

Age-related decline of contrast sensitivity for second-order stimuli: Earlier onset, but slower progression, than for first-order stimuli

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Many visual functions are known to decline during aging (P. D. Spear, 1993). However there has been no clear description as to how contrast sensitivity for second-order stimuli changes across the adult life span. Based on different mechanisms underlying perception of first-/second-order stimuli (Z. L. Lu & G. Sperling, 2001), and J. Faubert's (2002) theory of visual perception and aging, it is expected that perception of these two types of stimuli will change in different ways during aging. In this study we have measured contrast sensitivity for both first- and second-order stimuli in 141 subjects aged from 19 to 79 years old. The results have shown no gender effect but an evident aging effect, i.e., a progressive decline during aging, for perception of both types of stimuli. We have also proposed a piecewise linear model to interpret our data. Based on this model, contrast sensitivity for second-order stimuli begins to decline significantly earlier than for first-order stimuli, but with a slower rate of progression. We suggest the earlier decline for perception of second-order stimuli may be interpreted as reflecting a greater complexity of second-order processing.

Keywords: aging effect, gender effect, first-order stimuli, second-order stimuli, piecewise linear model

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Introduction

As the aging population increases, more and more attention has been attracted by age-related changes in visual perceptual capabilities. In the past thirty years, many psychophysical studies have been conducted to investigate changes in a number of visual functions, such as visual acuity (Frisen & Frisen, 1981; Owsley, Sekuler, & Siemsen, 1983), spatial contrast sensitivity (Crassini, Brown, & Bowman, 1988; Elliott, Whitaker, & MacVeigh, 1990; Owsley et al., 1983; Sloane, Owsley, & Jackson, 1988), spatiotemporal interactions (Elliott et al., 1990; Sloane et al., 1988; Tulunay-Keeseey, Ver Hoeve, & Terkla-McGrane, 1988), hyperacuity (Kline, Culham, Bartel, & Lynk, 2001; Odom, Vasquez, Schwartz, & Linberg, 1989), motion perception (Bennett, Sekuler, & Sekuler, 2007; Billino, Bremmer, & Gegenfurtner, 2008; Gilmore, Wenk, Naylor, & Stuve, 1992; Habak & Faubert, 2000; Snowden & Kavanagh, 2006) and 2-/3-dimensional shape perception (Norman, Clayton, Shular, & Thompson, 2004; Wist, Schrauf, & Ehrenstein, 2000). Most of these functions decline significantly during aging.

It has been suggested that senescent optical changes are insufficient to account for these functional declines (Spear, 1993). Age-related anatomical and physiological changes in the lateral geniculate nucleus (LGN), photoreceptors and retina ganglion cells are relatively minor (Spear, 1993; Spear, Moore, Kim, Xue, & Tumosa, 1994). Thus the functional declines cited above have been attributed to significant changes in the visual cortex during aging. This has been supported by anatomic studies (Peters, 2002; Peters, Moss, & Sethares, 2001) and electrophysiological recording studies on neurons in striate and extra-striate visual cortex (Hua et al., 2006; Leventhal, Wang, Pu, Zhou, & Ma, 2003; Liang et al., *in press*; Schmolesky, Wang, Pu, & Leventhal, 2000; Wang, Zhou, Ma, & Leventhal, 2005; Yang et al., 2008; Yu, Wang, Li, Zhou, & Leventhal, 2006).

First- and second-order stimuli are two types of patterns which have been used to characterize early visual processing. The former are defined by modulation of luminance, and the latter are defined by changes in features, such as contrast or texture (Lu & Sperling, 2001). It has been suggested that these two types of stimuli are ubiquitous in everyday visual scenes, and that

natural images are rich in both kinds of information (Johnson & Baker, 2004; Schofield, 2000). In a noisy environment, first- and second-order stimuli can be combined to improve perceptual accuracy (Johnson & Baker, 2004; Smith & Scott-Samuel, 2001). Therefore it seems likely that, perception of these two types of stimuli plays an important role in people's daily life, and so it is pertinent to elucidate age-related changes in their perception. The purpose of the present study is to make some progress in understanding this issue.

Converging evidence has suggested that there are two, at least partly, distinct mechanisms underlying perception of first- and second-order stimuli (Ashida, Lingnau, Wall, & Smith, 2007; Baker, 1999; Baker & Mareschal, 2001; Larsson, Landy, & Heeger, 2006; Lu & Sperling, 2001; Nishida, Ledgeway, & Edwards, 1997; Vaina & Cowey, 1996; Vaina, Makris, Kennedy, & Cowey, 1998; Vaina & Soloviev, 2004). Different computational models (Chubb & Sperling, 1989; Landy & Graham, 2004; Lu & Sperling, 2001; van Santen & Sperling, 1984; Wilson, Ferrera, & Yo, 1992) have also been developed for the processing of these two types of stimuli. Now it is generally recognized that the latter requires additional stages, such as rectification (or other nonlinearity) and a second filter.

It was initially hypothesized that first- and second-order stimuli were processed in the V1-MT and V1-V2-MT pathways, respectively (Wilson et al., 1992). However, recent studies have indicated most retinotopically organized visual cortical areas contain neurons selective for both kinds of stimuli (Ashida et al., 2007; Dupont, Sáry, Peuskens, & Orban, 2003; Greenlee & Smith, 1997; Larsson et al., 2006; Nishida, Sasaki, Murakami, Watanabe, & Tootell, 2003; Seiffert, Somers, Dale, & Tootell, 2003). On the other hand, some studies (Dumoulin, Baker, Hess, & Evans, 2003; Smith, Greenlee, Singh, Kraemer, & Hennig, 1998; Wenderoth, Watson, Egan, Tochon-Danguy, & O'Keefe G, 1999) have revealed a response bias for second-order stimuli in some visual cortical areas, such as V3 and VP.

Perception of first-order stimuli has been widely studied as a function of aging, typically measuring spatial contrast sensitivity or spatiotemporal interactions. In a large-sample study, Owsley et al. (1983) found that only the sensitivity to low spatial frequency static gratings remained the same throughout adulthood. For medium to high spatial frequencies, sensitivity decreased with age. Moreover, the sensitivity was found to be higher to moving than to static 1 cycle/degree gratings for all subjects, but the sensitivity enhancement also decreased with age. Similar results were also obtained for both central and peripheral vision by Crassini et al. (1988). For flickering gratings, Sloane et al. (1988) measured contrast sensitivity as a function of target luminance in younger and older adults and found a decreased sensitivity for older adults across all eight luminance levels. Additionally, sensitivity differences between younger and older adults are larger at some spatial frequencies and flickering

rates. Tulunay-Keesey et al. (1988) studied the effect of aging on spatiotemporal contrast sensitivity at both threshold and suprathreshold levels and found a progressive age-related decline of sensitivity for high spatial and temporal frequencies. Similarly, Elliott et al. (1990) measured contrast sensitivity over a range of spatial and temporal frequencies in both young and old observers, and also showed significantly reduced performance of older observers for some spatial and temporal frequencies.

On the other hand, few studies have investigated the effect of aging on the perception of second-order stimuli. Habak and Faubert (2000) measured contrast thresholds of nine young observers (mean age 23.0 ± 1.58 years) and nine elderly observers (mean age 69.7 ± 4.42 years) for static and moving gratings defined by luminance or by contrast, and for a temporally segmented second-order motion stimulus. Their results showed that the contrast sensitivity for both types of stimuli significantly decreased in elderly observers and there was a larger effect of aging on the perception of contrast-defined stimuli. However their study was based on a small sample size ($n = 18$) and covered a limited age range (range 21–26 and 64–79 years old).

Based on a series of studies on aging and its effect on perceptual processing and working memory capacity for visual stimuli, Faubert (2002) has suggested that both low and higher-level perceptual functions are probably altered during aging, but that the extent of age-related perceptual deficits depends on the complexity of the neural circuitry involved for processing a given task. Some perceptual functions involving minor neural circuitry may still be performed at similar performance levels because of the recruitment of alternate neural networks. However, when processing is more complex or requires larger simultaneous networks, performance will break down. On this basis it can be expected that, during aging, second-order processing will break down earlier than first-order processing.

