Development and aging of visual hemifield asymmetries in contrast sensitivity

Maria Fatima Silva* Visual Neuroscience Laboratory, IBILI, Faculty of Medicine, University of Coimbra, Coimbra, Portugal

Otília C. d'Almeida* Visual Neuroscience Laboratory, IBILI, Faculty of Medicine, University of Coimbra, Coimbra, Portugal; ICNAS, University of Coimbra, Coimbra, Portugal

Bárbara Oliveiros Laboratory of Biostatistics and Medical Informatics, IBILI, Faculty of Medicine, University of Coimbra, Coimbra, Portugal

Catarina Mateus Visual Neuroscience Laboratory, IBILI, Faculty of Medicine, University of Coimbra, Coimbra, Portugal

Miguel Castelo-Branco Visual Neuroscience Laboratory, IBILI, Faculty of Medicine, University of Coimbra, Coimbra, Portugal; ICNAS, University of Coimbra, Coimbra, Portugal

The relation of development and aging with models of visual anisotropies and their influence on low-level visual processing remain to be established. Our main goal was to explore visual performance asymmetries in development and normal aging using low-level contrast sensitivity behavioral tasks [probing two distinct spatiotemporal frequency channels, (a) intermediate spatial and null temporal frequency (3.5 cycles per degree (cpd) and 0 Hz); and (b) low spatial and high temporal frequency (0.25 cpd undergoing 25 Hz counterphase flicker)]. Different patterns of functional asymmetries were investigated within four (two neurodevelopmental and two adult) age groups ($N = 258$ participants; 8–65 years). We found a left visual hemifield/right hemisphere advantage for only the intermediate spatial frequency channel that was present early in life and remained stable throughout adulthood. In contrast, inferior/superior visual hemifield asymmetries, with a direct ecological meaning, were found for both spatiotemporal frequency channels. This inferior visual hemifield advantage emerged early in life and persisted throughout aging. These findings show that both right hemispheric and dorsal retinotopic patterns of dominance in low-level vision emerge early in childhood, maintaining during aging.

Introduction

The visual system is characterized by a clear functional asymmetry across distinct processing channels, which resembles the patterns identified for other brain functions (Hugdahl & Davidson, 2003). This fact is not surprising, given the available anatomical and physiological data for anisotropies in early visual pathways, including cortical retinotopic areas and the retina (Connolly & Van Essen, 1984; Curcio & Allen, 1990; Curcio, Sloan, Kalina, & Hendrickson, 1990; Curcio, Sloan, Packer, Hendrickson, & Kalina, 1987; Liu, Heeger, & Carrasco, 2006; Van Essen, Newsome, & Maunsell, 1984). Over the last few decades, perceptual and functional differences in spatial vision have been identified, such as foveal versus peripheral asymmetries (the radial eccentricity effect); the pseudoneglect leftward bias; the inferior/superior visual hemifield asymmetries; left/right visual hemifield asymmetries (reflecting interhemispheric laterizations) (Carrasco, Evert, Chang, & Katz, 1995; Danckert & Goodale, 2001; Jewell & McCourt, 2000; for a review, see Karim & Kojima, 2010; Levine & McAnany, 2005; Previc, 1990; Silva, Maia-Lopes, Mateus, Guerreiro, &

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Sampaio, 2008; Silva, Mateus, Reis, Nunes, & Fonseca, 2010; Thomas & Elias, 2011). Despite the wide variety of studies on visual asymmetries, they were mainly performed with adults, and little is known regarding their relation to neurodevelopment.

