

Visual Spatial Integration in the Elderly

Maria Michela Del Viva^{1,2} and Rachele Agostini¹

PURPOSE. To investigate the effect of ageing on contour integration in subjects whose ages ranged from 20 to 99 years.

METHODS. Detection thresholds were measured for a closed chain of Gabor patches oriented tangentially to a circle (target) embedded in a background of randomly positioned and oriented Gabors (noise). Detection thresholds were measured for different distances of elements composing the target.

RESULTS. Sensitivity decreases gradually with age at all interelement distances. Sensitivity decreases with increasing interelement distance, in both young and elderly subjects. The decrease of integration capability with age is not related to a decrease in contrast sensitivity.

CONCLUSIONS. Overall, the data provide evidence of a deterioration of cortical functionality with age, in agreement with other studies on texture and motion processing. (*Invest Ophthalmol Vis Sci.* 2007;48:2940–2946) DOI:10.1167/iov.06-0729

Visual abilities decline during normal (nonpathologic) ageing, but our understanding of the nature and causes of visual changes in the elderly is still limited. Damages to optical properties of the eyes (e.g., presbyopia, senile miosis) are the most common cause of visual deficits in the old population, producing deterioration of low-level visual functions, such as visual acuity and contrast sensitivity.^{1–3} However, visual acuity reduction is not exclusively due to changes in the eye's optical properties.^{4–7} Ageing produces loss of photoreceptor, bipolar, or ganglion cells and changes in their connections that could account for visual acuity losses.^{8,9} The decrease in contrast sensitivity observed with ageing (for frequencies higher than 2 cyc/deg),¹⁰ is also due to a natural deterioration of optical properties,^{11,12} as well as to retinal or central visual damage Zuckermann JL et al. *IOVS* 1973;12:ARVO Abstract 213^{4,13–16} Porciatti et al.¹⁷ found small differences in PERG, whereas VEP amplitudes and phases of old subjects were lower than those of young subjects, suggesting that visual impairment in the elderly occurs primarily in V1. More in general, ageing affects PERG and VEPs at low temporal frequencies, producing lower amplitudes and increased latency, particularly at high spatial frequencies.^{17–21} Despite the well-documented anatomic and physiological age-related changes in the primary visual pathway, the extent to which they contribute to specific nonpathologic deficits in low-level visual function remains unresolved.²²

If our understanding of age-related changes in low-level processes is limited, it is also true that not much is known about the effects of ageing on the way neurons elaborate and integrate complex information from the external environment

and about the relationship between behavior and diminished neural functions. There are several studies indicating a decreased activity in the ageing brain related to high-level cognitive tasks. Measurements of cerebral blood flow (rCBF) by standard positron emission tomography (PET) reveal differences in activation between young and old subjects in object-recognition tasks,^{23,24} face recognition,²⁵ and stimulus encoding.²⁶

In some recent studies, investigators have begun to examine also the consequences of ageing on visual perception, finding some abilities to be particularly affected by ageing whereas others are relatively spared. Snowden and Kavanagh²⁷ have explored several aspects of motion perception and found a variety of deficits not accompanied by a significant loss in contrast sensitivity. These deficits were ascribed to a deterioration of the brain areas responsible for global motion perception, such as the medial temporal area.^{28–30} O'Brien et al.³¹ also found a diminished sensitivity to optic flow motion in healthy elderly subjects. Changes due to ageing do not necessarily bring about a deterioration of visual function. Some investigators have found that motion perception of large, high-contrast stimuli is even better in old subjects than in young adults.³² This effect was attributed to age-related reductions in GABA-mediated inhibition³³ that, while having a detrimental effect on a broad range of cognitive, perceptual, and behavioral functions, could weaken center-surround antagonism and increase performance in motion perception.³⁴ Some studies report particularly low performance of the elderly in midlevel tasks, such as bilateral symmetry detection,³⁵ and in tasks requiring high-level or second-order processing, such as second-order motion and texture,³⁶ in comparison with tasks requiring first-order processing. These results led the authors to formulate the hypothesis that deficits in perceptual processing due to ageing become evident when the computational load of the task reaches a certain level of complexity, requiring larger or more complex networks that are not available in the ageing brain.³⁷

Contour integration is a complex ability, widely investigated in multiple-choice detection tasks, in which a chain of Gabor patches (GPs)—sinusoidal luminance signals within a Gaussian envelope—must be segregated from a noisy background.^{38–40} In these stimuli, there is no global cue—orientation, color, or texture—for the segregation of the chain. The global patterns seem to emerge from interactions between local mechanisms, influenced by variables such as relative orientation of nearby cues, relative distance, and colinearity.^{38,41–43} In particular, the critical distance between GPs that allows integration to occur for a given stimulus is a crucial parameter and may be related to connections between simple cortical units.^{41,44} In fact, several lines of anatomic,^{45–47} physiological,^{48,49} and imaging⁵⁰ evidence suggest that horizontal connections can link cells with nonoverlapping receptive fields, with similar orientation preferences, as early as in V1.

This contour segregation ability, which is part of a more general task of figure-ground segmentation,⁵⁹ is a second-order task, involving integration of locally oriented elements in a global percept. This task would require larger networks that, according to some investigators,³⁷ could generate age-related deficits. A multiple-stage analysis could also explain why this ability undergoes protracted development during child-

From the ¹Department of Psychology, University of Florence, Florence, Italy; ²Istituto di Neuroscienze, CNR Area di Ricerca di Pisa, Pisa, Italy.

Submitted for publication June 29, 2006; revised December 12, 2006; accepted April 19, 2007.

