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The effect of senescence on orientation discrimination and mechanism tuning

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Accurately processing orientation information is a fundamental component of visual performance. Single-unit recordings have shown that the orientation tuning of individual neurons in macaque cortical areas V1 and V2 is reduced dramatically with age (M. T. Schmolesky, Y. Wang, M. Pu, & A. G. Leventhal, 2000; S. Yu, Y. Wang, X. Li, Y. Zhou, & A. G. Leventhal, 2006). These researchers suggest that losses in single-unit orientation selectivity result in declines in orientation discrimination and object recognition in older humans. Three experiments were conducted to determine whether human performance is affected by putative age-related changes in tuning of cortical neurons. Ten younger and ten older observers participated in this study. [Experiment 1](#) demonstrated significant differences in the contrast sensitivity of the two age groups. [Experiment 2](#) showed significant differences in orientation discrimination thresholds. However, when thresholds were plotted in terms of multiples of detection threshold, age-related differences were not observed. In [Experiment 3](#), perceptual orientation tuning curves did not significantly differ in shape for younger and older subjects. As in [Experiment 2](#), at any given contrast, there is a large difference in sensitivity between younger and older adults. This implies a model of orientation processing that allows the adult visual system to maintain consistent and reliable orientation information at the network and ultimately the perceptual level.

Keywords: aging, contrast sensitivity, masking, orientation discrimination, orientation tuning, spatial vision, plasticity

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Introduction

Accurately encoding orientation information in a scene is a fundamental component of cortical visual processing. Neurons in primary visual cortex respond preferentially to specific orientations, with all orientations represented by a set of cortical columns for each region of visual space. Orientation tuning is one of the most robust and reliably observed characteristics of cortical information processing (DeValois, Yund, & Hepler, 1982; Hubel & Weisel, 1968).

The human visual system undergoes myriad anatomical and physiological changes with age. For example, senescence of the optical components of the eye results in less light reaching the retina chiefly due to reduced pupil size (Kadlecová, Peleska, & Vasko, 1958) and lens brunescence (van de Krats & van Norren, 2007; Weale, 1988). There is an age-related reduction in photoreceptor numbers (Curcio, Millican, Allen, & Kalina, 1993; Panda-Jonas, Jonas, & Jakobczyk-Zmija, 1995) and a loss of retinal ganglion cells (Curcio & Drucker, 1993; Harman,

Abrahams, Moore, & Hoskins, 2000). These changes are accompanied by substantial losses in sensitivity of all three cone pathways (Werner, Bieber, & Scheffrin, 2000). Nevertheless, color perception is remarkably stable with age (Hardy, Frederick, Kay, & Werner, 2005) unless the stimuli are below a critical size (Knau & Werner, 2002). Stability of color perception across the life span has been taken to reflect a continuous renormalization of color mechanisms to compensate for early stage losses (Delahunt, Webster, Ma, & Werner, 2004). Similar processes may support stability of spatial vision with losses in contrast sensitivity (Owsley, Sekuler, & Siemsen, 1983) across the life span (Elliott, Hardy, Webster, & Werner, 2007), but this has been studied less extensively.

Recent neurophysiological studies in the macaque monkey have shown that the proportion of V1 and V2 cells showing a high degree of selectivity to stimulus orientation is reduced dramatically with advanced age (Schmolesky, Wang, & Leventhal, 2000; Yu, Wang, Li, Zhou, & Leventhal, 2006). For example, cells in V1 that were characterized as “significantly tuned” were reduced

from 90% in the younger group to 42% in the older group. Cells characterized as “strongly tuned” were reduced from 73% in the younger group to 15% in the older group. Subsequent studies showed that this reduction in orientation tuning can be temporarily reversed by local application of GABA agonists (Leventhal, Wand, Pu, Zhou, & Ma, 2003), suggesting that reduced effectiveness of GABA-mediated inhibition may be a critical component in these senescent changes, and that the losses in orientation tuning occur in cortex itself rather than in the afferent inputs to visual cortex, consistent with receptive field properties of the lateral geniculate nucleus in old monkeys (Spear, Moore, Kim, Xue, & Tumosa, 1994).