Contrast sensitivity across multiple functional channels has been widely used as a robust estimate of the functional status of the visual system. Low-level visual asymmetries have been frequently studied in healthy adults, regarding the contrast sensitivity performance in orientation, discrimination, detection, and localization tasks (Cameron, Tai, & Carrasco, 2002; Carrasco, Talgar, & Cameron, 2001; Corbett & Carrasco, 2011; Fuller, Rodriguez, & Carrasco, 2008). Concerning identified patterns of visual hemifield asymmetry, an inferior visual hemifield advantage has been found in spatial and temporally based contrast sensitivity tasks. This pattern is found for low spatial frequencies and becomes gradually more pronounced for medium and higher spatial frequencies (Cameron et al., 2002; Carrasco et al., 2001; Carrasco, Williams, & Yeshurun, 2002; Levine & McAnany, 2005; Rubin, Nakayama, & Shapley, 1996; Silva et al., 2008; Silva et al., 2010). In addition, some psychophysical studies have shown a right hemisphere (RH) advantage for low spatial frequency processing with grating identification tasks (see reviews of Grabowska & Nowicka, 1996; Ivry & Robertson, 1998). By contrast, it was absent for low spatial and high temporal modulated stimuli, using contrast sensitivity detection tasks (Silva et al., 2008). Previously, we have examined contrast sensitivity asymmetries, using low-level psychophysical detection tasks, but only in young healthy adults. There, we were able to discriminate retinal from cortical mechanisms underlying these visual asymmetries (Sampaio et al., 2011; Silva et al., 2008). These previous results showed unequivocal evidence for preattentive low-level visual anisotropies, including early contrast processing, prior to the dual spatial frequency filtering stages (Ivry & Robertson, 1998) which occur at later cortical pathways, underlying visual attention.

Despite the extensive research on visual hemifield asymmetry, few studies have examined the effect of aging in such asymmetries (Spry & Johnson, 2001). Also, the influence of normal aging in low- and high-level visual processing is still poorly understood (for a review, see Owsley, 2011). A recent study addressed the deterioration of visual function from young to older adults in a large cohort using a comprehensive array of tasks up to 3D visual integration (Mateus et al., 2013), however, visual hemifield asymmetries were not addressed.

The information about the effect of aging on low-level visual interhemispheric lateralization is also very scarce. Visual lateralization studies have a limited scope, focusing mainly on high-level processing and/or based on restricted age cohorts (De Sanctis et al., 2008; Park, Polk, Minear, Savage, & Smith, 2004; Reuter-Lorenz, Stanczak, & Miller, 1999). Here, we considered cohorts that are still within periods of neural development (young children ([8:13[y) and adolescents ([13:20[y) age groups) and of "aging" (mature young ([20:40[y) and older ([40:65]y) adults age groups. The present study aims to investigate the patterns of low-level visual hemifield asymmetries during normal development and healthy aging. We measured achromatic contrast sensitivity under two spatiotemporal conditions that provide a distinct magno/parvocellular activation bias (Callaway, 2005; Lee, Martin, Valberg, & Kremers, 1993; Mateus et al., 2013; Merigan, 1989; Merigan & Maunsell, 1993, Silva et al., 2008; Silva et al., 2010). The ISF stimuli (parvocellular-biased) were static (0 Hz temporal frequency) sinusoidal gratings of intermediate spatial frequency (3.5 cpd). This spatial frequency provides only relative isolation of the visual pathways particularly in central visual field locations. However, it is relatively higher toward the periphery (beyond central 5°), which was the focus of our analysis of contrast sensitivity asymmetries. The LSF stimuli (tuned to high temporal and low spatial frequency channels, strongly magnocellular biased) were grating stimuli counterphasing at a temporal frequency of 25 Hz and at spatial frequency of 0.25 cpd. To our knowledge, this is the first study evaluating the modulation of low-level visual hemifield asymmetries within normal development and healthy aging.

Methods

Ethics statement

This study followed the tenets of the Declaration of Helsinki and all procedures were reviewed and approved by the Ethics Commission of the Faculty of Medicine of the University of Coimbra. Written informed consent was obtained from all participants older than 18 years of age and from the parents/guardians of children and adolescents younger than 18 years of age.

Participants

All participants performed contrast sensitivity tests under monocular conditions in a darkened room; only one eye was evaluated. Complete description of the demographic details is shown in Table 1. For the intermediate spatial/null temporal frequency channel, the total sample size was 123 participants, mean age of 30.2 ± 1.51 (*SEM*) years; age range: 8 to 65 years; 47

	Development cohorts		Aging cohorts	
	[8:13[y	[13:20[y	[20:40[y	[40:65]y
ISF				
Sample size (*N*)	21	19	45	38
Gender (m:f)	9:12	9:10	16:29	13:25
Mean age [*SEM*] (y)	10.4 [0.27]	14.1 [0.24]	28.1 [0.77]	51.8 [1.24]
LSF				
Sample size (*N*)	23	25	45	42
Gender (m:f)	9:14	15:10	16:29	15:27
Mean age [*SEM*] (y)	10.5 [0.26]	14.5 [0.22]	29.7 [0.86]	53.7 [1.23]

Table 1. Demographic characteristics of the population under study.

males. For the low spatial/high temporal frequency channel, the total sample size was 135 participants, mean age of 31.1 ± 1.53 (*SEM*) years; age range: 8 to 65 years; 55 males.