In this study we have made a large-sample investigation of the contrast sensitivity of subjects at different ages for both first-order (luminance-defined) and second-order (contrast-defined) stimuli. In [Experiment 1](#), we find a progressive decline in perception of both first- and second-order stimuli during aging. We have also proposed a piecewise linear model to interpret our data. Based on this model, it is clear that in adulthood, log contrast sensitivity for first- and second-order stimuli remains stable during the first stage and declines linearly during the second stage. In line with the prediction cited above, log contrast sensitivity for second-order stimuli begins to decline earlier than for first-order stimuli. However, the slope of decline is faster for the latter. In the control experiment ([Experiment 2](#)), we have excluded the possibility that the later decline in contrast sensitivity for first-order stimuli found in [Experiment 1](#) is due to its lack of the noise carrier used for second-order stimuli. Additionally, since older subjects have a smaller pupil size (Owsley et al., 1983; Weale, 1963), which will reduce the retina illuminance (Weale, 1963) and thereby reduce

contrast sensitivity (Kelly, 1972), we have also considered this effect in the control experiment. Our results showed that this effect was not statistically significant in the present study.

Furthermore, because of previous conflicting reports of gender effects on motion perception during aging (Billino et al., 2008; Gilmore et al., 1992; Owsley et al., 1983; Snowden & Kavanagh, 2006), we have also considered this in the present study. Our results in Experiment 1 suggest there is no gender effect on contrast sensitivity for both types of stimuli, either static or moving, when subjects are well matched for age.

Experiment 1

Methods

Subjects

One hundred and forty-one subjects aged from 19 to 79 years old were recruited in the present study. Subjects younger than 30 years old were students of the University of Science and Technology of China, while others were recruited from local communities. All subjects had normal or corrected-to-normal visual acuity (better than 20/25) and were free from ocular diseases. The Mini-Mental State Examination (MMSE) was performed on old subjects to exclude probable dementia. Alcoholism, stroke and depression were also exclusion criteria. Subjects were divided into five groups according to their ages. Table 1 gives the characteristics of these subjects in detail. All subjects were naive to the psychophysical experiments, and their informed consent was obtained before participation. This research has been approved by the ethics committee in University of Science and Technology of China, and was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Group (age range)	Gender	Sample size	Age (years)	Visual acuity
1 (19–29)	Female	16	21.31 ± 1.49	0.87 ± 0.16
	Male	16	22.25 ± 1.77	0.85 ± 0.10
2 (30–49)	Female	16	37.88 ± 5.69	0.85 ± 0.12
	Male	16	36.81 ± 4.71	0.78 ± 0.10
3 (50–59)	Female	14	54.79 ± 3.02	0.90 ± 0.18
	Male	16	56.06 ± 2.35	0.99 ± 0.25
4 (60–69)	Female	12	63.08 ± 2.15	0.97 ± 0.12
	Male	16	64.06 ± 2.81	1.04 ± 0.11
5 (70–79)	Female	10	72.67 ± 3.04	1.19 ± 0.11
	Male	9	72.10 ± 2.88	1.10 ± 0.20

Table 1. Characteristics of five age groups. Visual acuity is expressed as minimum angle of resolution (MAR). Data are expressed as mean ± SD.

Apparatus and visual stimuli

All stimuli were generated by a PC running Matlab software based on version 2.50 of Psychtoolbox (Brainard, 1997; Pelli, 1997), and were presented on a gamma-corrected Sony G220 CRT monitor, which had a refresh rate of 160 Hz, a resolution of 640 × 480 pixels and 36 cd/m² mean luminance. Using a custom-built device, the display system produced 14-bit gray-levels (Li, Lu, Xu, Jin, & Zhou, 2003). Subjects viewed the display binocularly in a dimly lit room at a viewing distance of 0.93 m.

The first-order stimulus was a luminance-defined 2 cycle/degree sine wave grating (Figure 1a) while the second-order stimulus was a static gray-scale noise carrier whose contrast was modulated by a 2 cycle/degree sine wave grating (Figure 1b). The luminance profile at point (x, y) of the first- (Equation 1) and second-order (Equation 2) stimuli are defined as:

$$l(x, y) = L_{mean} \{1 + C \cdot \sin\{2\pi[f(y\cos\theta - x\sin\theta) + \omega t] + \phi\}\}, \quad (1)$$

$$l(x, y) = L_{mean} \{1 + R(x, y)C_c \{1 + C \cdot \sin[2\pi(f(y\cos\theta - x\sin\theta) + \omega t) + \phi]\}\}, \quad (2)$$

where L_{mean} is the background luminance of the display; $R(x, y)$ is the static noise carrier, consisting of single-pixel dots whose values were randomly assigned as 1 or -1 ; C_c is the contrast of the noise carrier (here set to 0.5); f is the spatial frequency of the sine wave grating (here set to 2 cycle/degree); θ represents the orientation of the grating (0 or 90 in the static orientation task, or 90 in the motion direction discrimination task); ω is the temporal frequency of the moving grating (when ω is set to 0, the stimulus is static); ϕ is the (random) initial spatial phase; and C is the grating contrast.

Experimental design

An orientation task and a direction of motion task were used to measure contrast thresholds for static and moving stimuli, respectively. In the orientation task, the subject was required to indicate the orientation of the static grating (vertical vs. horizontal). In the direction of motion task, the subject was required to indicate the direction of the grating's motion (leftwards vs. rightwards). Two short sessions were used for the static first- and second-order orientation task. Each short session contained 100 trials and lasted about five minutes. Another two long sessions, each about twenty-five minutes, were used for the direction of first- and second-order motion tasks. Each long session contained 4 blocks (100 trials each). Before the formal session began, each subject was provided with a short training session.

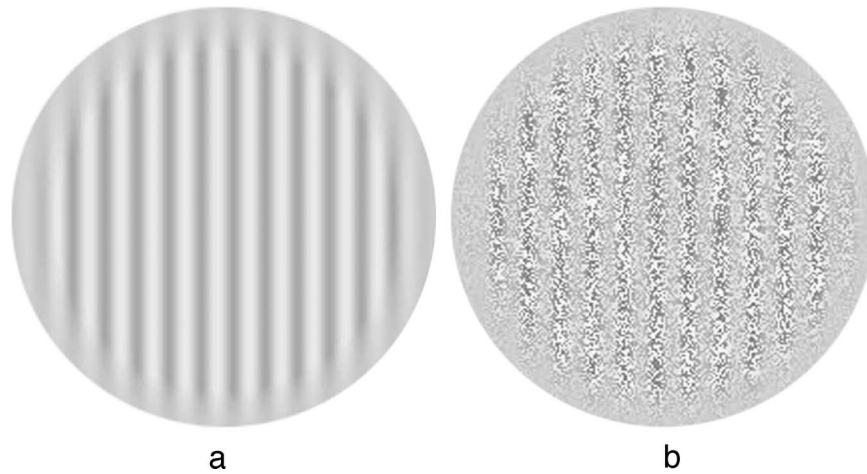


Figure 1. Stimuli, (a) first-order grating and (b) second-order grating, used in these experiments.

In the direction of motion task, the grating was drifted at 1, 2, 4 or 8 cycles/second. In each block, the moving gratings with different speeds were mixed together.

By using a two-alternative-forced-choice design and a three-down one-up staircase procedure (Levitt, 1971), a contrast threshold (converging at 79.4% correct) of each subject was measured for each task. Contrast sensitivity (reciprocal of contrast threshold) was used for data analysis.

Procedure

All trials were initiated by the subjects. In each trial, the stimulus was preceded by a short beep and presented for 300 ms. Then the subject indicated her/his decision with a keyboard button press. No feedback was provided.

Statistical analysis and model fitting

An analysis of covariance (ANCOVA) was first conducted to assess the gender and aging effects on the contrast sensitivity for first- and second-order stimuli. Visual acuity, expressed as minimum angle of resolution (MAR), was defined as a covariate. Correlation analysis was then used to reveal the relation between age and contrast sensitivity.

Finally, we compared how well different models of age-related decline would fit our data. The first idea is that contrast sensitivity declines log-linearly throughout adulthood (Figure 2a). Inspection of our data (see Figure 4) suggested two other candidates (Figures 2b and 2c) which specified two stages of change in log contrast sensitivity, having different log-linear slopes. In the first stage, log contrast sensitivity remains stable for one model (Figure 2b) while it changes for the other (Figure 2c). These three models have the following forms:

$$\log(S) = k \times \log(\text{Age}) + c_0, \quad (3)$$

$$\log(S) = \begin{cases} c & (\log(\text{Age}) \leq bp) \\ k \times (\log(\text{Age}) - bp) + c & (\log(\text{Age}) > bp) \end{cases}, \quad (4)$$

$$\log(S) = \begin{cases} k_1 \times (\log(\text{Age}) - bp) + c & (\log(\text{Age}) \leq bp) \\ k_2 \times (\log(\text{Age}) - bp) + c & (\log(\text{Age}) > bp) \end{cases}, \quad (5)$$

where S is the contrast sensitivity for the static stimuli or the mean of the contrast sensitivities for moving stimuli with different speeds; k , k_1 and k_2 are slopes of linear functions, c_0 and c are intercepts and bp corresponds to the break point of the piecewise linear function.