Disclosure: **M.M. Del Viva**, None; **R. Agostini**, None

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be marked "advertisement" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

Corresponding author: Maria Michela Del Viva, Istituto di Neuroscienze, CNR Area di Ricerca di Pisa via Moruzzi 1 56100 Pisa, Italy; michela@in.cnr.it.

hood.^{51,52} It is therefore interesting to study contour integration during ageing to verify whether the complexity of the task affects visual performance in the elderly.

The knowledge of natural evolution of contour integration during ageing is also useful to discriminate the normal trend in the ageing brain from a deterioration of this ability observed in some degenerative diseases.⁵³

In this study, we measured how visual integration ability changes with age, by measuring detection thresholds of a closed chain of GPs, oriented tangentially to a circle (target), embedded in a dense field of Gabors oriented randomly (noise), at different ages. We also tested whether in older people there is the same dependency on interelement distance in the target observed in younger subjects.³⁸

METHODS

Apparatus and Stimuli

Sensitivity for integration of local elements into a global pattern was measured by the ability of subjects to detect a circle (target) embedded in noise, where both the circle and noise elements were GPs^{38,39} (Fig. 1).

All GPs in the circle were oriented perpendicularly to its radius, whereas orientation of noise elements was randomly distributed. Noise elements were randomly placed within the display area, provided that they were never superimposed. Spatial frequency of GPs was 1.5 cyc/deg, each GP subtended 1°, and the target had a radius equal to

4.9° of the visual angle. Thresholds were measured for different distances between the GPs comprising the target: 4.9°, 3.8°, 2.9°, and 2.1° of visual angle, obtained by varying their number (Fig. 1).

Stimuli were presented on a 60-Hz frame-rate liquid crystal display (LCD) driven by a laptop computer. The distance of the subjects from the screen was 57 cm. The whole stimulus had a mean luminance of 20 cd/m², subtended 24° × 24° of visual angle, and was displayed for 1 second. All measurements were performed in a darkened room.

Procedure

The presentation of the stimuli was always preceded by a sound to catch the subjects' attention. The target could be positioned randomly in one of four quadrants of the computer screen (Fig. 1), and the subject's task was to locate the circle with a four-alternative, forced-choice procedure. Responses were reported verbally by the subjects and recorded manually by the experimenter. The subjects had no time limit for response, and no verbal or sound feedback was given.

For each separation between GPs comprising the target, the integration ability was quantified by measuring detection thresholds for the circular target, varying the number of noise GPs. Target-detection thresholds were defined by the number of noise GPs yielding 75% correct detection.

To minimize tiredness and boredom, data on elderly subjects were obtained in four sessions on different days, each of them measuring all conditions. Data on younger subjects were obtained in four sessions on the same day. We checked that the different data-taking procedures do

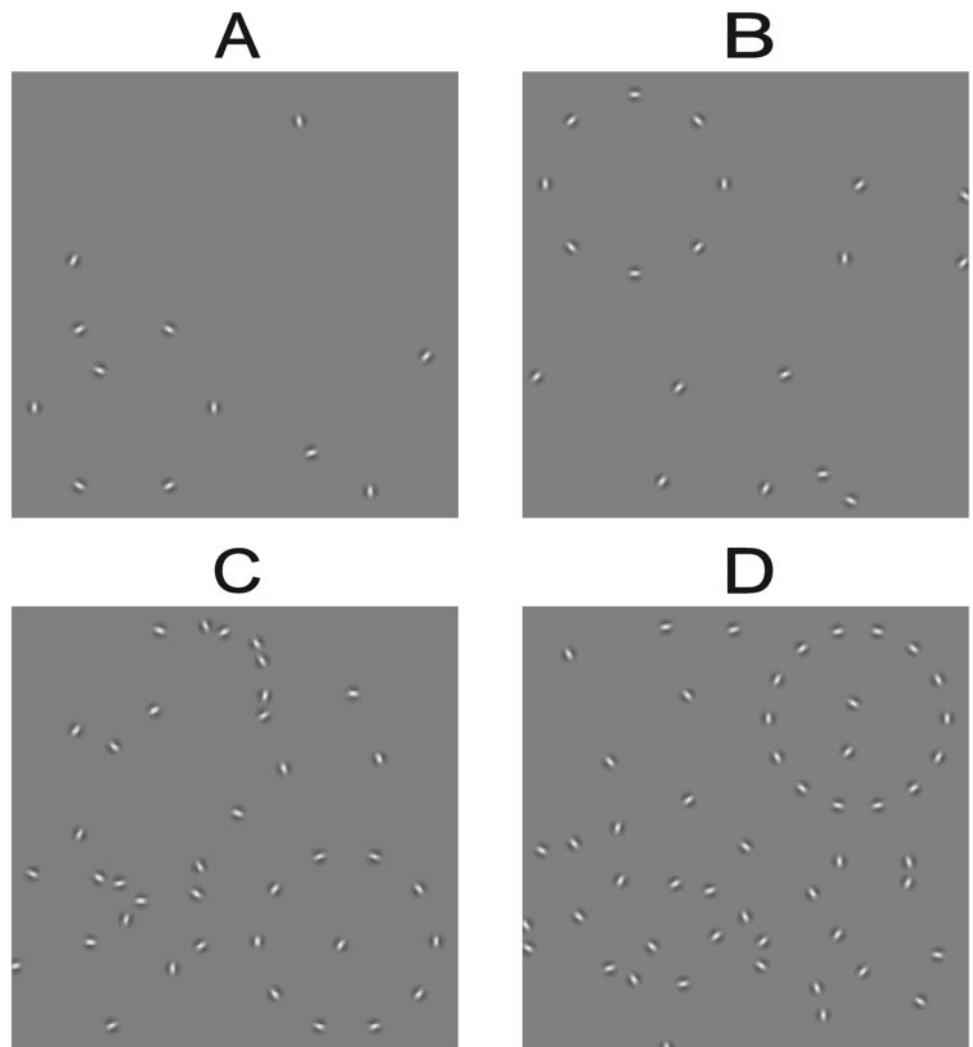


FIGURE 1. Examples of stimuli. Targets composed of (A) 6 GPs (interelement distance, 4.9°), (B) 8 GPs (interelement distance, 3.8°), (C) 10 GPs (interelement distance, 2.9°), and (D) 14 GPs (interelement distance, 2.1°).