All participants were recruited from our database of volunteers. A complete neuro-ophthalmological examination was performed in all participants. This exam consisted of best corrected visual acuity (VA) obtained with Snellen chart (observers were refracted for the target distance of each test), ocular tension (Goldman applanation tonometer), slit lamp biomicroscopy and fundus examination (Goldman lens). Exclusion criteria included retinal and neurological diseases, optic nerve pathology, diabetes even in the absence of retinopathy, significant media opacities precluding fundus examination and high ammetropy (sphere $> \pm$ 4D; cylinder $> \pm$ 2D). All participants had normal or corrected-to-normal visual acuity and were right-handed and naïve to the purpose of the tests performed.

Stimuli and task description

Intermediate spatial frequency achromatic contrast sensitivity task—ISF

Achromatic contrast sensitivity was measured within an intermediate spatial and null temporal frequency channel, labeled intermediate spatial frequency (ISF) task, using the same in-house test described in our previous studies on visual field asymmetries (Silva et al., 2008; Silva et al., 2010). Briefly, stimuli were static vertical gratings with a spatial frequency of 3.5 cpd and were displayed on a 21-in. Trinitron GDM–F520 Sony monitor (frame rate of 100 Hz) at a viewing distance of 36 cm. The stimulus, size (10° of visual angle), and locations tested within visual field are represented in Figure 1A. Calibration procedures were performed with software and hardware provided by Cambridge Research Systems, Rochester, UK (Minolta colorimeter; calibration software and CRS/VSG 2/5 graphics card, with 15-bit contrast resolution per pixel). An adaptive logarithmic staircase strategy was used to obtain the psychophysical thresholds. Staircases were run for a total of four reversals, with the contrast at the final two reversals being averaged to estimate the contrast threshold. The results were expressed in terms of decibels (dB) units, $dB = 20 * \log(1/c)$, with contrast c measured as a percentage. The mean background luminance was 51 cd/m^2, the stimulus duration was 200 ms, and interstimulus interval was jittered between 2300–2800 ms. The participant had up to 1800 ms to reply. In this task, the stimuli were used as detection targets in multiple locations of the visual field and subjects' responses were recorded with a button from the CT3 button response box (Cambridge Research Systems (CRS) Ltd., Rochester, England) with millisecond resolution. Participants were instructed to fixate the black square (1° × 1°) in the center of the screen and report the presence of vertical "striped" targets (detection task) in any of the nine locations by means of button press (only one button was used). Performance reliability was evaluated by randomly interleaving false positive (with 0% contrast stimuli) and negative (100% contrast) catch trials. Fixation loss was monitored with our custom eye-tracking methodology (CRS device) which provides detailed measurements of eye position.

Low spatial frequency achromatic contrast sensitivity task—LSF

The achromatic contrast sensitivity of low spatial and high temporal frequency channel, labeled low spatial frequency (LSF) task, was measured using the Humphrey Matrix perimeter (Frequency-Doubling Technology Perimetry, Welch Allyn, Skaneateles, NY; Zeiss Humphrey, Dublin, CA). Stimuli were sinusoidal vertical gratings with low spatial frequency (0.25 cpd) undergoing counterphase flicker at 25 Hz, that are best suited to assess the magnocellular system (Castelo-Branco et al., 2006; Mendes et al., 2005; Silva et al., 2005; Silva et al., 2008). We used the N-30-F strategy (with a staircase threshold method known as Modified Binary Search with a four reversals rule to determine