To estimate the model parameters, subjects were divided into twelve groups according to their age ranges: [19, 25], [25, 31], [31, 36], [36, 41], [41, 45], [45, 51], [51, 56], [56, 61], [61, 66], [66, 71], [71, 75] and [75, 79]. The $\log(S)$ and $\log(\text{Age})$ of subjects in the same group were averaged, and these data, weighted by their standard deviations, were then fit with each of the functions listed above.

The model fitting procedures were implemented in Matlab with the Curve Fitting Toolbox (Mathworks). The sum of squared differences ($\sum\{[\log(S)]_{theory} - [\log(S)]_{measured}\}^2$) between the log measured sensitivity ($[\log(S)]_{measured}$) and the log model-predicted sensitivity ($[\log(S)]_{theory}$) was minimized. The goodness-of-fit was evaluated by the r^2 statistic:

$$r^2 = 1.0 - \frac{\sum\{[\log(S)]_{theory} - [\log(S)]_{measured}\}^2}{\sum\{[\log(S)]_{measured} - \text{mean}[\log(S)]_{measured}\}^2}. \quad (6)$$

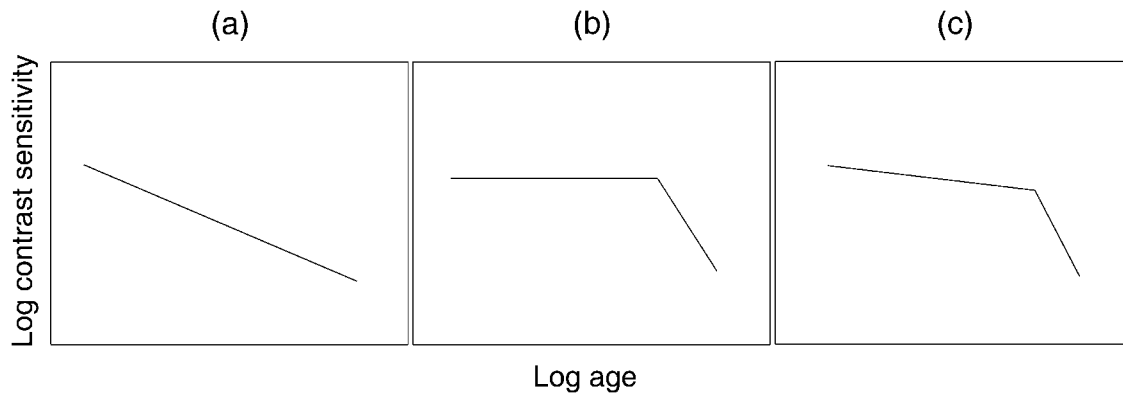


Figure 2. Three models used to fit our data. (a) A linear function, which predicts that the contrast sensitivity declines log-linearly throughout adulthood. (b, c) Piecewise linear functions, which specify two stages of change in log contrast sensitivity, having different log-linear slopes. In the first stage, log contrast sensitivity remains stable for b, while it changes for c.

Because these three models are nested (i.e., their parameters are proper subsets or supersets of one another), an *F*-test could be used to compare a full to a reduced model (Hays, 1988):

$$F(df_1, df_2) = \frac{(r_{full}^2 - r_{reduced}^2)/df_1}{(1 - r_{full}^2)/df_2}, \quad (7)$$

where $df_1 = k_{full} - k_{reduced}$ and $df_2 = N - k_{full} - 1$. The k 's are the number of parameters in each model and N is the number of predicted data points. The model which had the fewest parameters but provided a fit that was statistically equivalent to the other models, was selected as the best model.

The standard error of the mean (*SE*) of each model parameter for the best-fitting model was estimated using a re-sampling method (Maloney, 1990). Each data point was assumed to have a Gaussian distribution with its mean

value and standard deviation equal to the estimated values from the experimental data. Then a set of data points could be generated by sampling each of the Gaussian distributions once. We repeated this process to generate 1000 data sets, each of which was used to find a curve-fit; the *SE*s of these 1000 parameter sets provided error estimates for the model parameters.

Results

Aging and gender effects

The contrast sensitivities of five different age groups for first and second-order stimuli are shown in Figures 3a and 3b, respectively. Since there were no significant differences between the data for females and males (statistical analyses are shown in the following paragraphs), we collapsed them here. Data for static and moving stimuli

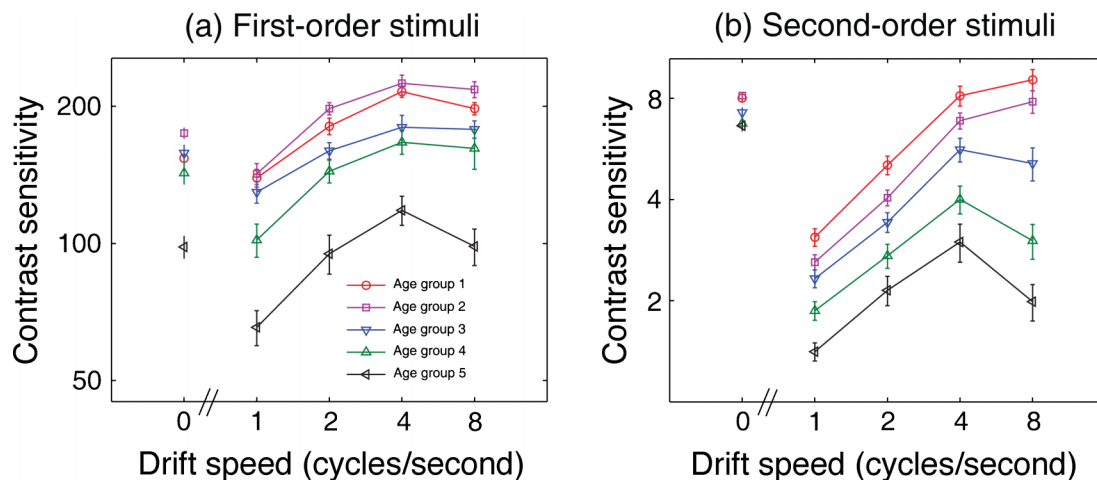


Figure 3. Contrast sensitivities of five age groups for (a) first-order stimuli and (b) second-order stimuli. Contrast sensitivity for the static stimuli is shown on the left side of each figure, with the drift speed of 0. Note that contrast sensitivities for both types of stimuli gradually decline during aging. Error bars indicate standard error of the mean.

are shown on the left and right side of each figure, respectively.

A first within-subject ANCOVA (group \times gender \times stimulus type \times drift speed with MAR as a covariate) was conducted on all our data. Age group and gender were defined as between-subject factors, while stimulus type and drift speed were defined as within-subject factors. The static stimuli were regarded as those with a drift speed of 0 Hz. The results showed a significant three-way interaction ($F[16,520] = 1.817, p = 0.026$) between stimulus type, drift speed and age group. As can be seen in [Figure 3](#), this three-way interaction was characterized by a smaller degradation with age in perception of static second-order stimuli, slightly different shapes of the temporal contrast sensitivity functions of age groups 1 and 2 for second-order motion (compared with other age groups), and various degradation patterns for different stimulus types during aging. In order to further explore the effects of gender and aging on perception of both types of stimuli, separate ANCOVAs were conducted.

Separate two-way ANCOVAs (group \times gender with MAR as a covariate) were conducted for the static first- and second-order orientation tasks. The results showed a significant effect of age group (for first-order stimuli, $F[4,130] = 7.208, p < 0.001$; for second-order stimuli, $F[4,130] = 4.424, p = 0.002$), while the effects of gender (for first-order stimuli, $F[1,130] = 2.162, p = 0.144$; for second-order stimuli, $F[1,130] = 2.259, p = 0.135$) and the age group \times gender interaction (for first-order stimuli, $F[4,130] = 1.060, p = 0.379$; for second-order stimuli, $F[4,130] = 1.171, p = 0.327$) were not significant. Therefore there were no main or interaction effects involving gender but there was a significant age effect for the static orientation task.

Similarly, separate two three-way ANCOVAs (group \times gender \times drift speed with MAR as a covariate) were conducted for first- and second-order motion tasks. Age group and gender were defined as between-subject factors, while drift speed was defined as a within-subject factor. Again, a significant effect of age (for first-order motion, $F[4,130] = 15.295, p < 0.001$; for second-order motion, $F[4,130] = 12.515, p < 0.001$) was found. In contrast, the effect of gender (for first-order motion, $F[1,130] = 0.054, p = 0.817$; for second-order motion, $F[1,130] = 1.732, p = 0.190$) and group \times gender interaction (for first-order motion, $F[4,130] = 0.463, p = 0.763$; for second-order motion, $F[4,130] = 0.455, p = 0.769$) were not significant. Thus the effects of age and gender were the same as in the static orientation task.