Similar changes in the tuning of orientation sensitive cells are likely to occur in the human visual cortex. This conclusion was supported by a recent study (Betts, Sekuler, & Bennett, 2007) in which orientation thresholds were measured for different levels of external noise. When external noise levels were low, orientation discrimination thresholds were higher in older observers, but not when external noise was high. This result is generally consistent with physiological studies demonstrating that elevated noise in cortical neurons of older primates may impair orientation tuning. In our study, the differences in contrast sensitivity between younger and older observers were taken into account by measuring orientation discrimination at constant multiples of threshold. Then, using a masking paradigm, the bandwidth of orientation tuning could be compared psychophysically for younger and older observers. We find that at a fixed physical contrast, sensitivity (Experiment 2) and selectivity (Experiment 3) for orientation information is reduced in older adults relative to younger adults; however, these differences can be completely explained by differences in overall contrast sensitivity. Observed age-related changes in the local noise conditions at the level of single units appear to be compensated by plastic changes at the network level to maintain constant *relative* orientation tuning properties of the system, reducing or eliminating perceptual distortions that would otherwise occur due to poorly represented orientation information.

General methods

Subjects

Ten younger (5 male/5 female, mean age 26.7, range 20–33) and ten older (5 male/5 female, mean age 71.5, range 65–85) participants were tested. All observers were examined for the presence of abnormal ocular media and retinal disease using slit lamp examination and by taking fundus photographs of the macula and optic disc that were examined by a retinal specialist. Intraocular pressure was ≤ 22 mmHg for all observers. All were normal trichromats based upon testing with the Neitz anomaloscope, the HRR

pseudoisochromatic plates, and the Farnsworth F-2 plate. Written informed consent was obtained following the Tenets of Helsinki and with approval of the Office of Human Research Protection of the University of California, Davis, School of Medicine.

Stimuli and procedures

Stimuli were presented on a 17-in. CRT monitor (Eizo FlexScan T566) driven by a Macintosh G4 400-MHz computer using the OS 9 operating system. The custom experimental software was written in MATLAB (<http://www.mathworks.com/>, version 5.2.1) using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). An ATI Radeon 9000 Pro graphics card was employed to provide 10 bits of intensity resolution per color channel. It has been verified that this graphics card provides 10-bit resolution when used with the PsychToolbox and the Macintosh OS 9 operating system (see <http://psychtoolbox.org/PTB-2/mac.html>). The monitor was calibrated using a Minolta colorimeter (CS 100 Chroma Meter), following the procedures described by Brainard, Pelli, and Robson (2002). The experiment took place in a dark room following a minimum of 3 minutes of dark adaptation before starting an experimental session.

The monitor was viewed at a distance of 2 m, and head position was stabilized using a chin rest. A level was used to ensure the monitor was horizontal. No attempt was made to mask the edge of the monitor, allowing this to be used as a vertical reference by observers. The stimuli were viewed monocularly with the fellow eye patched. Testing was conducted monocularly to simplify correction of refractive error for the test distance and to aid comparison to previous studies in this domain (e.g., Delahunt, Hardy, Okajima, & Werner, 2005; Delahunt et al., 2004; Hardy, Delahunt, Okajima, & Werner, 2005). All subjects had corrected acuity of 20/25 or better in the tested eye. For subjects over age 60, the crystalline lens has little remaining accommodative power (Glasser & Campbell, 1998). Therefore, the subjects in this group wore trial lenses for proper refraction at the test distance. The test stimuli were luminance-varying Gabor patches consisting of sinusoids having a two-dimensional Gaussian profile with a sigma equal to 1/4 of the stimulus size. Spatial frequencies of 1 and 4 cpd were used. To reduce adaptation effects, we randomized the phase on each trial.

All thresholds were estimated by averaging the results of two randomly interleaved staircases. A QUEST adaptive staircase procedure was used (Watson & Pelli, 1983). Observers responded using a number keypad. All stimuli were achromatic with a chromaticity of CIE Illuminant C (CIE xy chromaticity values of 0.310, 0.316) and a mean luminance of 40 cd/m². The stimuli were presented on a background of the same mean luminance and chromaticity.