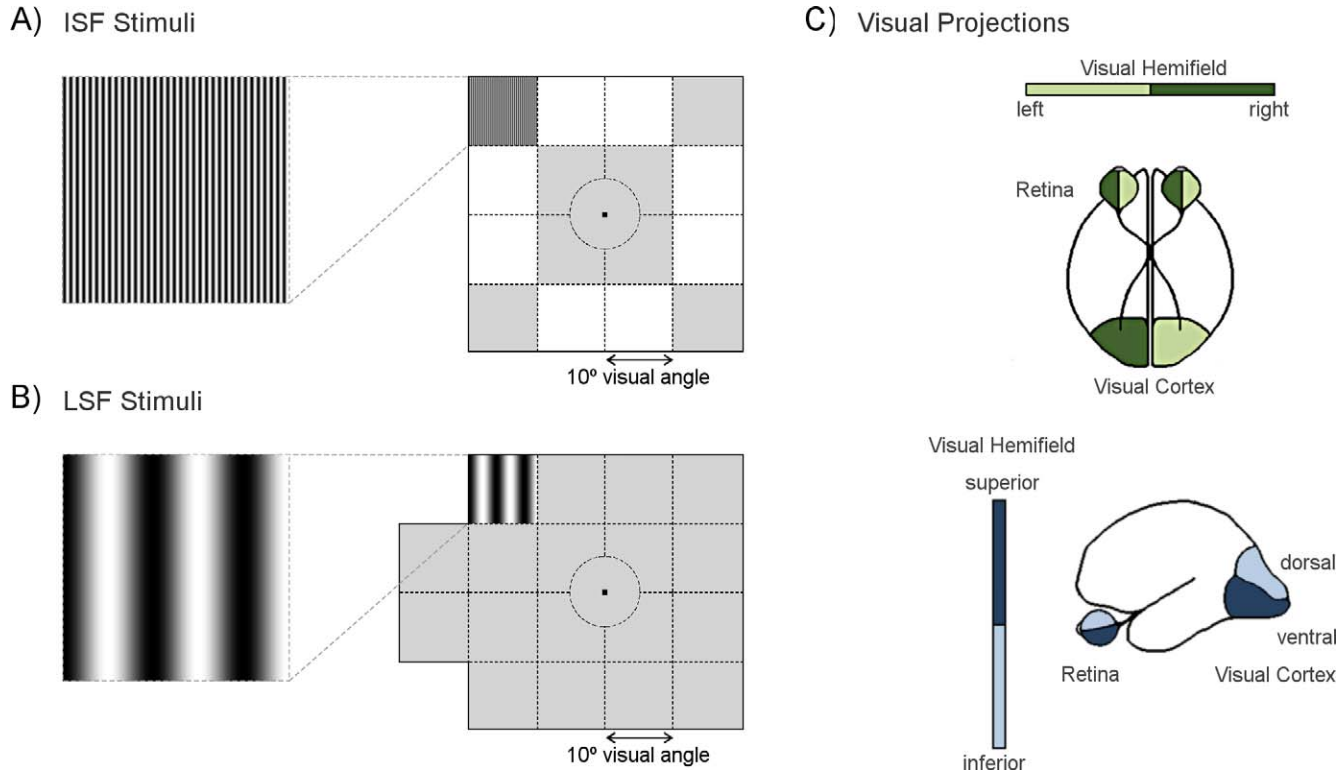

Figure 1. Schematic representation of the sizes and shapes of the visual field locations and magnified insets of the stimuli. The locations where the stimuli were presented are colored gray. The black square in the middle of the figures represents the fixation square. Contrast sensitivity was measured in two spatiotemporal conditions. (A) Intermediate spatial and low temporal frequency (ISF) stimuli were presented pseudo randomly within nine locations of the visual field. The white squares indicate locations where the ISF stimulus was not shown. (B) Low spatial and high temporal frequency (LSF) stimuli were presented within 19 locations of the visual field. However, in the analysis, we have excluded the two nasal periphery locations. (C) Scheme of the hemifield representations' projections along the visual pathway.

the threshold level and a dynamic luminance ratio range from 56 to 0 dB) which tests a total of 19 locations (Figure 1B). Mean background luminance was 100 cd/m^2, and each stimulus was presented for a maximum of 720 ms. During the first 160 ms, stimulus contrast was increased gradually from zero to the contrast selected for that trial. If the stimulus was not seen, it remained at that contrast for up to 400 ms and was then gradually decreased to zero during the final 160 ms. There was an interval of up to 500 ms between stimulus presentations. Testing with or without a ramp (commercial FDT and custom FDT/LSF tests) does not change the spatial pattern of CS asymmetry results (Silva et al., 2008).