From [Figure 3](#), it is clear that the sensitivity for first-order stimuli is significantly higher than for second-order stimuli and that they both gradually decline during aging. There is a larger sensitivity decline for the perception of the static first-order stimuli (about 1 log unit in [Figure 3a](#)) than for the perception of the static second-order stimuli (about 0.5 log units in [Figure 3b](#)). In contrast, the decline of motion perception remains approximately the same

(about 1 log unit) across different drift speeds and stimulus types (1.13, 1.02, 0.92 and 1.10 log units for different drift speeds of first-order motion, respectively; 1.10, 1.28, 1.56, 2.25 log units for different drift speeds of second-order motion, respectively).

Correlation between age and contrast sensitivity

To further reveal the relationships between these contrast sensitivity measurements and age, correlation analyses were conducted. Because there were differences in the mean visual acuity of the five age groups, a Pearson correlation coefficient between contrast sensitivity and visual acuity was also calculated. The results ([Figure 4](#)) showed that contrast sensitivities were significantly correlated with both age ($p < 0.001$) and visual acuity ($p < 0.001$) in all cases. Since visual acuity also had a significant effect on contrast sensitivity, partial correlation analyses were further conducted to exclude this influence. The results revealed significant negative effects of aging on contrast sensitivities for both first- ($p < 0.05$) and second-order ($p < 0.001$) stimuli.

Model fitting

We employed a model to further reveal the exact relations between the contrast sensitivity measurements and age. As described in the [Methods](#), we considered three different candidates ([Equations 3–5](#)) here. Goodness-of-fit of these models was evaluated and these different variants of the models were compared using an F -test for nested models. The results ([Table 2](#)) showed that the piecewise linear functions, models 2 and 3 ([Equations 4 and 5](#)), were both significantly better ($p < 0.05$) than the simple linear function, model 1 ([Equation 3](#)). Although the goodness-of-fit of model 3 was slightly better than that of model 2, the differences between them were not statistically significant. Because model 2 has fewer parameters, we choose it as the best-fitting model. Model 2 could account for 85.3%–93.8% of the variance of our data ([Table 2](#)).

The age-related contrast sensitivity functions (contrast sensitivity for the static stimuli or the mean of the contrast sensitivities for moving stimuli with different speeds vs. age) for both types of stimuli fit with model 2 are shown in [Figure 5](#). Based on this model, it is clear that the change of contrast sensitivity for both types of stimuli comprises two stages throughout adulthood. In the first stage, log contrast sensitivity remains stable and in the second stage, it declines log-linearly.

It can be seen in [Figure 5](#) that the location of the break point between these two stages varied for different stimuli. The locations of break points for first-order stimuli (1.790 in the static orientation task and 1.748 in the direction of motion task) were later than for second-order stimuli (about 1.63 in both the static orientation task and the direction of motion task). In other words, contrast

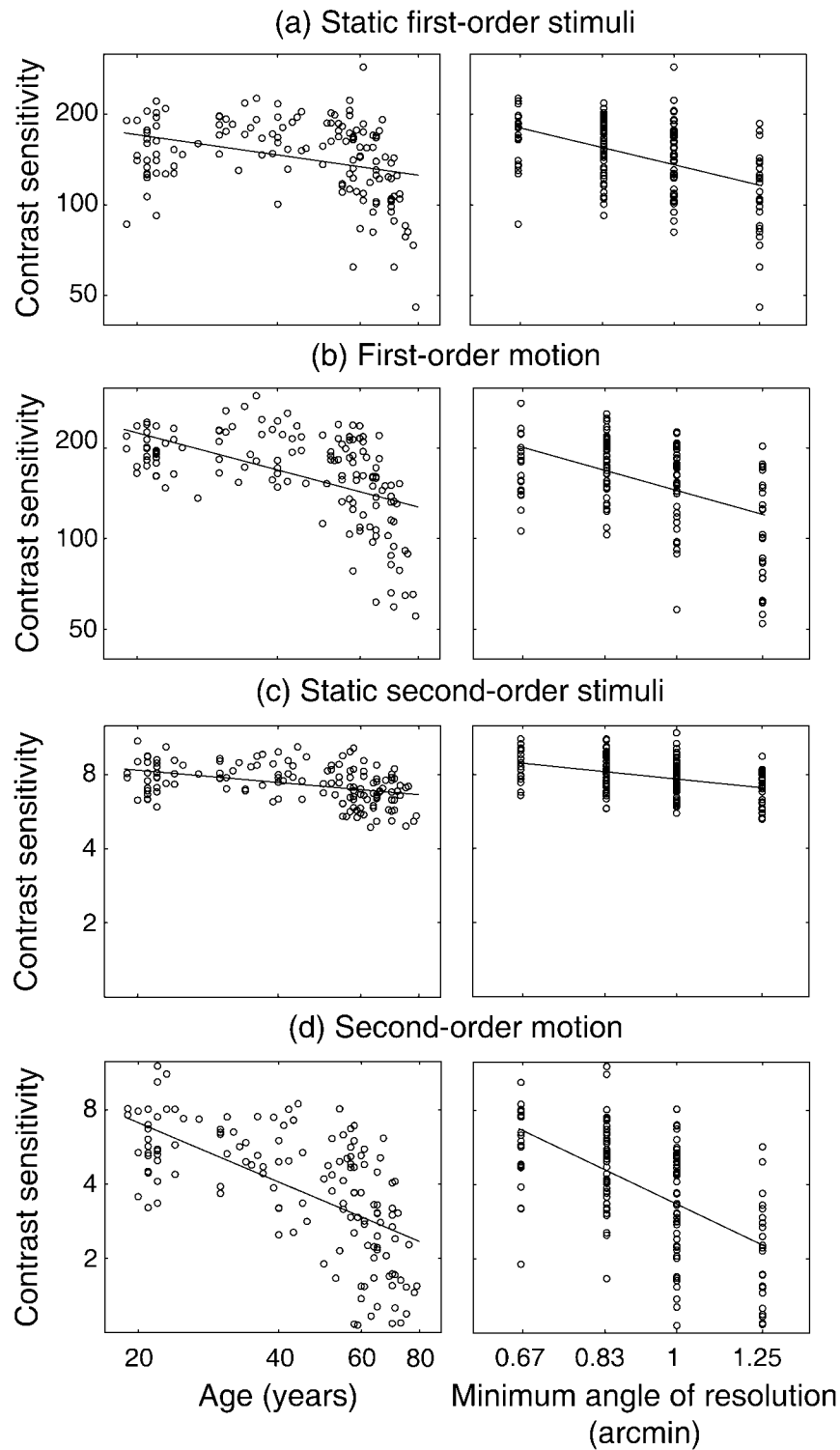


Figure 4. Correlations between age/visual acuity and contrast sensitivities for (a) static first-order stimuli, (b) first-order motion, (c) static second-order stimuli and (d) second-order motion. Visual acuity is expressed as minimum angle of resolution. Contrast sensitivity of each subject for motion, used here to conduct correlation analysis, is the mean of that for motion with different speeds.

sensitivity for static and moving second-order stimuli declines earlier than for first-order stimuli (at the ages of about 42 and 42 years old vs. 62 and 56 years old, respectively). This hypothesis was supported by statistical analyses based on a re-sampling procedure (see [Methods](#)),

the results of which are shown in [Table 3](#). From [Table 3](#), it is clear that the differences between locations of break points for first- and second-order stimuli in both the orientation task (1.800 ± 0.001 vs. 1.681 ± 0.005 , $t(1259) = 23.493$, $p < 0.001$) and the direction of motion

Parameters	Static first-order stimulus	Static second-order stimulus	First-order motion	Second-order motion
Model 1 <i>c</i>	2.900	1.231	3.225	2.258
<i>k</i>	-0.450	-0.219	-0.631	-1.017
<i>r</i> ²	0.450	0.645	0.577	0.778
Model 2 <i>c</i>	2.210	0.906	2.264	0.738
<i>bp</i>	1.790	1.628	1.748	1.628
<i>k</i>	-3.454	-0.431	-2.768	-1.874
<i>r</i> ²	0.916	0.853	0.938	0.902
Model 3 <i>c</i>	2.200	0.909	2.245	0.605
<i>bp</i>	1.793	1.628	1.753	1.738
<i>k</i> ₁	-0.044	0.028	-0.075	-0.504
<i>k</i> ₂	-3.453	-0.446	-2.768	-2.609
<i>r</i> ²	0.918	0.855	0.941	0.915
Comparison between 1 & 2				
<i>F</i> (1, 8)	44.380	11.320	46.581	10.122
<i>p</i>	<0.001	0.001	<0.001	0.013
Comparison between 1 & 3				
<i>F</i> (2, 7)	19.976	5.069	21.593	5.641
<i>p</i>	0.013	0.044	0.001	0.035
Comparison between 2 & 3				
<i>F</i> (1, 7)	0.171	0.097	0.356	1.071
<i>p</i>	0.692	0.765	0.570	0.335

Table 2. Parameters of three different model fits and results of comparison.

task (1.783 ± 0.002 vs. 1.675 ± 0.004 , $t(1442) = 23.683$, $p < 0.001$) are significant.