not affect the results, by repeating some measurements on young subjects with the same method used on elderly subjects. The measurements obtained in these two manners were compatible at the 95% confidence level. Data for each condition were collected in five blocks of 30 trials. In each block, the number of noise Gabors was varied along different trials according to a staircase QUEST procedure.⁵⁴

For every tested condition and for each subject, a cumulative maximum-likelihood fit was performed off-line with all data obtained in all sessions, by using a Weibull psychometric function.⁵⁵ Thresholds were defined as the point of the fitting curve where probability of correct response equals 0.75. We plotted sensitivities rather than thresholds, to represent and compare performances. Sensitivity is defined as $(S+N)/S$ where S is the number of target GPs, and N is the number of noise GPs at threshold.

Contrast sensitivities were measured with a portable test chart system (VCTS 6000; Vistech Consultants, Dayton, OH). For all subjects, young and old, environmental luminance level was kept constant around 115 cd/m², and test charts were positioned 46 cm away from subjects by using an apposite chart-holder. Contrast sensitivity curves were obtained for spatial frequencies of 1.5, 3, 6, 12, and 18 cyc/deg. Each measurement is the average of three different trials.

Dependence of sensitivity on age was estimated fitting data with a straight line. Statistical significance of angular coefficients obtained from fit was tested with normal distribution tests (Table 1), used also to test differences between them. Dependence of average performance on integration distance and group was tested with two-way ANOVA (with Bonferroni correction). Post hoc Student's *t*-tests were used to compare performances of old and young subjects (Table 1). Dependence of contrast sensitivity on age was also estimated fitting data at a particular frequency with a straight line.

Subjects

The young sample was composed of 11 observers (mean age, 25 ± 1 years; range, 24–27), and the elderly sample comprised 21 observers (mean age, 65 ± 8 years, range, 51–83). We also tested one observer who was 99 years old, well outside the range (subject GB). Younger subjects were middle-class Italian university students, and the older subjects were selected among their relatives (i.e., grandparents, uncles) in good general health, and living in the same area. All subjects had normal or corrected-to-normal vision with their glasses or contact lenses. Old subjects did not have eye defects (such as cataract and glaucoma) or neurologic deficits such as Alzheimer disease or other forms of dementia associated with age. Both experimental groups had similar socioeconomic status and educational background. The measurement of contrast sensitivity was performed in a later session (2 weeks later) in which 6 young and 15 old subjects from the initial group were available.

This research adhered to the tenets of the Declaration of Helsinki, and informed consent was obtained from all subjects after explanation of the nature and possible consequences of the study.

TABLE 1. Decline in Sensitivity with Age at Different GP Separations

Distance	α	σ	P ($\alpha = 0$)
4.9°	-0.079	0.017	<0.00001
3.8°	-0.082	0.018	<0.00001
2.9°	-0.126	0.020	<0.00001
2.1°	-0.216	0.035	<0.00001

The amount of decline is represented by angular coefficients (α) of the best-fit curves shown in Figure 2 and relative standard deviations (σ). P denotes the probability of the null hypothesis (Gaussian probability distribution test).

RESULTS

Age-Related Effects

Figure 2 shows sensitivity for detection of the circular target as a function of age for different interelement distances, indicated by the cartoons in each panel. Subjects' performance decreased with age for every distance of GPs (see Table 1 for fit parameters). In other words, old subjects, to locate the target correctly, needed less background noise than did younger subjects, which could indicate that the ageing visual system becomes more sensitive to background and progressively diminishes its capacity to integrate separated elements. Note that, in all conditions, on average, spatial integration sensitivity diminished at about a factor 2 between 25 and 80 years. Data obtained from our older subject suggest that over 90 years this loss in sensitivity is even more marked.

From inspection of Figure 2, one could deduce that age dependency is due only to the performance of the oldest subject (GB, 99 years). To exclude this possibility, we also fitted the data excluding the oldest subject from the sample and compared the results obtained with and without subject GB. Angular coefficients obtained excluding GB from the analysis were not significantly different from those obtained when using all data ($P = 0.37$ for 4.9°; $P = 0.41$ for 3.7°; $P = 0.42$ for 2.9°, and $P = 0.49$ for 2.1°). This demonstrates that the decline in sensitivity was not due solely to the performance of our oldest subject but reflected a characteristic of the whole sample.

Effects of Interelement Distance

Values of angular coefficients of best-fit curves in Figure 2, reported in Table 1, indicate that sensitivity decreased with age at different rates at different interelement distances. The rate of decline with age was more marked for short interelement distances, becoming constant over 3° ($P < 0.05$).

Figure 3 shows the average sensitivities of young and old subjects as a function of separation of GPs in the target (see also Table 2). Sensitivities of the 99-year-old subject (GB) are plotted apart, in that he was much older than the others (more than 3 SD). Straight lines represent best linear fits of data and highlight the trend of performance. In both samples, sensitivity to spatial integration increased with the proximity of Gabors comprising the target ($F = 18.9$; $P < 0.000001$). This result means that detection of all subjects improved when the elements were closer. ANOVA shows also that there is a significant difference between the two age groups, GB excluded, at all distances ($F = 6.1$; $P < 0.000001$). The performance of subject GB exhibits the same general trend as the rest of the old population. In other words, he benefitted in the same way from the proximity of GPs in the target. However, his sensitivity was much lower than that of the others, being well below the 99% lower confidence limit of the older sample (Student's *t*-test).

Relationships between Contrast Sensitivity and Integration Sensitivity

What is the origin of the decline of contour integration with age observed so far? Since all our subjects had normal or corrected-to-normal vision and did not have eye diseases or neurologic deficits, the observed deficit could be ascribed to contrast sensitivity losses, often present during ageing.¹⁰ We therefore measured contrast sensitivity in a subsample of our subjects (young and old) and found a distribution compatible with that in the normal population between 20 and 70 years, as shown in Figure 4A (confidence limits band provided by manufacturers of the VCTS 6000; Vistech). Sensitivities of elderly

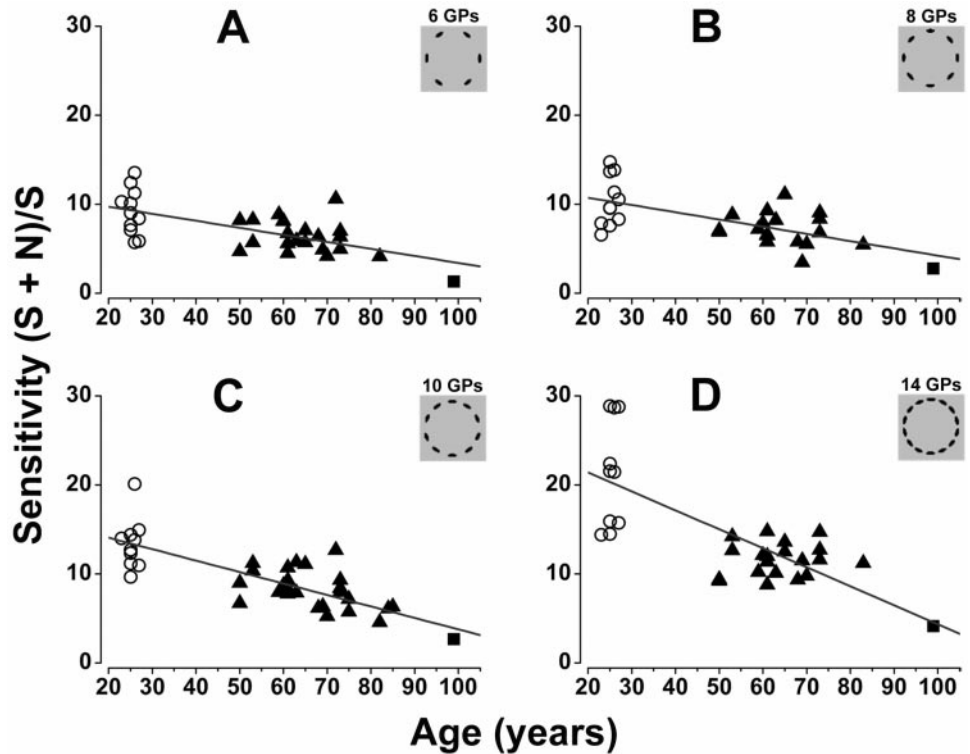


FIGURE 2. Individual integration sensitivities, plotted as a function of age, for different interelement distances, shown by cartoons (insets). Sensitivities of young (○) and old (▲) subjects and subject GB (■) are plotted together with their best-fit curves (see also Table 1).

subjects, however, were on average systematically lower than those of young observers at all spatial frequencies, indicating impairment with respect to the younger population. This is more evident in Figure 4B, which shows how contrast sensitivity varied with age for a particular value of spatial frequency chosen from those presented in Figure 4A (3 cyc/deg). There is a steady decrease of sensitivity with age ($P < 0.00001$) in agreement with Owsley et al.¹⁰

Contrast sensitivity results, although the presence of major deficits were excluded, demonstrate a general impairment with age that could be the cause of the observed decline of contour integration. Alternatively, ageing could impair independently the two sensitivities. To ascertain which possibility

is supported by our data, we compared in the same subject contrast sensitivity, measured at 3 cyc/deg (Fig. 4B), and integration sensitivity, measured at 2.9° (Fig. 2C). The comparison between these two values seemed reasonable, because they corresponded to similar distances. To remove the effect of age dependence and reveal the possible direct correlations between contrast and integration sensitivity, we evaluated the residual of each data point from the best-fit curve. We then plotted in Figure 5 the contrast sensitivity residual versus the integration sensitivity residual and correlated these values. The best-fit curve, in fact, represents in both cases the dependence of sensitivity on age; thus, subtracting from the observed value the best-fit value is equivalent to eliminate age dependency from sensitivities. We found no correlation between integration sensitivity residuals CI and contrast sensitivity residuals CS (Pearson's $r^2 = 0.0147651$; $P = 0.13$). A fit to a linear model $CI = \alpha CS$ returns $\alpha = -0.015 \pm 0.013$. Conversely, if the decline of contrast sensitivity with age were responsible for the limited performance in the contour detection task, one would expect $\alpha = 0.13 / 1.6 = 0.08$. The latter is excluded at 7- σ level from our data.