Performance reliability was assessed by monitoring fixation loss and computing false positive and negative errors. Participants were instructed to rest their forehead on the visor, fixate the small black square in the center of the screen and report the presence of "striped" targets by button presses (only one button was used).

Statistical analysis

The mean contrast sensitivity was measured for each visual hemifield (left, right, inferior and superior visual hemifields) defined by the vertical and horizontal meridians beyond the central 10° diameter circular target (Figure 1). For analysis purposes, the two additional nasal locations (Figure 1B) measured by the LSF task were excluded, so that comparisons between the two testing approaches could be made in matched locations within the same range of eccentricity, 20° of visual angle.

All results with false positive and false negative errors $\geq$ 33% and fixation loss $\geq$ 20% were excluded from analysis. Four age groups were considered: children ([8:13[y), adolescents ([13:20[y), young adults ([20:40[y) and older adults ([40:65]y). Statistical analysis was performed with IBM SPSS Statistics 20 (SPSS Inc., Chicago, IL). Parametric tests were performed after verification of normality assumption (Kolmogorov–Smirnov with Lillieforce's correction). Visual hemifield asymmetries, evaluated by contrast sensitivity

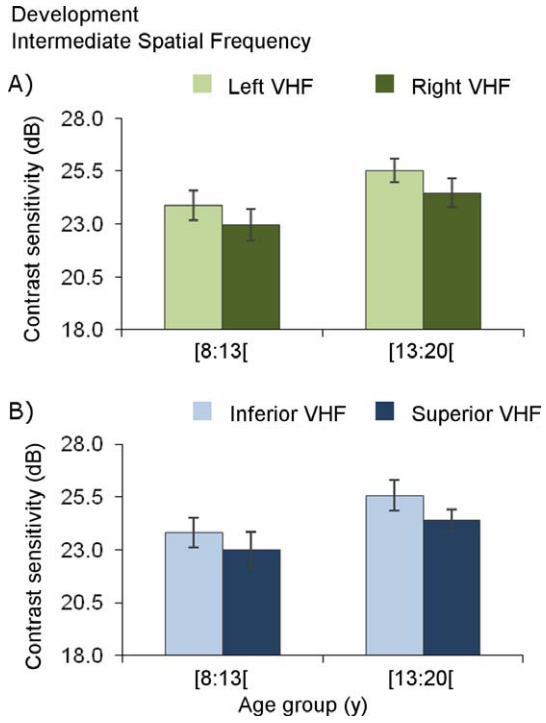

Figure 2. Mean visual contrast sensitivity for the intermediate spatial frequency task during development in (A) the left and right visual hemifields and in (B) the inferior and superior visual hemifields. Contrast sensitivity was significantly higher on the left and inferior visual hemifields (compared to the right and superior visual hemifields, respectively) for both children and adolescents. Error bars denote standard error of the mean ($\pm SEM$). $^{***}p \leq 0.001$ (repeated-measures ANOVA).

measures were analyzed using repeated-measures ANOVA, with visual hemifield (right and left or inferior and superior visual hemifields) as within-subjects factors and age group as between-subjects factors for both development and aging groups. Two tailed hypothesis testing was performed at a 0.05 significant level. Effect size (partial η^2) of statistically significant results was calculated using SPSS.

Results

Analysis of low-level visual asymmetries in developmental groups

Contrast sensitivity asymmetries measured during intermediate spatial and null temporal frequency condition (ISF)

We examined the anisotropy of contrast sensitivity between visual hemifields in developmental cohorts (children and adolescents), as illustrated in Figure 2A. Global patterns of left/right visual hemifield asymmetry were analyzed using intermediate spatial frequency/static stimuli in an achromatic contrast sensitivity detection task. Repeated-measures ANOVA revealed a significant main effect of left/right visual hemifield, $F(1, 38) = 9.913$, $p = 0.003$; effect size, $\eta_p^2 = 0.21$, with higher contrast sensitivity in the left visual hemifield (corresponding to right hemisphere dominance). The interaction visual hemifield $\times$ age group was not significant, $F(1, 38) = 0.051$, $p = 0.823$. The main effect of age group was also not significant, which means that there were no differences between children and adolescents age groups, $F(1, 38) = 2.972$, $p = 0.093$, concerning asymmetry. A left hemifield advantage (right hemisphere dominance) for ISF contrast sensitivity was present in both children and adolescents age groups, for the intermediate spatial frequency channel.