Notice that although contrast sensitivity for static and dynamic second-order stimuli begin to decline at similar ages (both about 42 years old), there seems to be a much faster rate of decline for the latter: the slope of decline for second-order motion (3.508 ± 0.083) is about 3.5 times as large as that for static second-order stimuli (1.034 ± 0.040). In contrast, the slopes of decline for static and dynamic first-order stimuli are similar (5.681 ± 0.112 vs. 5.631 ± 0.107). Furthermore, the slopes of decline for first-order stimuli are significantly larger ($p < 0.001$) than those for second-order stimuli.

Experiment 2

We have shown that contrast sensitivity for second-order stimuli declines significantly earlier than for first-order stimuli. However in [Experiment 1](#), the second-order stimuli contained a noise carrier that was not present in the first-order stimuli. The same results might also be expected if the performance in handling the noise carrier significantly degraded while there were no other significant differences between the processing for first- and second-order stimuli during aging. To test this possibility (suggested by an anonymous referee of an earlier version of this manuscript), we have measured the contrast sensitivities of young and old subjects for first-order stimuli with

and without an added noise carrier. If the sensitivity reduction due to the noise carrier has no significant difference between the two groups, the possibility cited above can be excluded.

Additionally, as described in the [Introduction](#), the smaller pupil size of old subjects is a potential factor resulting in reduced contrast sensitivity. In this experiment, we also considered this effect on both types of stimuli.

Methods

Twenty-eight subjects from [Experiment 1](#) participated in this experiment. They were divided into two groups, young ($n = 14$, mean age 23.43 ± 2.90 years) and old ($n = 14$, mean age 71.00 ± 3.62 years). Pupil diameters were measured under the experimental conditions for all these subjects. Mean pupil sizes of the young and old groups were 6.0 ± 0.7 mm and 4.2 ± 0.5 mm, respectively.

When evaluating the influence of the noise carrier in the first-order stimuli, the luminance profile at the point (x, y) of the first-order stimuli with noise carrier ([Equation 8](#)) were defined as:

$$l(x, y) = L_{mean} \{ 1 + R(x, y)C_c + C \cdot \sin \{ 2\pi [f(y \cos \theta - x \sin \theta) + \omega t] + \phi \} \}, \quad (8)$$

The luminance profile at the point (x, y) of the first-order stimuli without noise carrier and the parameter definitions were the same as those in [Experiment 1](#). Contrast

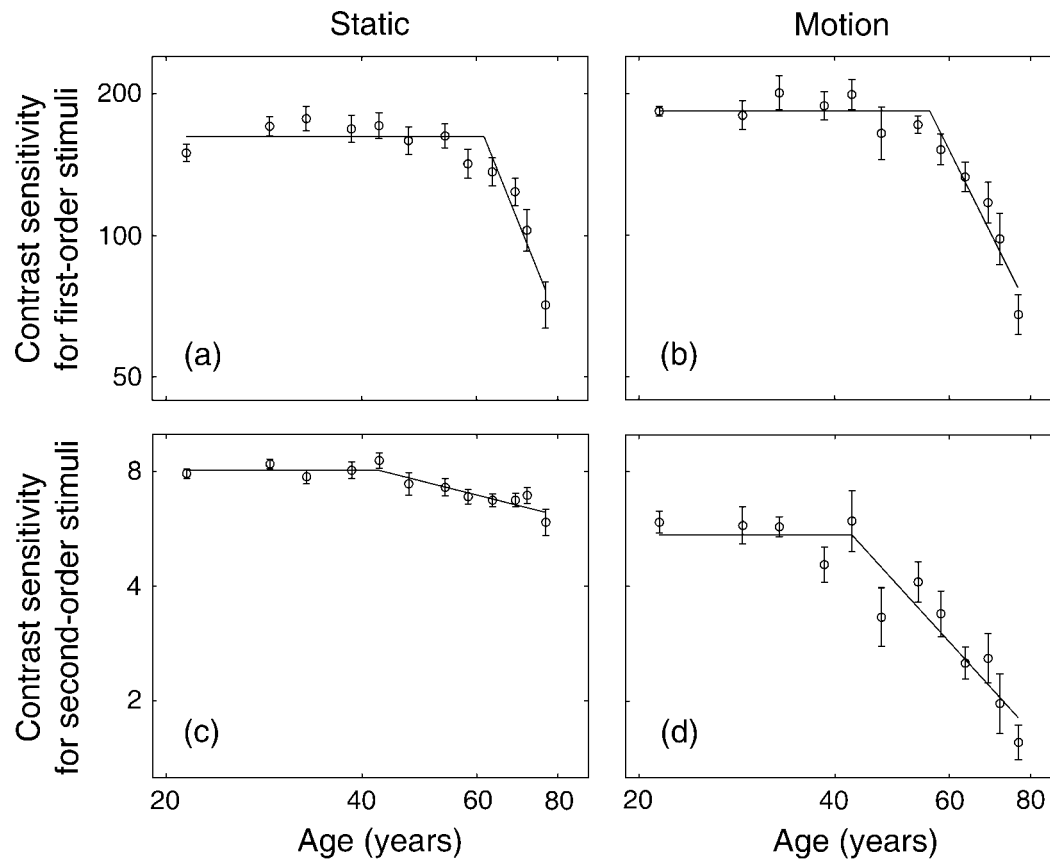


Figure 5. Perception of first- and second-order stimuli as a function of age. Data were fit with the piecewise linear model (Equation 4), with r^2 of 0.916, 0.853, 0.938 and 0.902 for (a) static first-order stimuli, (b) first-order motion, (c) static second-order stimuli and (d) second-order motion, respectively. In all cases, $p < 0.001$. Error bars indicate standard error of the mean.

thresholds for the first-order stimuli with and without the noise carrier were simultaneously measured within one session. Consequently, the number of trials in each block was twice in contrast with Experiment 1. As before, separate sessions were used for the orientation and direction of motion tasks. The contrast sensitivity ratio for these two types of stimuli was calculated for each subject and then used to conduct the data analysis.

When evaluating the influence of the smaller pupil size of old subjects, the stimuli were the same as those in Experiment 1. Since the difference in pupil sizes would result in a reduction of the retinal illuminance by a factor of about 2 for old subjects, contrast thresholds of young subjects for both types of stimuli were re-measured with the screen luminance halved.

All other details of method and procedure were described in Experiment 1.

Results

As shown in Figure 6, contrast sensitivities of both groups were lower for first-order stimuli with noise carrier than without noise carrier, but there were no significant differences between contrast sensitivity ratios of the two groups for both the static orientation task ($t(26) = 1.542$, $p = 0.135$) and the direction of motion task ($F(1, 26) = 0.013$, $p = 0.910$). Thus the later decline in contrast sensitivity for first-order stimuli could not be attributed to the lack of the noise carrier.

	Static first-order stimulus	Static second-order stimulus	First-order motion	Second-order motion
c	2.210 ± 0.001	0.909 ± 0.002	2.254 ± 0.001	0.735 ± 0.001
bp	1.800 ± 0.001	1.681 ± 0.005	1.783 ± 0.002	1.675 ± 0.004
k	-5.681 ± 0.112	-1.034 ± 0.040	-5.631 ± 0.107	-3.508 ± 0.083

Table 3. Distributions of parameters (mean \pm SE) in the best-fitting model, estimated by a re-sampling method.

