* represent the 68% confidence interval.

photon noise, which affected sensitivity at the low luminance intensities (right graph), was affected by a factor of 4.0.

The 4-fold age-related increase in photon noise found in the current study suggests that the cones of older adults absorbed four times fewer photons than the ones of the young adults. This lower absorption rate cannot be due to age-related miosis (i.e., smaller pupil) because observers were wearing an artificial pupil equating the amount of photons entering the eye. Furthermore, the lower absorption rate cannot be due to an age-related yellowing of the lens reducing the amount of short-wavelength photons reaching the retina, because a similar age-related effect was observed even when using only high wavelengths (i.e., red, Fig. 8) that are little affected by the yellowing of the lens. The absence of a considerable age-related yellowing of the lens effect in the current study can be explained by the strict inclusion criteria, which asserted that participants were healthy and had a good visual acuity ($\geq 6/7.5$). We conclude that the main known age-related factors reducing retinal illumination, namely, miosis and the yellowing of the lens, had little impact on the age-related contrast sensitivity losses observed in the current study.

If the lower number of photons absorbed by the elderly was not due to a reduction in the number of photons reaching the retina, then it must be due to a loss of cones or a lower absorption efficiency of cones. The exact loss of cones with aging remains debated,[38,39] but no study found evidence of a large loss of cones with aging that could explain the 4-fold decrease of photon absorption rate observed in the current study. This suggests that the age-related decrease in photon absorption rate was mainly due to lower absorption efficiency

L) as a function of SF, at which photon noise was the dominating noise source. The *third graph* represents equivalent input noise (N_{eq}) at the high luminance condition as a function of SF at which neural noise was the dominating noise source. The slopes of the fits are represented by s_A for the older adults and by s_Y for the young adults. The data are represented by *gray dots* fitted by our model with *dashed lines* for the older adults and by *black dots* fitted with our model with *solid lines* for the young adults. Data are all in energy. The *error bars* represent the standard error of the mean (most of them are not visible, being smaller than the size of the marker). The *last graph* summarizes the aging effect in energy units on each parameter of the model, which are the Modulation Transfer Function (MTF) at 16 cyc/deg, the photon noise, the neural noise slope (sl), and the neural noise average (av) across SF. The *error bars* represent the 95% confidence interval.
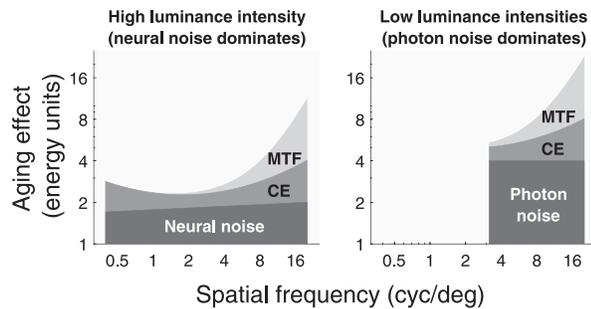
FIGURE 9. Impact of the different internal factors on the age-related sensitivity loss. The age-related sensitivity loss is represented for the different SFs at high luminance intensity on the *left graph* and at low luminance intensities on the *right graph*. Each factor responsible for the aging effect is represented with a different graduation of *gray*.

of the cones, not to a loss of cones. The results of the current study therefore suggest that a lower absorption efficiency of the cones considerably affects vision of older observers in low-brightness environments (e.g., driving at night[40]). This conclusion differs from the one reached by previous studies,[32,41] which mainly attributed age-related contrast sensitivity losses to an increase of the lens opacity and miosis reducing the amount of light reaching the retina, whereas the current study mainly attributes them to less efficient cones. Note that both conclusions suggest that persons who are elderly absorb fewer photons, but only our conclusion is consistent with our data as the pupil diameter was controlled for using an artificial pupil and similar age-related sensitivity losses were observed when using only high wavelengths (i.e., red), which are little affected by the yellowing of the lens.

A possible explanation of the lower absorption rate of cones is a change of morphology related to the decreased density of rods (i.e., approximately a 30% loss[39,42,43]) occurring with aging. Indeed, the loss of rods disorganizes the alignment of the cones by giving less support to the cones and therefore induces a change in the orientation of the cones, reducing their absorption rate.[44]

Optical aberrations (i.e., MTF) were found in the literature to greatly degrade contrast sensitivity with aging.[45,46] A reason that the aging effect on the MTF was not significant in the current study could be that the older participants had to have a good acuity ($\geq$6/7.5) and healthy eyes to be included in the study, and a relatively small artificial pupil (2.5 mm) was used, which reduces the impact of optical aberrations. Consequently, the absence of a considerable age-related increase in optical aberrations observed in the current study is likely not representative of the elderly population.

The 2-fold increase in neural noise with aging found in the current study could be due to various age-related neurobiological alterations such as more spontaneous activity, less inhibition, a decrease of the myelin density, or fewer synapses.[4,47] In any case, this aging effect on neural noise was not specific to some SFs, which suggests that there was not a greater loss in density of neurons sensitive to low SFs than neurons sensitive to high SFs.

A modest age-related decline in calculation efficiency was observed and this effect was similar across SFs (i.e., no interaction between SF and age; Fig. 5). Taken alone, this result could be due to numerous factors affecting the ability of elderly persons to perform the task such as cognitive impairment, attention, lack of motivation, or fatigue. Indeed, an age-related factor affecting performance in both absence and presence of noise would affect calculation efficiency, not equivalent input noise (and thus, not the MTF, photon noise,

or neural noise). The fact that the effect of aging on calculation efficiency was modest suggests that age-related effects not related to perception per se, were, at most, modest. Nonetheless, combining the current results with the ones of a previous study[8] suggests that this modest age-related decline in calculation efficiency was due to a less efficient spatial integration, not to a nonperceptual factor like cognitive impairment, attention, or fatigue. This previous study[8] found no aging effect on the calculation efficiency at 1 cyc/deg, a modest decline at 3 cyc/deg, and a greater decline at 9 cyc/deg. The absence of an aging effect on calculation efficiency at 1 cyc/deg was due to the fact that young and older adults had similar contrast thresholds in high noise, which rules out any effect due to cognitive impairment, attention, lack of motivation, or fatigue, and implies that the effect observed in the other conditions was specific to perception per se. Because this previous study[8] used a spatial window with a size fixed to 4° of visual angle, the number of visible cycles of the signal increased with the SF (4, 12, and 36 visible cycles, respectively). Given that the number of cortical neurons stimulated is proportional to the number of visible cycles,[34] the ability to integrate across many cortical neurons would be more useful when more cortical neurons are stimulated (i.e., more visible cycles). Consequently, if older observers were less efficient at integrating across many visible cycles, then age-related calculation efficiency declines would be greater when more cycles are visible. In the current study, the same number of visible cycles were presented for all SFs (eight visible cycles for which it has been shown that contrast sensitivity reaches a plateau[48]) and the modest aging effect was similar across SFs. Taken together, the results of the current and the previous study[8] suggest that healthy aging impairs spatial integration as the decline in calculation efficiency depends on the number of visible cycles of the signal.

A limitation of the current study was that older adults were not representative of the aging population, having, for instance, higher visual acuity. However, we would expect a similar or lower absorption rate by photoreceptors in a more representative aging population, which would only reinforce the main finding of the current study. Another limitation was that a cross-sectional paradigm was used, so it is possible that the age-related effects may not be due to aging per se but to other confounding factors. To minimize the impact of this limitation, partial correlations were used to control for the more likely confounding factors. Another limitation is that the interpretation of the underlying causes of age-related contrast sensitivity loss (e.g., absorption rate of photoreceptors) relies on the application of a psychophysical noise paradigm.[9] The current conclusion that aging affects the absorption rate of photoreceptors is currently being tested by combining physiological and psychophysical approaches.

To summarize and in conclusion, the current study suggests that an age-related increase in neural noise (e.g., spontaneous neural activity) considerably impairs contrast sensitivity at high luminance intensities, whereas a considerable decline in the ability of cones to absorb photons greatly impairs contrast sensitivity at low luminance intensities. Furthermore, an age-related decline in calculation efficiency likely due to a decline in spatial integration would also impair contrast sensitivity to large targets at all luminance intensities.

Thus, besides the optical factors and the neural factors, the absorption rate of cones is an important factor impaired with aging that has been overlooked and considerably affects vision under dim light. In order to prevent this age-related decline, additional studies should investigate the causes of less efficient cones (e.g., morphologic changes).

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