Concerning the inferior/superior (dorsal/ventral) visual hemifield asymmetries, the repeated-measures ANOVA indicated that, under the ISF condition, contrast sensitivity in the inferior visual hemifield was significantly higher than in the superior visual hemifield (main effect of hemifield: $F(1, 38) = 6.061$, $p = 0.018$, $\eta_p^2 = 0.14$). No main effect of age group, $F(1, 38) = 2.798$, $p = 0.103$, nor visual hemifield $\times$ age group interaction, $F(1, 38) = 0.212$, $p = 0.648$, was found (Figure 2B).

Contrast sensitivity asymmetries measured within low spatial and high temporal frequency condition (LSF)

Contrast sensitivity was also measured using low spatial/high temporal frequency stimuli for the activation of the temporally modulated channel. Left/right visual hemifields (interhemispheric pattern of asymmetry) anisotropy was assessed in the developmental groups. The main effect of left/right hemifield was not significant, $F(1, 46) = 2.629$, $p = 0.112$. Also, no significant hemifield $\times$ age group interaction was present, $F(1, 46) = 1.539$, $p = 0.221$. However, a significant main effect of age group was found, $F(1, 46) = 36.070$, $p < 0.0001$, $\eta_p^2 = 0.440$, reflecting higher contrast sensitivity values for the adolescents group (Figure 3A).

In these developmental groups, as for the ISF condition, a pattern of inferior/superior hemifield asymmetry was identified, with an advantage of the inferior visual hemifield (projecting in the dorsal cortical pathway). Repeated-measures ANOVA revealed a significant main effect of hemifield, $F(1, 46) = 4.925$, $p = 0.031$, $\eta_p^2 = 0.097$. The hemifield $\times$ age group interaction was not statistically significant, $F(1, 46) = 0.543$, $p = 0.465$. The above mentioned main effect of age group was replicated, $F(1, 46) = 36.070$, $p < 0.0001$, $\eta_p^2 = 0.440$, with higher contrast sensitivity values in adolescents (Figure 3B).

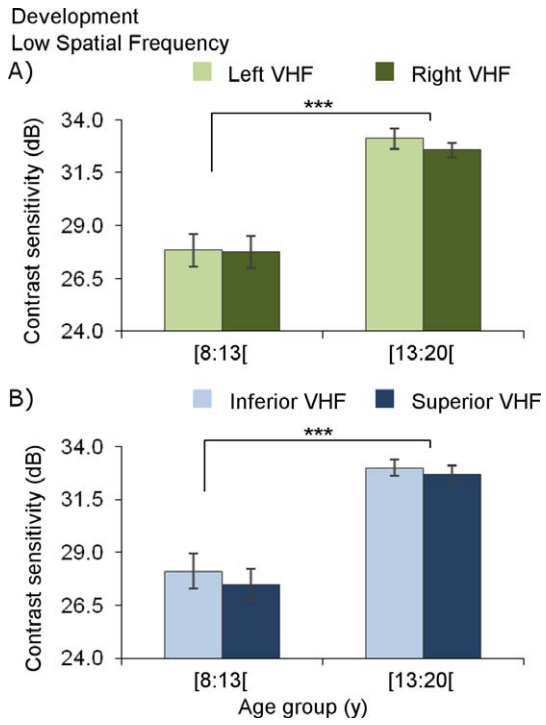

Figure 3. Mean visual contrast sensitivity for low spatial/high temporal frequency task during development in (A) the left and right visual hemifields and in (B) the inferior and superior hemifields. For development groups, contrast sensitivity was only significantly higher in the inferior visual hemifield compared to the superior visual hemifield. Error bars denote standard error of the mean ($\pm SEM$).***$p \leq 0.001$ (repeated-measures ANOVA).

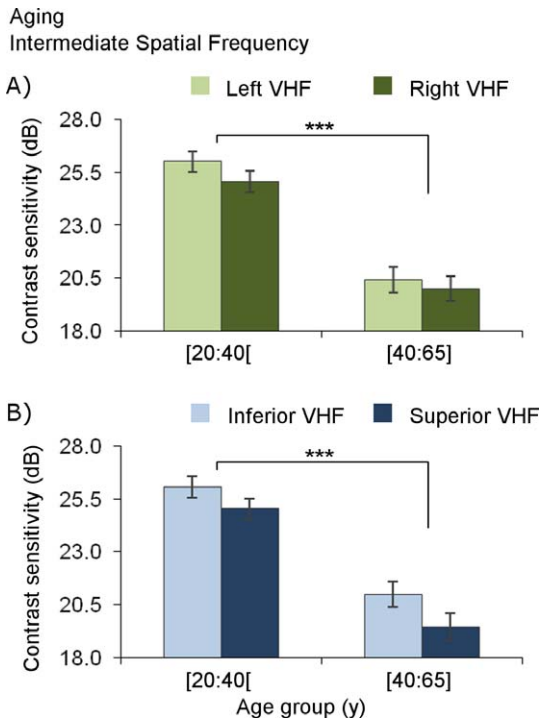

Figure 4. Mean visual contrast sensitivity for the intermediate spatial frequency task during aging in (A) the left and right visual hemifields and in (B) the inferior and superior visual hemifields. Contrast sensitivity was significantly higher on the left and inferior visual hemifields (compared to the right and superior visual hemifields, respectively) for both younger and older adults. Error bars denote standard error of the mean ($\pm SEM$).***$p \leq 0.001$ (repeated-measures ANOVA).

Analysis of the low-level visual asymmetries in aging cohorts

Contrast sensitivity asymmetries measured with intermediate spatial and null temporal frequency condition (ISF)

The anisotropy of contrast sensitivity within visual hemifields across aging was also assessed. Repeated-measures ANOVA revealed a significant main effect of hemifield, $F(1, 81) = 13.827$, $p = 0.0004$, $\eta_p^2 = 0.146$, with higher contrast sensitivity within the left visual hemifield, corresponding to the right hemisphere. The main effect of age group was also significant, $F(1, 81) = 50.858$, $p < 0.0001$, $\eta_p^2 = 0.386$, as expected, with younger adults exhibiting higher contrast sensitivity (Figure 4A). No interaction between visual hemifield $\times$ age group was found, $F(1, 81) = 2.565$, $p = 0.113$.

Next, the functional evaluation of the pattern of inferior/superior visual hemifield asymmetry (dorsal/ventral) was performed. Repeated-measures ANOVA showed a significant main effect of hemifield, $F(1, 81) = 29.544$, $p < 0.0001$, $\eta_p^2 = 0.267$. Mean contrast sensitivity was higher over the inferior visual hemifield (projecting in the dorsal cortical pathway) than over the superior visual hemifield. No hemifield $\times$ age group interaction was present, $F(1, 81) = 1.159$, $p = 0.285$. A main effect of age group was replicated, $F(1, 81) = 50.858$, $p < 0.0001$, $\eta_p^2 = 0.386$, with the younger adults presenting higher contrast sensitivity values (Figure 4B).

Contrast sensitivity asymmetries measured with low spatial and high temporal frequency condition (LSF)

Concerning the left/right visual hemifield asymmetries for the temporally modulated channel, no significant main effect of hemifield was found, $F(1, 85) = 0.514$, $p = 0.475$, neither hemifield $\times$ age group interaction, $F(1, 85) = 1.024$, $p = 0.314$. However, a main effect of age group was statistically significant, $F(1, 85) = 10.806$, $p = 0.001$, $\eta_p^2 = 0.113$, suggesting that there were significant differences of contrast sensitivity values between the two age groups (higher contrast sensitivity in the younger adults group, see Figure 5A).

The pattern of inferior/superior performance was also analyzed within aging. Differences in contrast sensitivity between the inferior and superior hemifields were found within aging cohorts, $F(1, 85) = 17.993$, $p <$

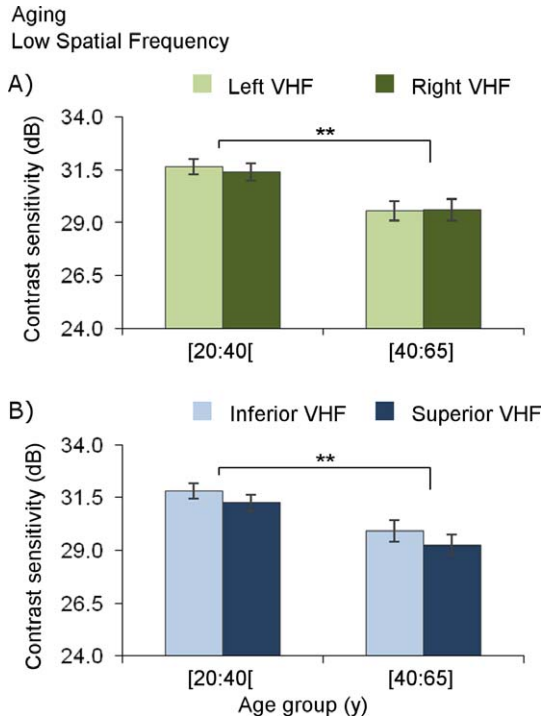

Figure 5. Mean visual contrast sensitivity for low spatial/high temporal frequency task during aging in (A) the left and right visual hemifields and in (B) the inferior and superior hemifields. For aging groups, contrast sensitivity was only significantly higher in the inferior visual hemifield compared to the superior visual hemifield. Error bars denote standard error of the mean ($\pm SEM$). $^{**}p \leq 0.01$ (repeated-measures ANOVA).

0.0001, $\eta_p^2 = 0.175$, an inferior visual hemifield advantage. No hemifield × age group interaction was present, $F(1, 85) = 0.179$, $p = 0.673$. A significant main effect of age group was found, $F(1, 85) = 10.860$, $p = 0.001$, $\eta_p^2 = 0.113$, with higher contrast sensitivity values in the younger adults group, Figure 5B.

Discussion

The current study extends previous evidence of contrast sensitivity asymmetries within two spatiotemporal channels for young adults (Silva et al., 2008; Silva et al., 2010). To our knowledge, this is the first behavioral study focusing on the role of development and healthy aging on low-level visual hemifield asymmetries. This study tested four age cohorts, two related to developmental stages and two with mature periods in life, and provides additional insights over the impact of development and aging on visual hemifield asymmetries and their implications on the role of visual experience. The visual hemifield advantage in this study was expressed by higher measures of contrast sensitivity. Left visual hemifield advantage (corresponding to right hemisphere dominance) appeared early in life for the intermediate spatial frequency condition (static spatial contrast sensitivity) and remained throughout aging. These findings extend the known right hemispheric dominance for high-level spatial vision tasks (Hugdahl & Davidson, 2003) to low-level vision mechanisms during both development and aging. We have previously documented a left hemifield and temporal visual field advantage using the same contrast sensitivity task, with gratings at 3.5 cpd but only in healthy young adults (Silva et al., 2008; Silva et al., 2010). In this study, we only performed the tasks at the monocular level, considering the dominant eye, which happened to be predominantly the right eye. Taking into account that retinal nasal/temporal effects interact with left/right asymmetries in an eye-dependent manner (for more details, see Silva et al., 2008), the potential nasal/temporal effects will only summate with left/right hemispheric outcomes for the left eye and will actually interfere negatively for the right eye. Therefore, any nasal/temporal effect would at best mask our left/right asymmetry and not enhance it.

In the case of low spatial and high temporal frequency condition (strongly magnocellular biased), the pattern of left/right hemifield asymmetry (interhemispheric lateralization) was not present at any stage of life. This result is in agreement with our previous study in young adults (Silva et al., 2008). On the other hand, the pattern of inferior/superior (dorsal/ventral) visual asymmetry, with an inferior hemifield advantage, was present for both spatiotemporal conditions. This pattern was consistent with the anisotropy found in anatomical and physiological data of early visual pathways (Connolly & Van Essen, 1984; Van Essen, Newsome, & Maunsell, 1984). Anatomically, the ventral pathway receives inputs mainly from the superior visual field, whereas visual information in the inferior visual field is largely projected to the dorsal pathway. Therefore, dorsal and ventral stream processing differences might be modulated by inferior/superior visual hemifield asymmetries. Both anatomical and physiological data are generally consistent with this anisotropy. Photoreceptors and ganglion cells are more densely packed in the superior human retina (Curcio & Allen, 1990; Curcio et al., 1990). Also, asymmetries are present in the nonhuman dorsal lateral geniculate nucleus, striate cortex, MT and V6A, with greater representation for the inferior field (Connolly & Van Essen, 1984; Danckert & Goodale, 2001; Galletti, Fattori, