Effects of Aging on Visual Contour Integration and Segmentation

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Purpose. Perception of circular disconnected contours requires the integration of relevant local orientation information across space and the suppression of irrelevant orientations. Using a detection of deviation from circularity (DFC) task, the present study examined whether the efficiency of either integrative or suppressive visual mechanisms, or both, declines with age.

Methods. Younger and older observers' sensitivities in detecting the DFC of a contour formed by Gabors were compared in three conditions: when all elements were oriented tangentially to the contour, with and without the presence of randomly oriented background noise; and when they had alternated tangential and orthogonal orientations, without background noise.

Results. In agreement with previous studies, the authors found that younger observers were not impaired in the mixed condition with respect to the tangential condition, suggesting the involvement of a high-level mechanism responding to the global closure information provided by tangential local orientations, even if they are interspersed with orthogonal ones. Instead, older observers were specifically impaired in the mixed condition, suggesting a reduced capability of suppressing nontangential information along the contour, and were also less efficient in suppressing irrelevant orientations in the background.

Conclusions. These results support the suggestion that, whereas integrative mechanisms are not affected by age, suppressive mechanisms are. (*Invest Ophthalmol Vis Sci.* 2011;52: 3955–3961) DOI:10.1167/iovs.10-5439

Human visual functions degrade with age. Although there are age-related degenerations of the optics of the eye,[1,2] those optical changes are insufficient to explain the decline of both low-level visual abilities (acuity,[3] contrast sensitivity for spatial or chromatic patterns,[4–6] and orientation discrimination[7,8]) and more complex visual functions (motion perception,[9–12] bilateral symmetry perception[13] and spatial integration and segregation[14–16]). Here we investigated the complex visual functions that involve deriving a meaningful percept from fragmented visual information in the retinal image.

In particular, these experiments investigated whether aging affects the integration of local fragments into contours and the segmentation of contours from the background.

The ability of the visual system to reconstruct contours from a fragmented retinal image has been investigated extensively in young adults by the use of contours formed by oriented disconnected elements. Numerous studies have examined the detection of linear,[17–20] curvilinear,[21,22] or closed contours[23–26] embedded in a cluttered background of elements of different orientation from those forming the contour.[27,28] Those studies highlighted the spatial parameters that reduce contour integration and segmentation, the most powerful being orientation jitter of nearby contour segments that renders them not aligned to the contour path and relative distance between contour segments.[27] In particular, many studies have shown better detectability of contours composed of elements aligned along the global contour orientation, both in the absence[29,30] and in the presence of background noise.[18,20]

Comparison of the ability to detect a fragmented contour with and without noise is important because it highlights the combined action of the two mechanisms involved: one facilitatory and the other suppressive. The facilitatory mechanism mediates the integration of oriented contour segments, whose linking, according to the association field model, is strongest when they are aligned along their axis of preferred orientation.[21,31–33] The suppressive mechanism mediates a reduction in the response to the noisy background that may interfere with the integration process. Whereas facilitation probably relies on long-range excitatory horizontal connections between cells in the primary visual cortex (V1),[34,35] background suppression is more likely to result from short-range inhibitory connections.[36]

Despite the large number of previous studies on contour integration and segmentation, little is known about how aging affects the facilitatory and suppressive mechanisms involved in those tasks. That aging may affect facilitation and suppression is suggested indirectly by neurophysiological studies in cats and monkeys. Those studies show two age-related deficits that may affect the integrative and suppressive mechanisms: (1) decreased selectivity to orientation in senescent V1 neurons caused by reduced lateral inhibition and (2) increased spontaneous activity.[37,38] Both deficits may result from reduced γ-aminobutyric acid (GABA)–mediated inhibition.[39] Human studies provide no evidence of reduced orientation selectivity,[8,40] whereas there is an age-dependent increase in equivalent input noise or internal noise that may be related to increased spontaneous activity.[7]

If aging reduces the efficiency of neural inhibition, this could affect not only the response of individual channels but also the efficiency of lateral interactions between channels accounting for contour integration and segmentation. Two recent studies[15,41] examined the effect of aging on contour integration and segmentation within noisy backgrounds, but

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with contradictory results. One study[41] did not find evidence for a deficit in segmentation. Indeed, the results showed that the detrimental effect of adding the noise was the same for older and younger observers. The other study[15] showed reduced ability of older observers to detect closed circular contours embedded in noisy backgrounds, and the effect was greater for small rather than that for large inter-element distances. The results are contradictory perhaps because the different tasks used (shape discrimination[41] vs. contour detection[15]) affect different levels of processing involved in visual integration and segmentation, spanning from contextual influences in V1 to top-down influences such as attention and task demands.[19,20]

To interpret the contour-detection results of Del Viva and Agostini,[15] two further questions have to be answered. The first regards the relative contribution of facilitatory and inhibitory lateral interactions[20] in accounting for reduced sensitivity to circular contours. The paradigm used by Del Viva and Agostini[15] does not allow this distinction; the reduced ability of older observers to detect closed circular contours embedded in a noisy background may be attributable to a reduced capability to suppress noise, particularly when integration signals are weak. Alternatively, and regardless of the presence of noise, older individuals may be less efficient in integrating elements belonging to the contour.

The second question arises because Del Viva and Agostini[15] manipulated only inter-element distance. As a consequence, it is unclear whether there is an aging effect on contour integration that depends on the relative orientation of the elements defining the circular contour in addition to their distance. One previous study[16] examined the effect of relative local orientations on contour integration across different age groups. The results showed that the contrast threshold for detecting and discriminating the global orientation of a C-shaped contour against a blank background depended on the orientation of the local elements for younger but not for older observers. However, this result cannot be generalized to suprathreshold stimuli since it is well established that facilitation by alignment in contrast detection is a low-level, monocular phenomenon,[42] and its role in higher-level tasks such as detection of a smoothly curved suprathreshold path has often been questioned.[43,44] That is, the contrast-detection paradigm used by Roudaia et al.[16] may have pinpointed age differences in local low-level facilitatory mechanisms of contrast enhancement instead of, or in addition to, age differences in the global long-range facilitation involved in suprathreshold circular contour integration.[45]

To summarize, the question of whether aging affects the dependence of contour-integration mechanisms on the relative orientation of elements along a contour and in the background remains open. Such dependence could be accounted for by reduced orientation selectivity highlighted by primate studies.[37,38] In that case, the effect of aging on contour integration and segmentation would be general. Indeed, reduced orientation selectivity should reduce both the facilitatory interactions that mediate contour integration and the inhibitory interactions that mediate suppression of nontangential elements along the contour and in the background. Also, nonsensorial factors, if affected by age, should have a general effect on contour integration and segmentation. However, the effect of aging could be specific for either integration or segregation (i.e., selective for one type of low-level cortical lateral interactions).

To compare the efficiency of integrative and segregative operations in younger and older adults we measured detectability of deviation from circularity (DFC) in the shape of suprathreshold circular contours,[46,47] defined by oriented Gabor elements, sinusoidal gratings (carriers) seen through a Gaussian window. We compared a condition where Gabors were aligned along the contour with a condition where Gabors had alternating tangential and orthogonal orientations to establish how aging affects the capacity to suppress irrelevant orientation information along the contour. Moreover, by comparing performances with and without background noise we intended specifically to establish whether the capacity to suppress random orientations not belonging to the contour is reduced by aging.

Contrast sensitivity was also measured to confirm that the contrast of the carrier was above threshold for both age groups. Indeed, there is evidence of an age-related loss in sensitivity at high and middle spatial frequencies in photopic vision,[48] whereas only in scotopic vision does an age-related decline occur for spatial frequencies < 1.2 cycles/deg, consistently with age-related changes in the magnocellular pathway.[49]

Methods

This research adhered to the tenets of the Declaration of Helsinki and was approved by the bioethics committee of the Psychology Faculty of the University of Padua. Informed consent was obtained from all participants.

Stimuli

In the spatial integration and suppression experiment the target stimuli were composed of cosine-phase Gabor patches. The SD of the two-dimensional Gaussian envelope was subtended 0.16° of visual angle and the sinusoidal grating had a wavelength λ of 0.32° of visual angle (spatial frequency = 3.13 cycles/deg). Stimuli were achromatic with a Michelson contrast of 0.87 and presented on a background with mean luminance of 38.9 cd/m^2. We used high-contrast Gabors to ensure that the lower sensitivity that older observers have for carriers of this spatial frequency[48] could not be the cause of group differences in integration and segmentation.

The circular contour was created by placing eight equally spaced Gabors (center-to-center distance = 74.4 arcmin or 3.9λ) along an imaginary circle (radius = 97.2 arcmin) centered on the screen. One of these Gabors was positioned on an imaginary circle of larger radius that varied randomly in five levels: 98.7, 103.1, 107.5, 112.0, and 116.4 arcmin. Thus, five DFC levels were obtained: 1.5, 5.9, 10.3, 14.8, and 19.2 arcmin. The displaced Gabor was chosen randomly with equal probability on every trial among four different locations (0°, 90°, 180°, and 270°). These DFC levels were selected to allow the psychometric function fit.

Three different stimulus conditions were tested in three separate sessions (Fig. 1). In the "tangential" condition, all Gabors were tangential to the contour; in the "mixed" condition, Gabors had alternating tangential and orthogonal orientations, and the displaced Gabor was always tangential. The "noise" condition was the same as the "tangential" but with background noise consisting of randomly oriented, equally spaced Gabors. These Gabors were placed along two imaginary concentric circles centered on the screen. One had 4 Gabors and a radius of 41.3 arcmin; the other had 12 Gabors and a radius of 153.2 arcmin.

The stimuli for the contrast sensitivity measurement consisted of full-screen vertical sinusoidal gratings. Eight spatial frequencies (0.10, 0.19, 0.42, 0.90, 1.99, 4.41, 9.91, and 19.82 cycles/deg) were tested.

Apparatus

The stimuli for the spatial integration and suppression experiment were generated with a high-level interactive technical computing language (MATLAB 7.3.0.267 [R2006b], Mathworks; Natick, MA) and presented on a 17-in. cathode ray tube (CRT) monitor (P70f ViewSonic [Walnut, CA]; refresh rate, 100 Hz; resolution, 1024 × 768 pixels). A computer (Pentium 4; Intel, Santa Clara, CA) was used to generate and present the stimuli. Experiment control and collection of behavioral responses were undertaken using a software application suite (E-

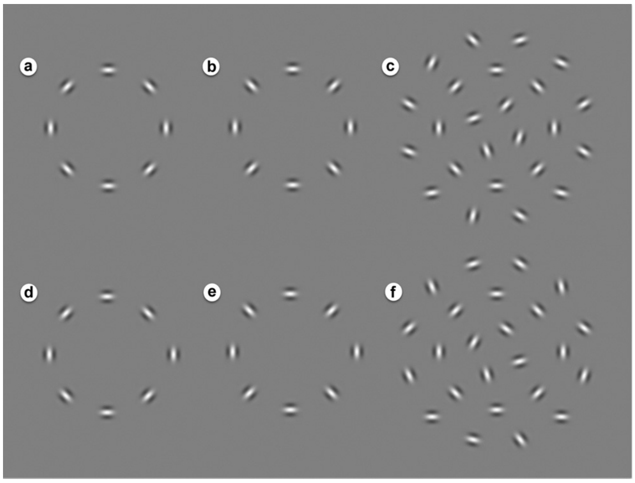

FIGURE 1. The circular stimuli used. (**a–c**) Contours without DFC. (**d–f**) Contours with DFC (here only a DFC of 14.8 arcmin and only for the Gabor on the *right* is shown). (**a**) and (**d**) show "tangential" stimulus conditions, (**b**) and (**e**) "mixed" conditions, and (**c**) and (**f**) "noise" conditions.

Prime, version 1.2; Psychology Software Tools, Inc., Sharpsburg, PA). Contrast sensitivity was measured using a software application tool (CRS Psycho 2.36; Cambridge Research Systems Ltd, Rochester, UK). The stimuli were generated by a graphics card (Cambridge Research Systems Ltd VSG2/3) and displayed on a 17-in. CRT monitor (Brilliance 107P; Philips [Amsterdam, The Netherlands] refresh rate, 70 Hz; resolution, 1024 × 768 pixels).

Procedure and Design

For all measurements (spatial integration and suppression and contrast sensitivity) stimuli were viewed binocularly in a darkened room at a viewing distance of 70 cm.

In each trial of the spatial integration and suppression experiment, a fixation cross presented for 200 ms was followed, after 300 ms, by two stimuli that were presented for 400 ms each and with an interstimulus interval of 600 ms. We used a two-interval, two-alternative forced choice (2I-2AFC) detection task in which observers had to choose, by pressing one of two alternative keys on the computer keyboard, which presentation contained a DFC. The contour with DFC was presented, with equal probability, either in the first or in the second stimulus interval. The other stimulus displayed a circular contour shape. Note that although the exposure time was relatively long, the psychophysical method used allowed comparisons, across stimulus conditions and groups, of the psychometric functions describing changes in detection over a range of DFC levels.

Each session consisted of 80 randomly presented trials, resulting from eight repetitions of each of the DFC levels (1.5, 5.9, 10.3, 14.8, and 19.2 arcmin) and presentation order (contour with DFC either in the first or in the second stimulus interval). The experiment (within-subjects design, three sessions with counterbalanced order) lasted approximately 2 hours, including resting intervals.

Displacement thresholds, defined as the DFC level that corresponds to the 0.75 correct detection probability (DFC thresholds), were calculated for each subject by fitting a psychometric function with the Probit analysis.[50] Dependence of DFC thresholds on stimulus type (tangential, mixed, and noise) and group was tested with two-way repeated-measures ANOVAs. Degrees of freedom (df) were corrected with the Greenhouse–Geisser procedure and corrected probability levels are reported. Post hoc pairwise comparisons were computed with Bonferroni correction. The α level was set at 0.05 for all statistical tests.

Contrast sensitivity was measured after the third experimental session. In each trial, a full-screen vertical sinusoidal grating was presented and the subjects' task was to indicate whether they could detect it. We used the method of limits with three ascending (from lower to higher grating contrast) and three descending (from higher to lower grating contrast) series. For each subject contrast sensitivity at each spatial frequency tested was calculated by averaging across series.

Subjects

Subjects tested on spatial integration and suppression belonged to two groups: the younger group was composed of 14 observers (mean age, 24.8 ± 3.4 years; range, 19–33 years), and the older group comprised 14 observers (mean age, 66.9 ± 6.3 years; range, 60–78 years). All participants had normal or corrected to normal vision such that binocular visual acuity was ≤ +0.10 logMAR at a distance of 70 cm (younger mean visual acuity [logMAR]: −0.11 ± 0.07; older mean visual acuity [logMAR]: +0.00 ± 0.09). Older observers did not have eye defects (such as cataract and glaucoma) or neurologic deficits (such as Alzheimer's disease or other forms of age-associated dementia). Both groups had similar socioeconomic status and educational background.

In nine younger (mean age, 24.8 ± 3.6 years; range, 20–33 years) and eight older (mean age, 65.9 ± 7.5 years; range, 60–78 years) observers contrast sensitivity was also measured in addition to visual acuity (younger mean visual acuity [logMAR]: −0.11 ± 0.08; older mean visual acuity [logMAR]: +0.02 ± 0.10).

For all measurements (spatial integration and suppression and contrast sensitivity) subjects wore their glasses or contact lenses.

RESULTS

Contrast Sensitivity

In agreement with previous findings,[48] we found that at the spatial frequency of the carrier (3.13 cycles/deg), sensitivity was lower (Fig. 2) for older than that for younger observers. However, since the contrast of the Gabors was very high, the low sensitivity to the carrier could not be the cause of group differences in integration and segmentation, even considering that a grating viewed through a Gaussian window produces a sensitivity reduction of approximately 0.5 log units.[51]

Spatial Integration

Figure 3 shows psychometric functions obtained in the tangential and mixed conditions by younger and older observers. The two-way ANOVA on threshold values, with group and condition (tangential versus mixed) as factors, showed a group effect [$F_{(1,26)} = 16.21$, $P < 0.001$, $\eta_p^2 = 0.384$], indicating that DFC thresholds are higher in the older group.

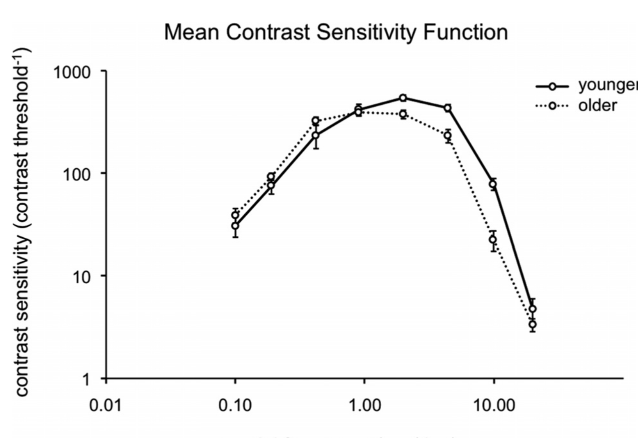

FIGURE 2. Mean binocular contrast sensitivity functions of younger (*continuous line*) and older observers (*dotted line*).

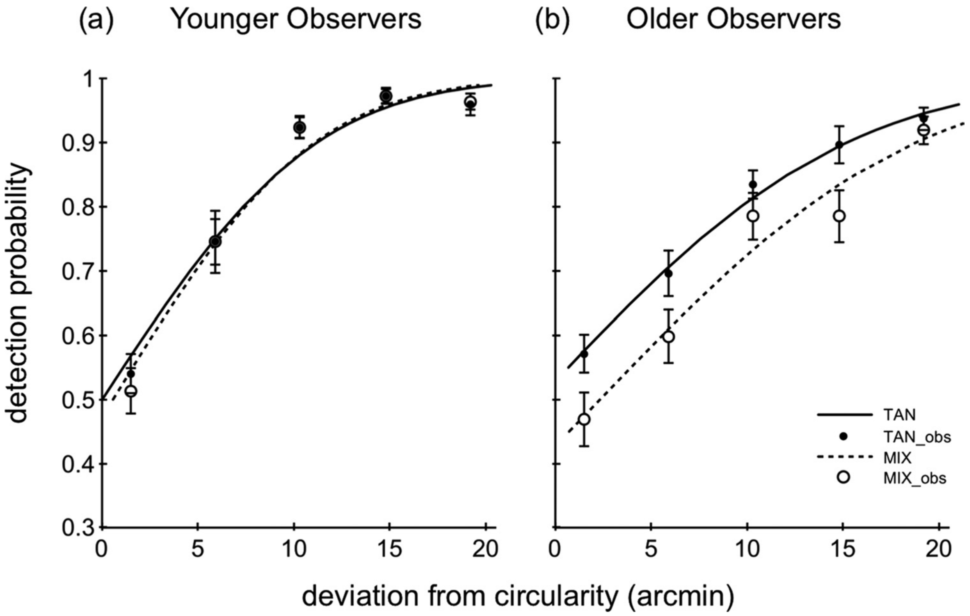

FIGURE 3. Psychometric functions for the (**a**) younger and (**b**) older groups in the tangential (TAN) and mixed (MIX) conditions, obtained by fitting observed mean detection probabilities (TAN_obs, MIX_obs) for each DFC level.

To detect the DFC, older observers need a larger displacement of the Gabor. Since the displaced Gabor had one of four randomly chosen positions along the circle its detection is unlikely to depend on local comparisons. Instead, detection is more likely to be mediated by the comparisons of the single displaced Gabor position with the whole contour shape. In that case, the finding that older observers have a higher DFC threshold may indicate a reduced efficiency in a global integrative process. The finding that both the factor condition [$F_{(1,26)}$ = 6.29, P = 0.019, η_p^2 = 0.195] and the condition × group interaction [$F_{(1,26)}$ = 7.71, P = 0.01, η_p^2 = 0.229] were significant supports this suggestion. Indeed, post hoc comparisons revealed that the difference between tangential and mixed conditions was not significant in the younger group (t_{26} = 0.19, two-tailed, P = 0.852, d = 0.118) but it was in the older group (t_{26} = −3.74, two-tailed, P = 0.001, d = 1.129). Moreover, the difference between groups was significant in the mixed (t_{26} = −4.98, two-tailed, P < 0.001, d = 1.830) but not in the tangential condition (t_{26} = −1.58, P = 0.127, two-tailed, d = 0.543).

Spatial Suppression

In the noise condition, background noise was added to the "tangential" target. The noise was made of randomly oriented, equally spaced Gabors, placed along two imaginary concentric circles centered on the screen.

Figure 4 shows psychometric functions describing detection probability as a function of DFC levels in the tangential (Figs. 1a, 1d) and noise conditions (Figs. 1c, 1f) in the two groups. The ANOVA on threshold values showed a group effect [$F_{(1,26)}$ = 8.95, P = 0.006, η_p^2 = 0.256], indicating a general increase of DFC thresholds with age. Moreover, the effect of condition was significant [$F_{(1,26)}$ = 17.90, P < 0.001, η_p^2 = 0.408], indicating that DFC thresholds are generally affected by background noise. The condition × group interac-

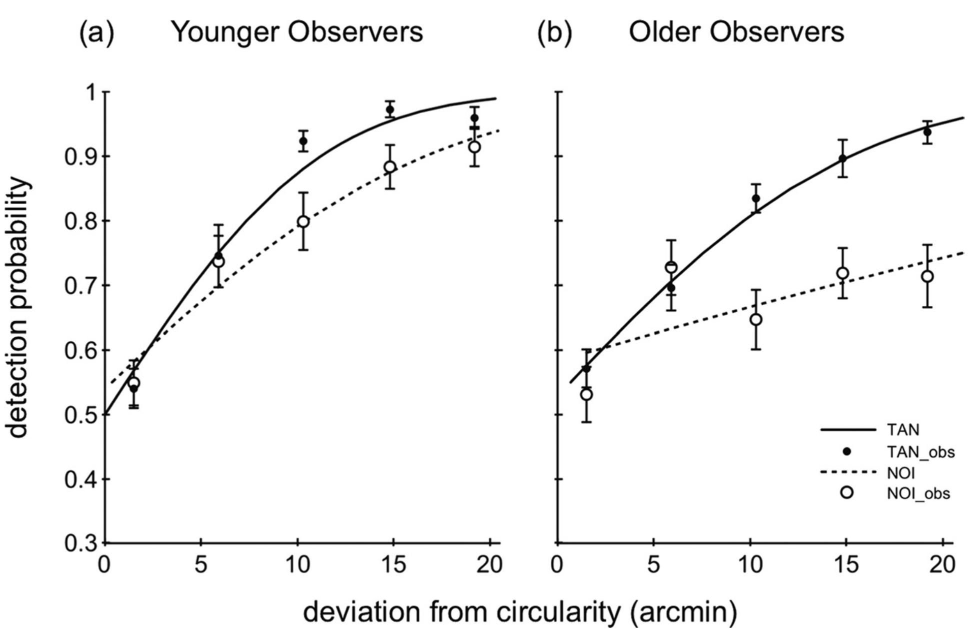

FIGURE 4. Psychometric functions for the (**a**) younger and (**b**) older groups in the tangential (TAN) and noise (NOI) conditions, obtained by fitting observed mean detection probabilities (TAN_obs, NOI_obs) for each DFC level.

tion was also significant [$F_{(1,26)} = 5.52$, $P = 0.027$, $\eta_p^2 = 0.175$]. Post hoc comparisons showed that the effect of noise was significant in the older group ($t_{26} = -4.65$, two-tailed, $P < 0.001$, d = 1.926) but not in the younger group ($t_{26} = -1.33$, two-tailed, $P = 0.195$, d = 0.589).

Furthermore, an inspection of the results of Figure 4 revealed an interesting finding. Indeed, although both groups are generally affected by noise, the largest DFC level illustrates a group dissociation: only older observers are strongly impaired. A post hoc *t*-test showed that the difference between the tangential and noise conditions at the largest DFC level was nonsignificant in the younger observers group ($t_{13} = 1.22$, $P = 0.246$, two-tailed, d = 0.474) but it was significant in the older observers ($t_{13} = 4.88$, $P < 0.001$, two-tailed, d = 2.219 group).

Discussion

Spatial Integration

Results show that older observers are strongly impaired in detecting the DFC when the circular contour contains mixed orientations. Nevertheless, performance of the two groups does not significantly differ in the detection of the DFC when the circular contour is defined by tangential Gabors. These results are relevant to the issue of whether there are age-related losses in the integrative operation involved in the detection of DFC of curvilinear contours and whether these depend on reduced orientation discrimination. To be integrated, oriented elements lying along a curved contour have to stimulate cells with relative orientations and spatial positions that optimize their encoding of the contour.[35] That is, the association of one cell with another is strong not only along the axis given by the cell's orientation but also along a curved contour as long as the orientation of the two cells is tangential to the contour. In this case, an association field is formed that integrates the response of the two cells through excitatory connections. This is possible for orientation differences up to ±60° among elements along the contour. Conversely, if oriented elements lying along the contour stimulate cells with relative orientations and positions that do not optimize their encoding of the contour, inhibitory connections are activated.[34,35]

The "association field model" predicts detection of curved contours but does not account for the difference between open and closed contours. Closed contours are better detected than open contours.[23] Moreover, the integration of elements lying along a closed contour tolerates larger inter-element distances than the integration of elements along an open contour.[23] Finally, for closed contours integration occurs with as few as four/five tangential signal elements, even when there are, as in our stimuli, four noise elements with nontangential orientation between each pair of tangential elements along the contour.[25,45–47] To account for the relative insensitivity to perturbation of local orientation, some authors have suggested that the detection of circular contours involves the comparison of the centroid of the contrast envelope because it does not vary with Gabor orientation.[52] Detection of DFC could be based on this strategy. However, if older observers were less efficient in this strategy they should also be impaired in the tangential condition. Alternatively, the insensitivity to local orientation perturbations could be ascribed to the activation of a shape-specific mechanism that integrates the relevant orientations along the closed contour while discarding interposed nontangential orientations. This mechanism may involve extrastriate areas in the ventral stream.[53]

The specific impairment in the mixed condition indicates that aging may reduce the efficiency of the shape-specific mechanism. However, it is unlikely that this impairment is the result of older observers requiring more than four relevant orientations. Although it has been claimed that older subjects need more elements for shape integration,[15,41] the evidence produced is not indisputable. Indeed, Del Viva and Agostini[15] found a group difference in the slope of the linear regression line fitting average sensitivity data as a function of the number of elements in the target. The shallower slope they observed for older adults reflects a lower rate of sensitivity improvement as the number of elements increased. Importantly, McKendrick et al.[41] found that thresholds (i.e., the minimum number of contour elements required for shape discrimination) were very similar in the two groups and did not differ from those of four/five elements needed to activate a shape-specific mechanism.[45] Instead, an age-dependent deficit in discarding nonrelevant orientations is more likely, a suggestion confirmed by the results in the noise condition of the present study's experiment.

Spatial Suppression

Comparison between the results obtained in the tangential and noise conditions indicates that older observers are more impaired than younger observers in the noise condition. Moreover, at the largest DFC level only older observers are significantly impaired, indicating that they do not take advantage of the largest DFC. We suggest that this is because although Gabors with large displacements from the circular contour are easily detected, they are also easily embedded in the background noise. The masking effect is increased in older subjects because of reduced suppression of the background noise.

Reduced Background Suppression or Lower Efficiency in Detecting Local Density Irregularity?

The display containing the DFC always has one displaced Gabor, and this creates a local density irregularity in that location. As such, rather than a reduced suppression of background noise, higher DFC thresholds in the older group may indicate reduced efficiency in detecting which interval contains a local density irregularity. To check for this second possibility we left the procedure unvaried but changed the task and used a stimulus constructed by modifying each contour in the noise condition as follows: we randomized the orientation of the elements defining the contour without changing their position to obtain patterns made up of randomly oriented Gabors placed along three circles and one displaced Gabor. We asked six younger subjects who did not participate in the main experiment to perform a 2I-2AFC task, indicating in which of the two presentations there was a density irregularity. *t*-Tests, testing whether accuracy was significantly different from 50% (chance level) at each DFC level, showed no significant results (*P*-values of 0.111 [$t_5 = 1.94$], 1.000 [$t_5 = 0.00$], 0.256 [$t_5 = 1.28$], 0.661 [$t_5 = 0.47$], and 0.090 [$t_5 = 2.10$] for DFC levels equal to 1.5, 5.9, 10.3, 14.8, and 19.2 arcmin, respectively).

These results rule out the possibility that higher DFC thresholds for the older group in the noise condition indicate lower efficiency in detecting which interval contains the local density irregularity.

Suppressive Mechanism, Attention, or Working Memory?

To summarize, we have shown that aging reduces the efficiency in integrating local oriented elements into a closed curvilinear contour when this task requires the exclusion of irrelevant orientations (in the mixed and noise conditions). This suggests an age-dependent reduction in the efficiency of the suppressive mechanism, a change that reduces the capacity to discard irrelevant orientations along the contour and in the background. Neurophysiological studies in cats and monkeys provide indirect support for this suggestion. They show reduced lateral inhibition as well as increased spontaneous activity in senescent V1 neurons selective for orientation and direction of motion.[37,38] Those changes might result from reduced GABA-mediated inhibition.[39] This could specifically affect the suppressive mechanism while leaving the integrative mechanism unperturbed. Indeed, intracortical interactions underlying these two visual operations are different: whereas the majority of the postsynaptic excitatory effects result from long-range intracortical interactions, intracortical inhibitory interactions between GABAergic inhibitory cells mediating the suppression of irrelevant orientations on contour detectability are predominantly short range[36] and largely independent of orientation.

It is also interesting to speculate whether the data can be explained by declining attentional capacity with age. Attentional factors cannot be excluded because they may affect the relatively low level perceptual operations investigated here. Indeed, it has been demonstrated that attention modulates both facilitatory and inhibitory contextual influences in contour integration and segmentation[19,54] and exclusion of distracters.[55] Declining attentional capacity with age should negatively affect all conditions tested in the present study's experiment and not only mixed and noise conditions. Thus, the reduction of attentional resources with age cannot be the only explanation. Similarly, differences in working memory cannot account for our results: indeed a general effect on all conditions tested should have emerged.

To conclude, we suggest that in older observers reduced inhibitory intracortical lateral connections may account for the increased effect of background noise. Those same changes can account for the reduced performance of a shape-specific mechanism that integrates only a few tangential Gabors along a circular contour while suppressing nontangential ones.

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