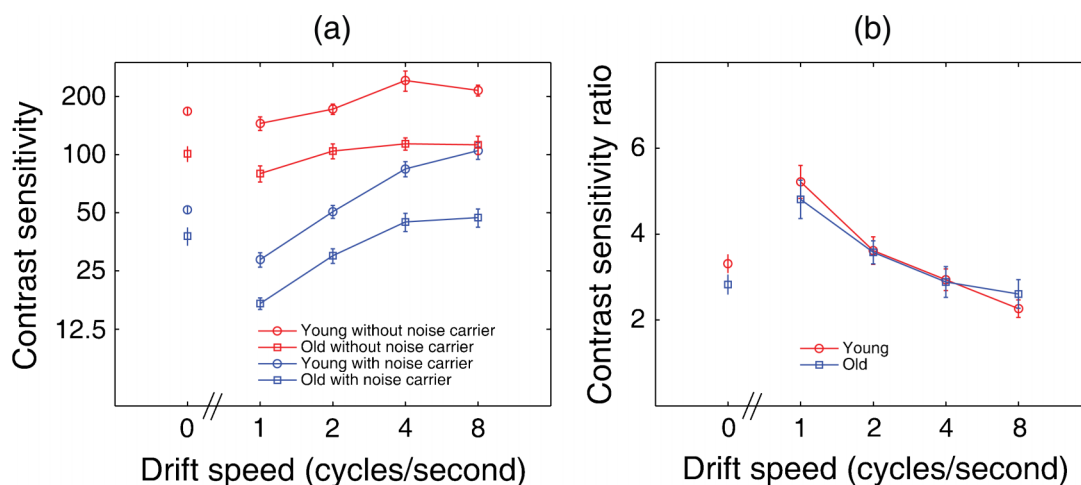


Figure 6. Data used to clarify the effect of noise carrier on contrast sensitivity for first-order stimuli in Experiment 2. (a) Contrast sensitivities of young and old groups for first-order stimuli with and without noise carrier in the static orientation task and direction of motion task, respectively. (b) Ratios between contrast sensitivities for first-order stimuli with and without noise carrier in the static orientation task and direction of motion task, for young and old groups. Contrast sensitivity for the static stimuli is shown on the left side of each figure, with the drift speed of 0. Error bars indicate standard error of the mean.

As shown in Figure 7, the contrast sensitivities of fourteen young subjects under reduced screen luminance were slightly lower than those measured with normal screen luminance. However these differences were not statistically significant for either the orientation task (paired *t*-test, for first-order stimuli, $t(13) = 2.050, p = 0.061$; for second-order stimuli, $t(13) = 1.128, p = 0.280$) or the direction of motion task (within-subject ANOVA, for first-order stimuli, $F(1, 13) = 3.722, p = 0.076$; for second-order stimuli, $F(1, 13) = 3.585, p = 0.081$).

Therefore it seems unlikely that our findings in Experiment 1 were a result of the smaller pupil size of old subjects.

Discussion

Contrast sensitivities for first- and second-order stimuli across the adult life span were investigated in this study.

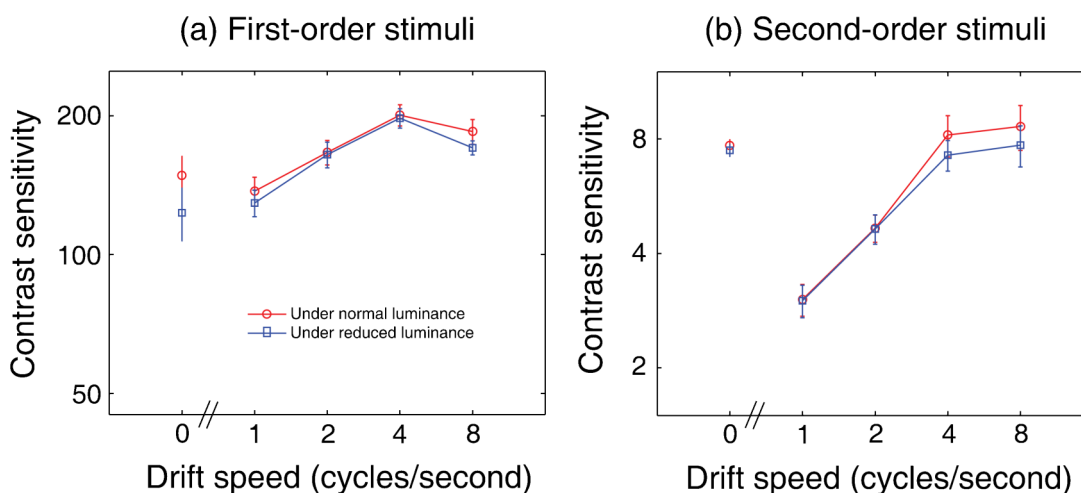


Figure 7. Data used to clarify the effect of retina illuminance on contrast sensitivity for first- and second-order stimuli in Experiment 2. (a) Contrast sensitivity of fourteen young subjects for first-order stimuli under normal and reduced screen luminance in the static orientation task and direction of motion task, respectively. (b) Contrast sensitivity of fourteen young subjects for second-order stimuli under normal and reduced screen luminance in the static orientation task and direction of motion task, respectively. Contrast sensitivity for the static stimuli is shown on the left side of each figure, with the drift speed of 0. Error bars indicate standard error of the mean.

No gender effect was found. But there was a progressive decline in contrast sensitivities for both types of stimuli, both static and dynamic, throughout adulthood. The change of contrast sensitivity across the adult life span can be modeled by a piecewise linear function. Based on this model, contrast sensitivity for second-order stimuli declines significantly earlier than that for first-order stimuli, but with a slower rate of progression. Our control experiments have indicated that these findings are not a result of the smaller pupil size of old subjects or the lack of a noise carrier for first-order stimuli.

Our data on static first-order stimuli is in accordance with previous studies which found a progressive age-related decline in the perception of 2 c/d gratings (Crassini et al., 1988; Elliott et al., 1990; Owsley et al., 1983). Our results on moving first-order stimuli are also similar to the results of Owsley et al. (1983), although their study used a slightly lower spatial frequency (1 c/d).

An effect of aging on perception of second-order stimuli has been reported by Habak and Faubert (2000). As described in the [Introduction](#), they measured contrast sensitivities of nine young subjects (mean age 23.0 ± 1.58 years) and nine old observers (mean age 69.7 ± 4.42 years) for second-order stimuli and found the perceptual performance of old subjects was significantly worse than that of young subjects, consistent with our results.

Using random dot cinematograms, significant gender differences were found in speed discrimination thresholds for translational motion (Snowden & Kavanagh, 2006), coherence thresholds for translational motion (Billino et al., 2008; Gilmore et al., 1992; Snowden & Kavanagh, 2006), radial flow (Billino et al., 2008) and biological motion (Billino et al., 2008). In contrast, a gender effect for dependence of age-related changes in motion perception was found by Gilmore et al. (1992) but not by others. As for first-order stimuli, Owsley et al. (1983) failed to find gender differences in the perception of both static and moving patterns when subjects were well matched for age, in agreement with the present study. Additionally, our results suggest this lack of gender effect is also the same for the perception of second-order stimuli, which has not been previously addressed.

An important issue in the present study is the analysis based on model fitting. The piecewise linear model has been suggested to be a viable model because it can account for most of the variance (85.3%–93.8% in different cases) in our data. Based on this model, we have found an earlier decline during aging for the perception of second-order stimuli, both static and dynamic. Although to our knowledge, no similar results have been reported, a study investigating the development of perception of first- and second-order stimuli in infants suggests something relevant. Ten-month-old infants showed little sensitivity to pure second-order motion but much higher sensitivity to first-order motion (Kato, de Wit, Stasiewicz, & von Hofsten, 2008), which suggested a later development of second-order processing. Since later development is often

associated with earlier decline for many functions, such as sensitivity to sine-wave gratings with high spatial frequencies compared with that with low spatial frequencies (Adams & Courage, 2002; Banks, 1982; Owsley et al., 1983), it might not be surprising that the second-order processing system declines earlier than the first-order processing system during aging.

As described in the [Introduction](#), this earlier decline for perception of second-order stimuli can be interpreted in terms of Faubert's theory (2002) on visual perception and aging. That is to say, the second-order processing system receives more age-related deterioration than the first-order processing system does since the former involves more complex neural circuitry, and therefore the contrast sensitivity for second-order stimuli declines earlier than that for first-order stimuli during aging.