The stimuli were 1 and 4 cycles per degree (cpd) Gabor patches with a constant number of cycles (4 cycles) to maintain a constant bandwidth in the frequency domain. The refresh rate of the monitor was set to 85 Hz. Before testing, each subject underwent a training session consisting of two detection threshold measurements for vertically oriented 1 and 4 cpd Gabors and two orientation threshold measurements using both 1 and 4 cpd Gabors of high contrast (64%).

A temporal two-alternative forced choice (2-AFC) task was used to obtain detection threshold measurements for vertically orientated Gabor patterns. The patterns were presented for 0.75 s with square-wave temporal modulation (i.e., no onset or offset ramp); ISIs were also 0.75 s. Participants responded by pressing appropriately labeled buttons on a number pad with all unused buttons masked.

Three experiments were conducted. In [Experiment 1](#), contrast threshold measures were obtained for Gabor patterns used in subsequent experiments. In [Experiment 2](#), orientation discrimination thresholds were obtained for stimuli at a range of contrast levels. In [Experiment 3](#), thresholds were obtained in the presence of sine wave maskers at a range of orientations to obtain an estimate of the orientation tuning properties of the visual system.

Experiment 1: Contrast threshold

Contrast thresholds were obtained as baseline measurements. The results were used in [Experiments 2](#) and [3](#) to equate stimuli across younger and older participants in terms of multiples of each individual's contrast detection thresholds.

Additional methods

Detection thresholds were measured for each observer using vertically oriented Gabor patches. A temporal two-interval AFC task was used; observers indicated in which time interval the Gabor was presented. Intervals were marked by auditory cues indicating the beginning of the interval. During the no-stimulus intervals, the background mean luminance blank field was presented. Thresholds were obtained for both 1 and 4 cpd patterns.

Results and discussion

Mean contrast thresholds for 1 and 4 cpd Gabor patterns are shown in [Figure 1](#). It is apparent that older individuals had higher thresholds for both spatial frequencies. A two-factor ANOVA confirmed that the main effect of age, $F_{1,36} = 11.624$, $p = 0.002$, and the main effect of spatial frequency, $F_{1,36} = 17.010$, $p = 0.0002$, were statistically

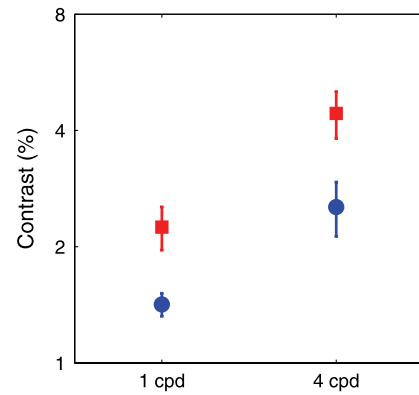


Figure 1. Contrast thresholds for older participants (red squares) and younger participants (blue circles) for 1 and 4 cpd Gabor patterns. Error bars represent ± 1 SEM across 10 participants.

significant; however, there was no significant interaction between age and spatial frequency, $F_{1,36} = 1.774$, $p > 0.05$. The magnitude of age-related sensitivity losses and their spatial frequency dependence are known to depend critically on the specific stimulus parameters and methods (Burton, Owsley, & Sloane, 2004; Owsley et al., 1983; Scheffrin, Hauser, & Werner, 2004). Our results are consistent with similar changes as a function of spatial frequency, but we did not explore the extremes of the spatial frequency range.

Experiment 2: Orientation discrimination sensitivity

The purpose of this experiment was to measure orientation discrimination thresholds for a range of stimulus contrasts. This simple task requires individuals to indicate whether a pattern is tilted to the left or to the right of vertical. In a two-alternative forced-choice task, this requires only a single stimulus presentation, as the observer compares the orientation to an internalized representation of vertical. Any bias in this response is eliminated by averaging across tilted-left and tilted-right thresholds. Observers generally find this task quite intuitive and easy to perform, and sensitivities on this type of task can reach near hyperacuity levels (Westheimer, 1996; Westheimer, Shimamura, & McKee, 1976).

Additional methods

Orientation discrimination thresholds were obtained for Gabor patches at six contrast levels. The first five were multiples of contrast threshold factors in equal logarithmic steps (1.41, 2.00, 2.83, 4.00, and 5.66). The contrasts were set for each participant individually based on their contrast

threshold obtained in Experiment 1. In addition, orientation thresholds were measured at maximum contrast. Therefore, a total of 12 orientation thresholds (2 spatial frequencies \times 6 contrasts levels) were obtained for each observer. The sequence of orientation testing was randomized and blocked so that the sequence followed by the younger group was matched by the older group.

A single presentation 2-AFC task was used with a presentation time of 0.75 s. The observer’s task was to indicate whether it was orientated to the left or to the right of the vertical axis. The maximum orientation was set at ± 60 degrees from vertical.

The Gabor was always created in one direction but was randomly displayed either in the original direction or in the mirror reversed direction (with the correct response also changed). This was done to average out any internal orientation biases and any slight errors in the display device setup.

Results and discussion

Orientation discrimination thresholds for each observer for each contrast are shown in Figure 2. Error bars (± 1 SEM

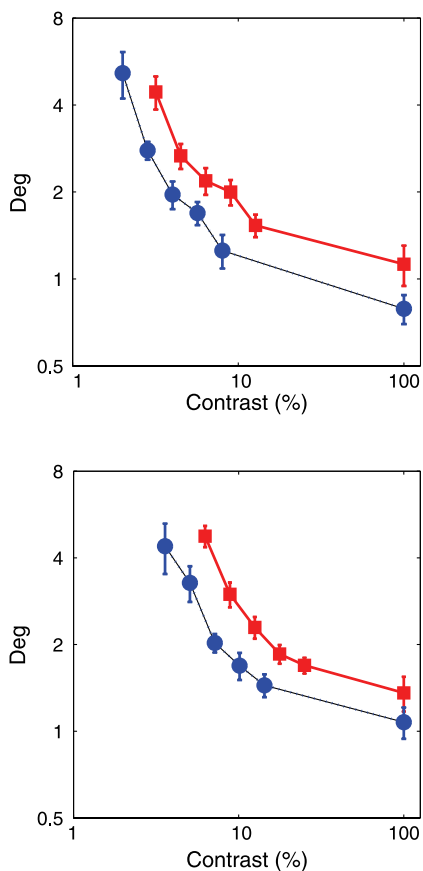


Figure 2. Orientation discrimination thresholds for older participants (red squares) and younger participants (blue circles) for 1 cpd (top panel) and 4 cpd (bottom panel). Error bars represent ± 1 SEM across 10 participants.

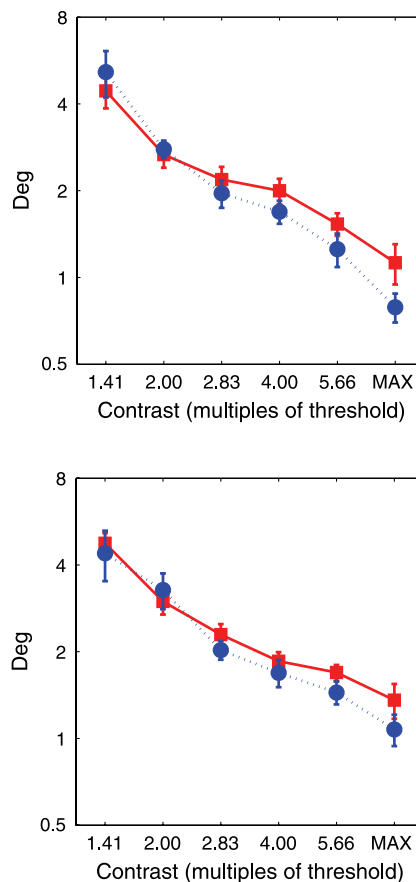


Figure 3. Orientation discrimination thresholds re-plotted as multiples of thresholds obtained in Experiment 1 for older participants (red squares) and younger participants (blue circles) for 1 cpd (top panel) and 4 cpd (bottom panel). Error bars represent ± 1 SEM across 10 participants.

of the threshold estimate) are used for both x and y axes; however, they are smaller on the x axis than the plotted points. ANOVAs based on the differences in contrasts reveal significant differences between older and younger adults at both 1 cpd, $F_{1,5} = 30.218$, $p < 0.001$, and 4 cpd, $F_{1,5} = 26.758$, $p < 0.001$.