TABLE 2. Mean Sensitivities of the Two Samples of Subjects for Each Interelement Distance

Distance	Young Subjects		Old Subjects		P*
	Mean	SD	Mean	SD	
4.9°	9.2	2.6	6.4	1.7	<0.00059
3.8°	10.3	2.8	7.2	1.8	<0.00001
2.9°	13.4	2.9	8.5	2.1	<0.00088
2.1°	21.3	6.0	11.7	1.7	<0.00089

Subject GB is excluded.
* Student's *t*-test.

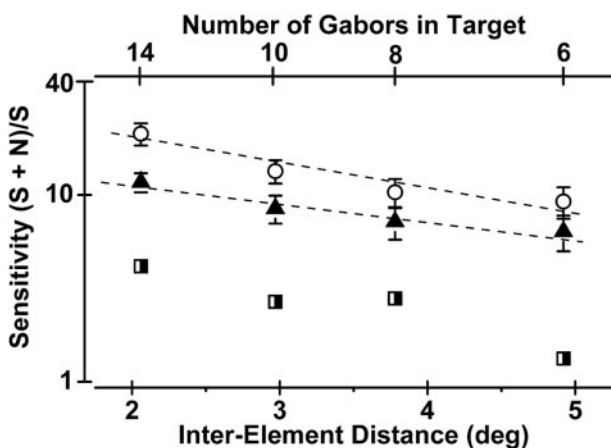


FIGURE 3. Mean sensitivity of young (○) and old (▲) subjects and subject GB (■) as a function of separation of GPs in the target (bottom abscissa). The top abscissa shows the correspondent numbers of GPs. Dotted lines: linear regressions of data that highlight the trend of performance of subjects (young sample: $y = 23.22 - 3.04x$; $\chi^2 = 0.5$; and old sample: $y = 15 - 1.87x$; $\chi^2 = 0.3$).

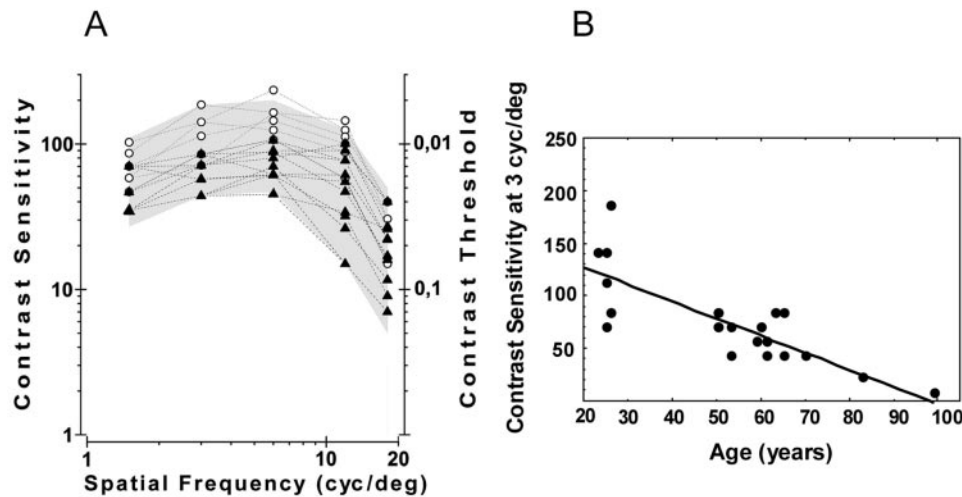


FIGURE 4. (A) Contrast sensitivity as a function of spatial frequency. Shaded area: 90% confidence limits of normal population between 20 and 70 years. (○) Young subjects; (▲) old subjects. (B) Contrast sensitivity for spatial frequency of 3 cyc/deg plotted as a function of age. Solid line: best fit ($160.53 - 1.628x$).

DISCUSSION

In the present study contour integration ability deteriorated during ageing. In fact, sensitivity for detection of a target composed of local elements, embedded in a noise field, decreased linearly with age, independent of the distance between local elements. One could argue whether the observed handicap in old people is purely perceptual or is caused by high-level cognitive ageing factors, such as less efficient search strategies, or by nonvisual factors, such as reduced motivation in completing a difficult task. Our data cannot rule out these possibilities, but the adopted procedure—limited presentation time, guessing factor of 25%—limits the influence of visual search in completing the task. The repetition of the same measurement—one for each distance—on five different days was a control for motivation.

In both age groups, contour integration deteriorated, as distance between local elements comprising the target increased, in agreement with previous studies in which improved performance was found with colinearity and proxi-

mity.^{38,41-43} However, the performance at short distances seemed to be more affected by age (Table 1).

Recently, some investigators devised a hypothesis to explain why some perceptual abilities are more affected by ageing than others.^{35-37,56} They suggest the magnitude of the observed age-related changes depends on stimulus complexity (given by the computational load or by the complexity of the underlying neural network). Our data are consistent only in part with this hypothesis: contour integration ability, which is a second-order complex task, is diminished with age, but age-related changes are more pronounced at shorter distances, when the task appears to be easier. These counter-intuitive results could be explained with different integration mechanisms, for large and small contour spacing, that evolve separately during life⁵¹ and are affected differently by ageing.

Elderly subjects who participated in our experiments were healthy, active, and independent, with contrast sensitivity within the norm of their age—therefore, without significant low-level deficits—nevertheless, we found a natural decline in contrast sensitivity with age. In the current study we demonstrate that there was no correlation between contrast sensitivity and integration sensitivity, when corrected for age dependency. Therefore, the observed impairment with ageing in contour integration cannot be due to ageing of the neural circuits that underlie contrast sensitivity, the precise localization of which remain unknown, occurring at any level between the retina and the visual cortex.^{4,15}

The exact localization of the circuits responsible for spatial integration of colinear elements over a certain distance is also still largely unknown. Many studies have demonstrated that long-range connections in the striate cortex, localized in the plexus of intrinsic horizontal connections of V1,^{46,57-60} connect cells with similar orientation preference.⁶¹ These connections could be altered in elderly individuals and, in principle, could be responsible for the observed deficit. These connections are not solely responsible for the contour-detection task, which may be modulated by feedback top-down connections originating in the extrastriate cortex. In particular, for global processing, functional neuroimaging studies have located the source of such a modulatory activity in the right temporoparietal junction.⁶² Other neurophysiological findings provide evidence of the existence of facilitatory top-down effects that could amplify and focus the activity of neurons in lower-order areas and thus facilitate figure-ground segmentation and improve the visibility of features and contribute to the “pop-out” phenomenon.⁶³ Studies of the development of the visual system⁶⁴ suggest also a role of feedback connections from V2 to

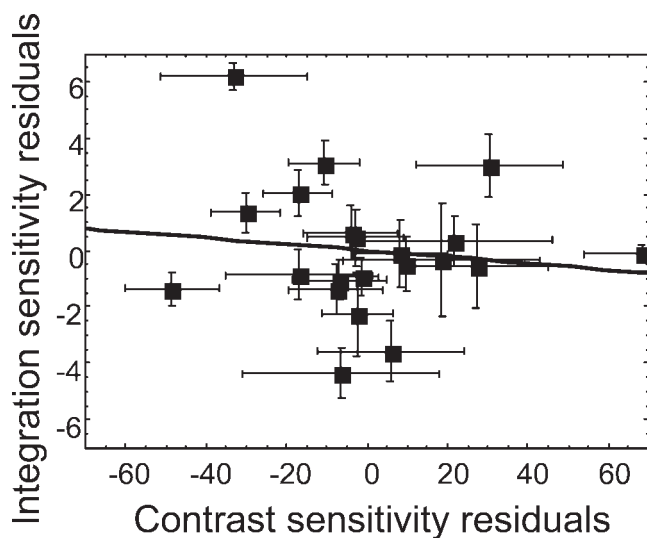


FIGURE 5. Correlation between integration and contrast sensitivity. Integration sensitivities in Figure 2C (distance: 2.9°) plotted against contrast sensitivities in Figure 4B (spatial frequency: 3 cyc/deg) after subtraction of respective best-fit values. The observed correlation (solid line) is not significant ($P = 0.13$).

V1 in contour integration.⁵¹ Although the lateral and feedback connections of V1 are essential in completing a contour-detection task, cortical areas concerned with form vision, such as V4,⁶⁵ probably also participate in this process. Given the complexity of circuits and areas involved in the contour-detection task, the anatomic substrates of modifications induced by ageing have yet to be identified.

Regarding the nature of modifications of these circuits, several studies have found in the ageing brain changes in neuronal discharges, neurotransmitter release, and response to neurotransmitters.^{33,66-71} In the visual system, ageing produces the loss of retinal cells^{8,9}; selective damage to the parvocellular pathway, perhaps related to changes in spatial contrast sensitivity^{72,73}; abnormal dendritic growth; dendritic regression; and reduction of the spinal density of striate cortex cells.⁷⁴⁻⁷⁶ Recent work provides evidence that both the orientation and direction selectivities of extrastriate V2 cells in old monkeys degrade significantly while spontaneous activity increases.⁷⁷ These modifications could underlie the decline in higher-order visual functions, such as contour integration, occurring during ageing. However, there is no direct evidence that similar modifications occur in the striate and extrastriate cortex of humans, and our understanding of the effects of ageing on the neuronal circuitry attributed to contour integration remains rudimentary.

Acknowledgments

The authors thank Concetta Morrone and David Burr for helpful discussions.