We have also found different rates of decline for perception of these stimuli based on the piecewise linear model. Firstly, the rates of decline are faster for perception of first-order stimuli than for second-order stimuli. This finding seems to contradict the larger decline in contrast sensitivity for second-order stimuli which has been found by Habak and Faubert (2000) in elderly subjects aged about 70 (69.7 ± 4.42) years old. However, our results indicate that the age when the decline begins and the rate of decline both contribute to the effect of aging, and that the larger decline found by Habak and Faubert may be mainly attributed to the earlier onset of decline, rather than its faster rate, for perception of second-order stimuli. Secondly, the rate of decline is faster for dynamic than for static second-order stimuli. Supposing that perception of the static and dynamic second-order stimuli used by Habak and Faubert (2000) begin to decline at similar age just as observed here, similar results could be expected from their study: i.e., a faster rate of decline for perception of second-order motion since it exhibits a slightly larger decline in their results. Additionally, a recent study (Bertone, Hanck, Cornish, & Faubert, 2008) has shown a faster developmental rate for perception of dynamic than of static second-order stimuli in school-aged children, which further suggested that our finding may not be an incidental phenomenon.

However, it should be noticed that the issue of rate of decline may be less important for the hypothesis that first- and second-order processing systems differ in their vulnerability to age-related neurophysiological changes than the issue of onset of decline. This is because the former may be quite spatial frequency dependent for the first-order stimuli: The slope of decline is highly dependent on the spatial frequency but less so on age of onset for perception of first-order stimuli with the spatial frequency from middle to high, which can be suggested from the data by Owsley et al. (1983). While second-order mechanisms may not depend on the contrast of the high spatial frequencies in the same manner since if the reverse was true, the slopes of decline for second-order stimuli

would be much sharper as the carrier is made of spatial frequency components that contain much higher spatial frequencies than the first-order grating signal. Additionally, the differences in the slope of static and dynamic second-order stimuli can be interpreted by Allard & Faubert's findings that even in carefully controlled conditions where global distortions are accounted for, it is not possible to dissociate first- and second-order mechanisms at high temporal frequencies, such as 4–8 Hz used in the present study. That is to say, since our data are globally presented with many temporal frequencies (from 1 to 8 Hz), the slope presented here for second-order motion may have both first- and second-order characteristics, which would make it steeper than the static second-order but less steep than the first-order data slopes.

Based on this piecewise linear model, we observe a larger effect of aging on the perception of second-order than first-order motion at the age of 70 years old, consistent with the findings of Habak and Faubert (2000). However for static stimuli, our analysis indicates the decline in log contrast sensitivity is smaller for second- than for first-order stimuli at the same age, inconsistent with their study. Our statistical analysis represents the effect of aging as the log contrast sensitivity decline ($\log S_{young} - \log S_{old}$) and its standard error. Based on the parameters listed in Table 3, and using the re-sampling method, we calculate the log contrast sensitivity decline for static first- (0.254 ± 0.003), static second- (0.166 ± 0.003), dynamic first- (0.351 ± 0.005) and dynamic second-order stimuli (0.600 ± 0.007) at the age of 70 years old. Thus, the log contrast sensitivity decline is significantly smaller for static second-order stimuli than for static first-order stimuli. This discrepancy between the results of Habak and Faubert's study (2000) and ours may be explained, we speculate, by the difference in spatial frequency of the gratings used in the two studies (1 c/d in their study and 2 c/d in ours), since a previous study (Owsley et al., 1983) has suggested varying patterns of decline for sine-wave gratings with different spatial frequencies.

Actually, a larger effect of aging on perception of second-order stimuli cannot always be expected because of the earlier onset but slower rate of progression for decline in perception of second-order stimuli. This is especially true for perception of static second-order stimuli, which exhibit the smallest rate of decline. For example, in the present study, the decline of log contrast sensitivity is significantly larger for static second-order stimuli at ages below 66 years old (at age 66, the log contrast sensitivity declines are 0.114 ± 0.002 and 0.146 ± 0.003 for first- and second-order stimuli, respectively) but the reverse is true for static first-order stimuli at ages above 68 years old (at age 68, the log contrast sensitivity declines are 0.186 ± 0.002 and 0.157 ± 0.003 for first- and second-order stimuli, respectively). Therefore, the earlier decline, rather than the larger effect of aging, may be more closely linked to the greater vulnerability to age-

related neurophysiological changes for second-order processing system.

In conclusion, our findings support the hypothesis that the first- and second-order processing systems differ in their vulnerabilities to neurophysiological changes during aging. We found an earlier onset of decline, but with a slower subsequent progression, for perception of second-order stimuli. We suggest the earlier decline for perception of second-order stimuli, the most important finding in the present study, is consistent with Faubert's theory of visual perception and aging.

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References

- Adams, R. J., & Courage, M. L. (2002). Using a single test to measure human contrast sensitivity from early childhood to maturity. *Vision Research*, *42*, 1205–1210. [PubMed]
- Ashida, H., Lingnau, A., Wall, M. B., & Smith, A. T. (2007). fMRI adaptation reveals separate mechanisms for first-order and second-order motion. *Journal of Neurophysiology*, *97*, 1319–1325. [PubMed] [Article]
- Baker, C. L., Jr. (1999). Central neural mechanisms for detecting second-order motion. *Current Opinion in Neurobiology*, *9*, 461–466. [PubMed]
- Baker, C. L., Jr., & Mareschal, I. (2001). Processing of second-order stimuli in the visual cortex. *Progress in Brain Research*, *134*, 171–191. [PubMed]
- Banks, M. S. (1982). The development of spatial and temporal contrast sensitivity. *Current Eye Research*, *2*, 191–198. [PubMed]
- Bennett, P. J., Sekuler, R., & Sekuler, A. B. (2007). The effects of aging on motion detection and direction identification. *Vision Research*, *47*, 799–809. [PubMed]
- Bertone, A., Hanck, J., Cornish, K. M., & Faubert, J. (2008). Development of static and dynamic perception for luminance-defined and texture-defined information. *Neuroreport*, *19*, 225–228. [PubMed]

- Billino, J., Bremmer, F., & Gegenfurtner, K. R. (2008). Differential aging of motion processing mechanisms: Evidence against general perceptual decline. *Vision Research*, *48*, 1254–1261. [[PubMed](#)]
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436. [[PubMed](#)]
- Chubb, C., & Sperling, G. (1989). Two motion perception mechanisms revealed through distance-driven reversal of apparent motion. *Proceedings of the National Academy of Sciences of the United States of America*, *86*, 2985–2989. [[PubMed](#)] [[Article](#)]
- Crassini, B., Brown, B., & Bowman, K. (1988). Age-related changes in contrast sensitivity in central and peripheral retina. *Perception*, *17*, 315–332. [[PubMed](#)]
- Dumoulin, S. O., Baker, C. L., Jr., Hess, R. F., & Evans, A. C. (2003). Cortical specialization for processing first- and second-order motion. *Cerebral Cortex*, *13*, 1375–1385. [[PubMed](#)]
- Dupont, P., Sáry, G., Peuskens, H., & Orban, G. A. (2003). Cerebral regions processing first- and higher-order motion in an opposed-direction discrimination task. *The European Journal of Neuroscience*, *17*, 1509–1517. [[PubMed](#)]
- Elliott, D., Whitaker, D., & MacVeigh, D. (1990). Neural contribution to spatiotemporal contrast sensitivity decline in healthy ageing eyes. *Vision Research*, *30*, 541–547. [[PubMed](#)]
- Faubert, J. (2002). Visual perception and aging. *Canadian Journal of Experimental Psychology: Revue Canadienne de Psychologie Experimentale*, *56*, 164–176. [[PubMed](#)]
- Frisen, L., & Frisen, M. (1981). How good is normal visual acuity? A study of letter acuity thresholds as a function of age. *Albrecht Von Graefes Archiv fur Klinische und Experimentelle Ophthalmologie*, *215*, 149–157. [[PubMed](#)]
- Gilmore, G. C., Wenk, H. E., Naylor, L. A., & Stuve, T. A. (1992). Motion perception and aging. *Psychology and Aging*, *7*, 654–660. [[PubMed](#)]
- Greenlee, M. W., & Smith, A. T. (1997). Detection and discrimination of first- and second-order motion in patients with unilateral brain damage. *Journal of Neuroscience*, *17*, 804–818. [[PubMed](#)] [[Article](#)]
- Habak, C., & Faubert, J. (2000). Larger effect of aging on the perception of higher-order stimuli. *Vision Research*, *40*, 943–950. [[PubMed](#)]
- Hays, W. L. (1988). *Statistics*. Fort Worth, TX: Holt, Rinehart & Winstone.
- Hua, T., Li, X., He, L., Zhou, Y., Wang, Y., & Leventhal, A. G. (2006). Functional degradation of visual cortical cells in old cats. *Neurobiology of Aging*, *27*, 155–162. [[PubMed](#)]
- Johnson, A. P., & Baker, C. L., Jr. (2004). First- and second-order information in natural images: A filter-based approach to image statistics. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, *21*, 913–925. [[PubMed](#)]
- Kato, M., de Wit, T. C., Stasiewicz, D., & von Hofsten, C. (2008). Sensitivity to second-order motion in 10-month-olds. *Vision Research*, *48*, 1187–1195. [[PubMed](#)]
- Kelly, D. H. (1972). Adaptation effects on spatio-temporal sine-wave thresholds. *Vision Research*, *12*, 89–101. [[PubMed](#)]
- Kline, D. W., Culham, J. C., Bartel, P., & Lynk, L. (2001). Aging effects on vernier hyperacuity: A function of oscillation rate but not target contrast. *Optometry & Vision Science*, *78*, 676–682. [[PubMed](#)]
- Landy, M. S., & Graham, N. (2004). Visual perception of texture. In L. M. Chalupa, & J. S. Werner (Eds.), *The visual neuroscience*. Cambridge, MA: MIT Press.
- Larsson, J., Landy, M. S., & Heeger, D. J. (2006). Orientation-selective adaptation to first- and second-order patterns in human visual cortex. *Journal of Neurophysiology*, *95*, 862–881. [[PubMed](#)] [[Article](#)]
- Leventhal, A. G., Wang, Y., Pu, M., Zhou, Y., & Ma, Y. (2003). GABA and its agonists improved visual cortical function in senescent monkeys. *Science*, *300*, 812–815. [[PubMed](#)]
- Levitt, H. (1971). Transformed up-down methods in psychoacoustics. *Journal of the Acoustical Society of America*, *49*, 467+. [[PubMed](#)]
- Li, X., Lu, Z. L., Xu, P., Jin, J., & Zhou, Y. (2003). Generating high gray-level resolution monochrome displays with conventional computer graphics cards and color monitors. *Journal of Neuroscience Methods*, *130*, 9–18. [[PubMed](#)]
- Liang, Z., Yang, Y., Li, G., Zhang, J., Wang, Y., Zhou, Y., et al. (in press). Aging affects the direction selectivity of MT cells in rhesus monkeys. *Neurobiology of Aging*. [[PubMed](#)]
- Lu, Z. L., & Sperling, G. (2001). Three-systems theory of human visual motion perception: Review and update. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, *18*, 2331–2370. [[PubMed](#)]
- Maloney, L. T. (1990). Confidence intervals for the parameters of psychometric functions. *Perception & Psychophysics*, *47*, 127–134. [[PubMed](#)]
- Nishida, S., Ledgeway, T., & Edwards, M. (1997). Dual multiple-scale processing for motion in the human visual system. *Vision Research*, *37*, 2685–2698. [[PubMed](#)]