To take the differences in contrast detection sensitivity (measured in Experiment 1) into account, we re-plotted the data in Figure 3 as multiples of individual contrast detection thresholds. Expressed in this manner, the main effect of age was not statistically significant for either 1 cpd, $F_{1,5} = 0.062$, $p = 0.804$, or 4 cpd, $F_{1,5} = < 0.776$, $p = 0.380$. The curves showing orientation discrimination against multiples of contrast detection threshold are nearly completely overlapping for the two age groups.

The performance for detecting the orientation of Gabor patterns set at the maximum contrast for both younger and older participants is shown in Figure 4. The disparity in performance can be accounted for by the differences in contrast sensitivity measured in Experiment 1. Note that the pattern of results in Figures 1 and 4 is similar and

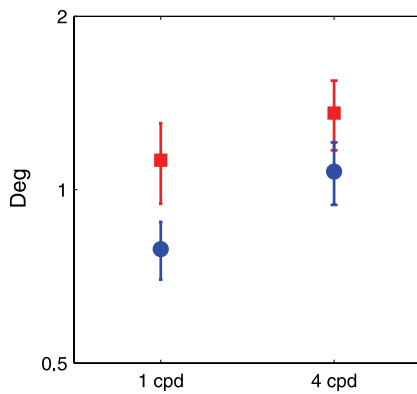


Figure 4. Orientation discrimination thresholds for Gabor patterns at the maximum contrast (same physical contrast for both groups) for older participants (red squares) and younger participants (blue circles) for 1 and 4 cpd. Error bars represent ± 1 SEM across 10 participants.

indicates that even at the highest contrasts used, the effect of elevated orientation tuning thresholds as a function of age can be accounted for by differences in effective contrast of the patterns. These results indicate that age-related differences in orientation discrimination performance do exist, even at high suprathreshold physical contrasts; however, the age-related elevation in orientation discrimination can be explained by age-related elevation in contrast sensitivity.

Experiment 3: Orientation tuning

Orientation tuning curves were obtained by measuring contrast sensitivity for vertical Gabor patches superimposed on sine wave gratings of various orientations.

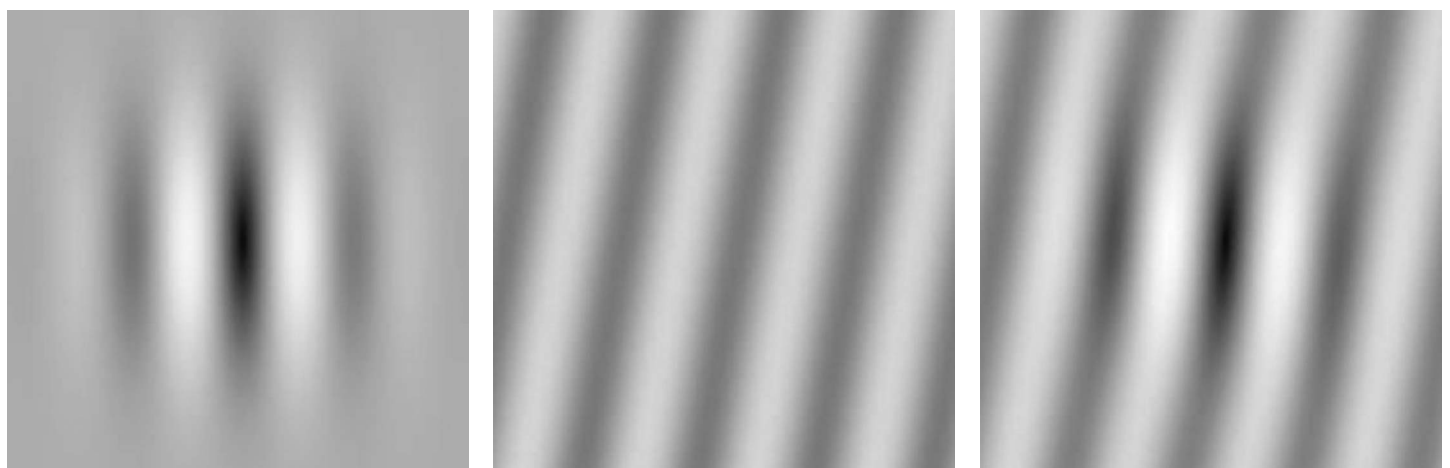


Figure 5. Illustration of the masker stimulus. Detection thresholds were measured for a vertically oriented Gabor (left panel) superimposed on a sine wave masker (middle panel) to produce a combined stimulus (right panel). Various masker orientations were used in the experiment. In this example, the masker is 10 degrees from vertical.

Contrast-masking effects occur when patterns are similar in spatial frequency and orientation (Graham, 1989; Phillips & Wilson, 1984; Regan & Beverley, 1985). Figure 5 illustrates the appearance of such patterns as used in our experiment.

Additional methods

Orientation tuning was measured using a masking paradigm; thresholds were measured for Gabor patches superimposed on a sine wave pattern. The contrast of the sine wave pattern was set for each participant at two times the contrast threshold measured in Experiment 1. Detection thresholds were measured for Gabors presented with maskers of 6 orientations (5, 10, 15, 20, 30, and 45 degrees). The spatial frequency of the sine wave pattern matched the frequency of the Gabor that it was presented with. The phase of each pattern was also matched.

Each observer ran through four practice runs (detection with and without a masker at both spatial frequencies). Then, contrast thresholds for each spatial frequency and masker orientation were tested separately. The experimental runs were randomized and blocked so that each pair of younger and older observers followed the same randomized sequence.

Results and discussion

Contrast thresholds as a function of masker orientation for older (red squares) and younger (blue circles) adults are shown in Figure 6. The differences are statistically significant (ANOVA 1 cpd, $p = 0.002$; 4 cpd, $p < 0.0001$). Note that the thresholds for older participants are higher than for the younger group, but the general shape of the curve is the same. In Figure 7, the data are presented as

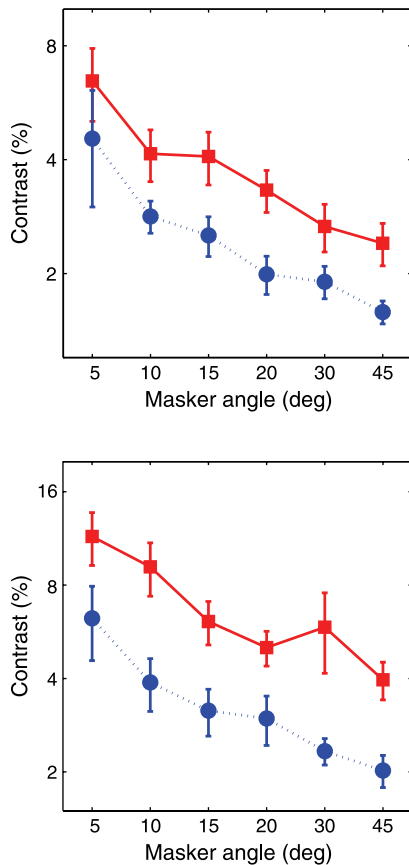


Figure 6. Orientation tuning curves for older participants (red squares) and younger participants (blue circles) for 1 cpd (top panel) and 4 cpd (bottom panel). Error bars represent ± 1 SEM across 10 participants.

multiples of contrast detection threshold. When plotted this way, the differences between the two groups are not significantly different (ANOVA 1 cpd, $F_{1,5} = 0.249$, $p = 0.619$; 4 cpd, $F_{1,5} = 3.672$, $p = 0.058$).