References

- Elliot DB, Whitaker D, MacFeigh D. Neural contribution to spatio-temporal contrast sensitivity decline in healthy ageing eyes. *Vision Res.* 1990;30:541-547.
- Pitts D. The effects of ageing on selected visual functions: dark adaptation, visual acuity, stereopsis and brightness contrast. In: Sekuler R, Kline D, Dismukes K, eds. *Ageing and Human Visual Function*. New York: Liss; 1982;131-159.
- Owsley C, Burton K. Aging and spatial contrast sensitivity: underlying mechanism and implications for everyday life. In: Bagnoli P, Hodos, W. eds. *The Changing Visual System: Maturation and Aging in the Central Nervous System*. London: Plenum; 1991; 119-136.
- Weale RA. Senile changes in visual acuity. *Trans Ophthalmol Soc UK.* 1975;95:36-38.
- Weale RA. The eye and the aging. *Interdisciplinary Topics in Gerontology.* 1978;13:1-13.
- Weale RA. Senile ocular changes, cell death, and vision. Sekuler R, Kline D, Dismukes K, eds. *Ageing and Human Visual Function*. New York: Liss; 1982:161-171.
- Jay JL, Mammo RB, Allan D. Effect of age on visual acuity after cataract extraction. *Br J Ophthalmol.* 1987;71:112-115.
- Curcio CA, Millican CL, Allen KA, et al. Aging of the human photoreceptor mosaic: evidence for selective vulnerability of rods in central retina. *Invest Ophthalmol Vis Sci.* 1993;35:783-784.
- Curcio CA, Drucker DN. Retinal ganglion cells in Alzheimer's disease and aging. *Ann Neurol.* 1993;33:248-257.
- Owsley C, Sekuler R, Siemsen D. Contrast sensitivity throughout adulthood. *Vision Res.* 1983;23:689-699.
- Dressler M, Rassow B. Neural contrast sensitivity measurements with a laser interference system for clinical screening application. *Invest Ophthalmol Vis Sci.* 1981;21:737-744.
- Kayazawa F, Yamamoto T, Itoi M. Clinical measurement of contrast sensitivity function using laser generated sinusoidal grating. *Jpn J Ophthalmol.* 1981;25:229-236.
- Weale RA. Retinal senescence. *Prog Retin Res.* 1986;5:53-73.
- Ordy MJ, Brizee KR, Johnson HA. Cellular alterations in visual pathways and the limbic system: Implications for vision and short-term memory. In: Sekuler R, Kline D, Dismukes K, eds. *Ageing and Human Visual Function*. New York: Liss; 1982:79-114.
- Morrison JD, McGrath C. Assessment of the optical contributions to the age-related deterioration in vision. *Q J Exp Physiol.* 1985; 70:249-269.
- Owsley C, Gardner T, Sekuler R, et al. Role of the crystalline lens in the spatial vision loss of the elderly. *Invest Ophthalmol Vis Sci.* 1985;26:1165-1169.
- Porciatti V, Burr DC, Morrone MC, et al. The effects of ageing on the pattern electroretinogram and visual evoked potential in humans. *Vision Res.* 1992;32:1199-1209.
- Bobak P, Bodis-Wollner I, Guillory S, et al. Aging differentially delays visual evoked potentials to checks and gratings. *Clin Vis Sci.* 1989;4:269-274.
- Sokol S, Moskowitz A, Towle VL. Age related changes in latency of the visual evoked potential: Influence of check size. *Electroencephalogr Clin Neurophys.* 1981;51:559-562.
- Tomoda H, Celesia GG, Brigell MG, et al. The effects of age on steady-state pattern electroretinograms and visual evoked potentials. *Doc Ophthalmol.* 1991;77:201-211.
- Trick GL, Trick LR, Haywood KM. Altered pattern evoked retinal and cortical potentials associated with human senescence. *Curr Eye Res.* 1986;5:717-724.
- Spear PD. Neural bases of visual deficits during aging. *Vision Res.* 1993;33:2589-2609.
- Levine BK, Beason-Held LL, Purpura KP, et al. Age-related differences in visual perception: a PET study. *Neurobiol Aging.* 2000; 21:577-584.
- Grady CL, Haxby JV, Horwitz B, et al. Dissociation of object and spatial vision in human extrastriate cortex: age-related changes in activation of regional cerebral blood flow measured with [¹⁵O] water and positron emission tomography. *J Cogn Neurosci.* 1992; 4:23-24.
- Grady CL, Maisog JM, Horwitz B, et al. Age-related changes in cortical blood flow activation during visual processing of faces and location. *J Neurosci.* 1994;14:1450-1462.
- Grady CL, McIntosh AR, Horwitz B, et al. Age-related reductions in human recognition memory due to impaired encoding. *Science.* 1995;269:218-221.
- Snowden RJ, Kavanagh E. Motion perception in the ageing visual system: minimum motion, motion coherence and speed discrimination thresholds. *Perception.* 2006;35:9-24.
- Tanaka K, Fukada Y, Saito HA. Underlying mechanisms of the response specificity of expansion/contraction and rotation cells in the dorsal part of the medial superior temporal area of the macaque monkey. *J Neurophysiol.* 1989;62:642-656.
- Morrone MC, Tosetti M, Montanaro D, et al. A cortical area that responds specifically to optic flow, revealed by functional magnetic resonance imaging. *Nat Neurosci.* 2000;3:1322-1328.
- Moutoussis K, Zeki S. Seeing invisible motion: a human fMRI study. *Curr Biol.* 2006;16:574-579.
- O'Brien HL, Tetewsky SJ, Avery LM, et al. Visual mechanisms of spatial disorientation in Alzheimer's disease. *Cereb Cortex.* 2001; 11:1083-1092.
- Betts LR, Taylor CP, Sekuler AB, et al. Aging reduces centre-surround antagonism in visual motion processing. *Neuron.* 2005; 45:361-366.
- Leventhal AG, Wang Y, Pu M, et al. GABA and its agonists improved visual cortical function in senescent monkeys. *Science.* 2003;300:721-722.
- Tadin D, Blake R. Motion perception getting better with age. *Neuron.* 2005;45:325-332.
- Herbert AM, Overbury O, Singh J, Faubert J. Aging and bilateral symmetry detection. *J Gerontol B Psychol Sci Soc Sci.* 2002;57: 241-245.
- Habak C, Faubert J. Larger effect of aging on the perception of higher-order stimuli. *Vision Res.* 2000;40:943-950.
- Faubert J. Visual perception and aging. *Can J Exp Psychol.* 2002; 56:164-176.
- Field DJ, Hayes A, Hess RF. Contour integration by the human visual system: evidence for a local "association field." *Vision Res.* 1993;33:173-193.

39. Kovacs I, Julesz B. A closed curve is much more than an incomplete one: effect of closure on figure-ground segmentation. *Proc Natl Acad Sci USA*. 1993;90:7495-7497.
40. Kovacs I, Julesz B. Perceptual sensitivity maps within globally defined visual shapes. *Nature*. 1994;370:644-646.
41. Li W, Gilbert CD. Global contour saliency and local collinear interactions. *J Neurophysiol*. 2002;88:2846-2856.
42. Saarinen J, Levi DM, Shen B. Integration of local pattern elements into a global shape in human vision. *Proc Natl Acad Sci USA*. 1997;94:8267-8271.
43. Saarinen J, Levi DM. Integration of local features into a global shape. *Vision Res*. 2001;41:1785-1790.
44. Polat U, Sagi D. Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments. *Vision Res*. 1993;33:993-999.
45. Gilbert CD, Wiesel TN. Morphology and intracortical connections of functionally characterised neurones in the cat visual cortex. *Nature*. 1979;280:120-125.
46. Gilbert CD, Wiesel TN. Clustered intrinsic connections in cat visual cortex. *J Neurosci*. 1983;3:1116-1133.
47. Gilbert CD, Wiesel TN. Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. *J Neurosci*. 1989;9:2432-2442.
48. Ts'o DY, Gilbert CD. The organization of chromatic and spatial interactions in the primate striate cortex. *J Neurosci*. 1988;8:1712-1727.
49. Kapadia MK, Ito M, Gilbert CD, et al. Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in V1 of alert monkeys. *Neuron*. 1995;15:843-856.
50. Das A, Gilbert CD. Receptive field expansion in adult visual cortex is linked to changes in strength of cortical connections. *J Neurophysiol*. 1995;74:779-792.
51. Kovacs I, Kozma P, Feher A, et al. Late maturation of visual spatial integration in humans. *Proc Natl Acad Sci USA*. 1999;96:12204-12209.
52. Del Viva MM, Iglizzi R, Tancredi R, et al. Spatial and motion integration in children with autism. *Vision Res*. 2006;46:1242-1252.
53. Piccini C, Lauro-Grotto R, Del Viva MM, et al. Agnosia for global patterns: when the cross-talk between grouping and visual selective attention fails. *Cogn Neurosci*. 2003;20:3-25.
54. Watson AB, Pelli DG. QUEST. A Bayesian adaptive psychometric method. *Percept Psychophys*. 1983;33:113-120.
55. Weibull WA. A statistical distribution function of wide applicability. *J Appl Mechanisms*. 1951;18:292-297.
56. Faubert J, Bellefeuille A. Aging effects on intra- and inter-attribute spatial frequency information for luminance, color, and working memory. *Vision Res*. 2002;42:369-378.
57. Rockland KS, Lund JS. Widespread periodic intrinsic connections in the tree shrew visual cortex. *Science*. 1982;215:1532-1534.
58. Mitchison GJ, Crick F. Long axons within the striate cortex: their distribution, orientation, and patterns of connection. *Proc Natl Acad Sci USA*. 1982;79:3661-3665.
59. Nelson JI, Frost BJ. Intracortical facilitation among co-oriented, co-axially aligned simple cells in cat striate cortex. *Exp Brain Res*. 1985;61:54-61.
60. Gilbert CD. Adult cortical dynamics. *Physiol Rev*. 1998;78:467-485.
61. Gilbert CD. Horizontal integration and cortical dynamics. *Neuron*. 1992;9:1-13.
62. Fink GR, Halligan PW, Marshall JC, et al. Where in the brain does visual attention select the forest and the trees? *Nature*. 1996;382:626-628.
63. Hupé JM, James AC, Payne BR, et al. Cortical feedback improves discrimination between figure and background by V1, V2 and V3 neurones. *Nature*. 1998;394:784-787.
64. Burkhalter A. Development of forward and feedback connections between areas V1 and V2 of human visual cortex. *Cereb Cortex*. 1993;3:475-487.
65. Wilson HR, Wilkinson F. Detection of global structure in glass patterns: implication for form vision. *Vision Res*. 1998;44:2629-2641.
66. Adams I, Jones DG. Effects of normal and pathological aging on brain morphology: neurons and synapses. *Current Topics in Research on Synapses*. New York: Liss. 1987;1-84.
67. Aston-Jones G, Rogers J, Shaver RD, et al. Age-impaired impulse flow from nucleus basalis to cortex. *Nature*. 1985;318:462-464.
68. Barnes CA, Foster TC, Rao G, et al. Specificity of functional changes during normal brain aging. *Ann NY Acad Sci*. 1991;640:80-85.
69. Coleman PD, Flood DG. Neuron numbers and dendritic extent in normal aging and Alzheimer's disease. *Neurobiol of Aging*. 1987;8:521-545.
70. Flood DG, Coleman PD. Neuron numbers and sizes in aging brain: comparison of human, monkey, and rodent data. *Neurobiol of Aging*. 1988;9:453-464.
71. Severson JA. Synaptic regulation of neurotransmitter function in aging. *Rev Biol Res into Aging*. 1987;3:191-206.
72. Lynch JJ, Silveira LC, Perry VH, et al. Visual effects of damage to P-ganglion cells in macaques. *Vis Neurosci*. 1992;8:575-583.
73. Merigan WH, Katz LM, Maunsell JH. The effects of parvocellular lateral geniculate lesions on the acuity and contrast sensitivity of macaque monkeys. *J Neurosci*. 1991;11:994-1001.
74. Connor JR Jr, Diamond MC, Johnson RE. Aging and environmental influences on two types of dendritic spines in the rat occipital cortex. *Exp Neurol*. 1980;70:371-379.
75. Leuba G. Aging of dendrites in the cerebral cortex of the mouse. *Neuropathol Appl Neurol*. 1983;9:467-475.
76. Peters A, Moss MB, Sethares C. The effects of aging on layer 1 of primary visual cortex in the Rhesus Monkey. *Cereb Cortex*. 2001;11:93-103.
77. Yua S, Wanga Y, Lia X, Zhoua Y, Leventhal AG. Functional degradation of extrastriate visual cortex in senescent rhesus monkeys. *Neuroscience*. 2006;140:1023-1029.