- Nishida, S., Sasaki, Y., Murakami, I., Watanabe, T., & Tootell, R. B. (2003). Neuroimaging of direction-selective mechanisms for second-order motion. *Journal of Neurophysiology*, *90*, 3242–3254. [PubMed]
- Norman, J. F., Clayton, A. M., Shular, C. F., & Thompson, S. R. (2004). Aging and the perception of depth and 3-D shape from motion parallax. *Psychology and Aging*, *19*, 506–514. [PubMed] [Article]
- Odom, J. V., Vasquez, R. J., Schwartz, T. L., & Linberg, J. V. (1989). Adult vernier thresholds do not increase with age; vernier bias does. *Investigative Ophthalmology & Visual Science*, *30*, 1004–1008. [PubMed] [Article]
- Owsley, C., Sekuler, R., & Siemsen, D. (1983). Contrast sensitivity throughout adulthood. *Vision Research*, *23*, 689–699. [PubMed]
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442. [PubMed]
- Peters, A. (2002). The effects of normal aging on myelin and nerve fibers: A review. *Journal of Neurocytology*, *31*, 581–593. [PubMed]
- Peters, A., Moss, M. B., & Sethares, C. (2001). The effects of aging on layer 1 of primary visual cortex in the rhesus monkey. *Cerebral Cortex*, *11*, 93–103. [PubMed]
- Schmolesky, M. T., Wang, Y., Pu, M., & Leventhal, A. G. (2000). Degradation of stimulus selectivity of visual cortical cells in senescent rhesus monkeys. *Nature Neuroscience*, *3*, 384–390. [PubMed]
- Schofield, A. J. (2000). What does second-order vision see in an image? *Perception*, *29*, 1071–1086. [PubMed]
- Seiffert, A. E., Somers, D. C., Dale, A. M., & Tootell, R. B. (2003). Functional MRI studies of human visual motion perception: Texture, luminance, attention and after-effects. *Cerebral Cortex*, *13*, 340–349. [PubMed]
- Sloane, M. E., Owsley, C., & Jackson, C. A. (1988). Aging and luminance-adaptation effects on spatial contrast sensitivity. *Journal of the Optical Society of America A, Optics and Image Science*, *5*, 2181–2190. [PubMed]
- Smith, A. T., Greenlee, M. W., Singh, K. D., Kraemer, F. M., & Hennig, J. (1998). The processing of first- and second-order motion in human visual cortex assessed by functional magnetic resonance imaging (fMRI). *Journal of Neuroscience*, *18*, 3816–3830. [PubMed] [Article]
- Smith, A. T., & Scott-Samuel, N. E. (2001). First-order and second-order signals combine to improve perceptual accuracy. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, *18*, 2267–2272. [PubMed]
- Snowden, R. J., & Kavanagh, E. (2006). Motion perception in the ageing visual system: Minimum motion, motion coherence, and speed discrimination thresholds. *Perception*, *35*, 9–24. [PubMed]
- Spear, P. D. (1993). Neural bases of visual deficits during aging. *Vision Research*, *33*, 2589–2609. [PubMed]
- Spear, P. D., Moore, R. J., Kim, C. B., Xue, J. T., & Tumosa, N. (1994). Effects of aging on the primate visual system: Spatial and temporal processing by lateral geniculate neurons in young adult and old rhesus monkeys. *Journal of Neurophysiology*, *72*, 402–420. [PubMed]
- Tulunay-Keeseey, U., Ver Hoeve, J. N., & Terkla-McGrane, C. (1988). Threshold and suprathreshold spatiotemporal response throughout adulthood. *Journal of the Optical Society of America A, Optics and Image Science*, *5*, 2191–2200. [PubMed]
- Vaina, L. M., & Cowey, A. (1996). Impairment of the perception of second order motion but not first order motion in a patient with unilateral focal brain damage. *Proceedings of the Royal Society of London B: Biological Sciences*, *263*, 1225–1232. [PubMed]
- Vaina, L. M., Makris, N., Kennedy, D., & Cowey, A. (1998). The selective impairment of the perception of first-order motion by unilateral cortical brain damage. *Visual Neuroscience*, *15*, 333–348. [PubMed]
- Vaina, L. M., & Soloviev, S. (2004). First-order and second-order motion: Neurological evidence for neuroanatomically distinct systems. *Progress in Brain Research*, *144*, 197–212. [PubMed]
- van Santen, J. P., & Sperling, G. (1984). Temporal covariance model of human motion perception. *Journal of the Optical Society of America A, Optics and Image Science*, *1*, 451–473. [PubMed]
- Wang, Y., Zhou, Y., Ma, Y., & Leventhal, A. G. (2005). Degradation of signal timing in cortical areas V1 and V2 of senescent monkeys. *Cerebral Cortex*, *15*, 403–408. [PubMed]
- Weale, R. (1963). *The aging eye*. London: Lewis.
- Wenderoth, P., Watson, J. D., Egan, G. F., Tochon-Danguy, H. J., & O’Keefe, G. J. (1999). Second order components of moving plaids activate extrastriate cortex: A positron emission tomography study. *NeuroImage*, *9*, 227–234. [PubMed]
- Wilson, H. R., Ferrera, V. P., & Yo, C. (1992). A psychophysically motivated model for two-dimensional motion perception. *Visual Neuroscience*, *9*, 79–97. [PubMed]
- Wist, E. R., Schrauf, M., & Ehrenstein, W. H. (2000). Dynamic vision based on motion-contrast: Changes

- with age in adults. *Experimental Brain Research: Experimentelle Hirnforschung*, *134*, 295–300. [[PubMed](#)]
- Yang, Y., Liang, Z., Li, G., Wang, Y., Zhou, Y., & Leventhal, A. G. (2008). Aging affects contrast response functions and adaptation of middle temporal visual area neurons in rhesus monkeys. *Neuroscience*, *156*, 748–757. [[PubMed](#)]
- Yu, S., Wang, Y., Li, X., Zhou, Y., & Leventhal, A. G. (2006). Functional degradation of extrastriate visual cortex in senescent rhesus monkeys. *Neuroscience*, *140*, 1023–1029. [[PubMed](#)]