To measure the bandwidth of the tuning curves, we first fitted the data with half-Gaussian and exponential functions. The exponential produced a better fit to our data (mean RMS error for the half-Gaussian was 1.187, and for the exponential it was 0.526) and was used to calculate the bandwidths using width at half height. The height was calculated as the difference between the values of each exponential curve fit at 5 and 45 degrees. For 1 cpd stimuli, the bandwidths were 11.72 degrees for older participants and 11.03 for younger participants. For 4 cpd stimuli, the bandwidths were 11.44 degrees for older participants and 11.19 for younger participants. The exponential curve fits and bandwidths are illustrated in Figure 8.

Despite an age-related increase in noise for individual neurons (Leventhal et al., 2003) as well as for the orientation detection system as a whole (Betts et al., 2007), the bandwidth of psychophysical channels mediating orientation discrimination is similar for younger and

older observers. In this experiment, we equated subjects in terms of equivalent input noise when plotting orientation thresholds as a function of multiples of threshold. These results are consistent with a senescent system that preserves the optimal *shape* of the orientation tuning function, despite changes in the baseline noise characteristics of the system. A complete explanation of the orientation tuning characteristics of the visual system must take into account the plastic processes driving this (presumably optimal) characteristic.

General discussion

Recent research in the macaque indicates that orientation tuning in early visual cortex becomes less precise with increased age (Schmolesky et al., 2000; Yu et al., 2006). The authors of those investigations suggest that such changes in cortical cells could account for observed

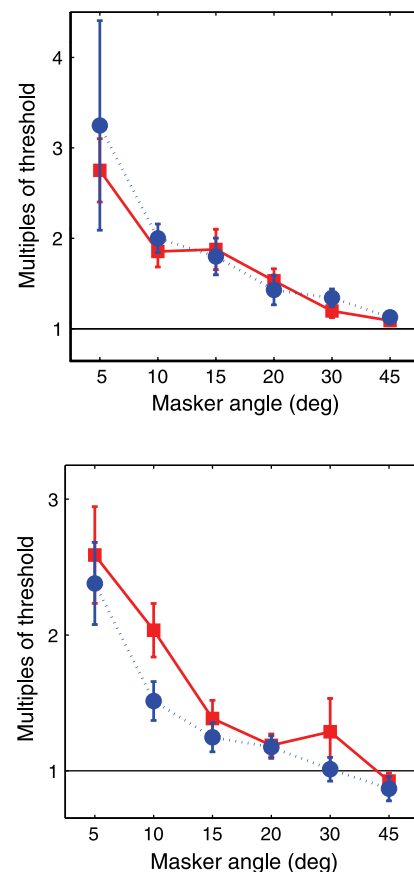


Figure 7. Orientation tuning curves re-plotted using multiples of detection thresholds obtained in Experiment 1 for older participants (red squares) and younger participants (blue circles) for 1 cpd (top panel) and 4 cpd (bottom panel). Error bars represent ± 1 SEM across 10 participants. The black horizontal line indicates no threshold elevation.

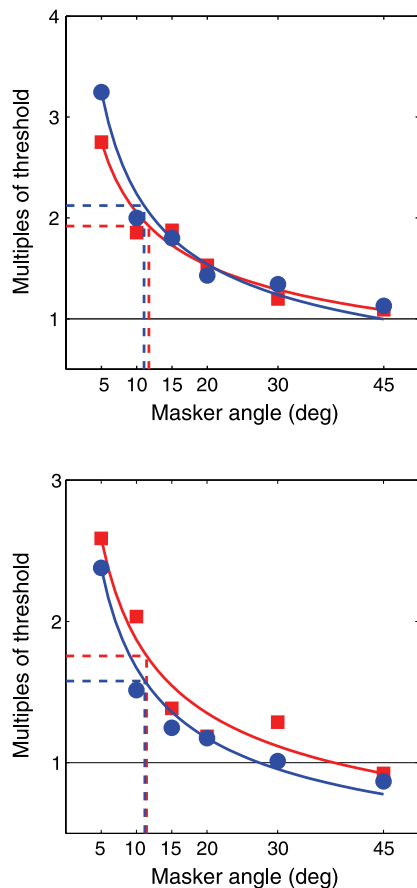


Figure 8. The multiples of threshold masking data from [Experiment 3](#) were fitted with exponential curves for both older (red squares) and younger (blue circles) participants. The bandwidths were calculated at half height and are illustrated with dashed lines. The black horizontal line indicates no threshold elevation.

losses in human performance with age, such as a reduction in the ability to discriminate faces. However, there is scant evidence to suggest that the representation of orientation is in fact impaired in the course of normal healthy aging in a manner that affects human perceptual performance. In this study, we investigated the impact of aging on (a) the ability to accurately discriminate fine orientation differences and (b) the shape of the psychophysical orientation tuning function. In both the orientation discrimination and the orientation-masking experiments, older adults showed relatively impaired performance compared with younger adults, when data are expressed in purely physical terms. However, when equated for differences in contrast detection sensitivity, the performance of the older group is similar to that of the younger group.

The bandwidths of the perceptual tuning curves were between 11 and 12 degrees for both younger and older participants for 1 and 4 cpd patterns. These bandwidths are consistent with previous psychophysical estimates of 10–20 degrees (Campbell & Kulikowski, 1966; Thomas &

Gille, 1979). Individual cortical neurons may have a similar bandwidth, but there is a wide range, and many are even more broadly tuned (DeValois et al., 1982; Hubel & Wiesel, 1968).

Betts et al. (2007) found differences in orientation sensitivity for younger and older participants when contrast was low. However, at high contrast levels, performance was similar for both groups. The authors suggested that this is because the equivalent input noise is similar for high contrast stimuli. In the current experiments, the results are similar to those of Betts et al. for low contrast stimuli. However, for high contrast stimuli, the difference between young and old groups remains (see [Figure 2](#)). Losses in contrast sensitivity alone are sufficient to account for these results. It is not clear why the results between the two studies differ at higher contrast. The Betts et al. study tested thresholds for stimuli embedded in noise, whereas the current study used stimuli of varying contrasts. To date, these are the only two studies examining this issue, and further work will be required to resolve this issue.

Single-cell recordings in macaque V1 and V2 (Schmolesky et al., 2000; Yu et al., 2006) show that the shape of orientation tuning functions becomes broader with age (orientation selectivity declines), even for high contrast stimuli. However, results from [Experiment 3](#) show that the shape of perceptual tuning curves remains unaffected by age. The lack of age-related changes in the shape of this characteristic at a behavioral level in humans is dissociated from the age-related changes seen in single-unit recordings in early visual cortex in monkeys.

The results of the experiments are consistent with a model in which threshold and discrimination are dissociated. Detection may depend on those neurons that are most sensitive to a particular orientation and spatial frequency, which in turn depend on the level of internal noise and hence neuronal bandwidth. This would be expected to change with observer age as has been shown in electrophysiological studies with monkeys. Discrimination of orientation, however, is more likely to depend on the relative activity of an ensemble of elements, which vary in their preferred orientation. The ability to discriminate orientation may thus occur only when the stimulus has sufficient energy to elevate neuronal responses above the spontaneous activity. Orientation sensitivity tuning therefore is affected little with age, but contrast detection thresholds are increased. The visual system appears to preserve the overall shape of the orientation tuning function across the lifespan. Plastic reorganization of network properties would be necessary to account for the consistency in these tuning characteristics despite the low-level increases in noise. Orientation tuning appears to be a perceptual feature that must be held constant in order to eliminate or to reduce perceptual distortions across the life span. In this way, the effects of aging on orientation tuning appear similar to the senescent effects seen in color vision (Delahunt et al., 2004; Hardy et al., 2005),

perceived contrast (Beard, Yager, & Neufeld, 1994), and blur perception (Elliot et al., 2007). Perceptual characteristics are preserved in the face of degrading optical and neural inputs with age.

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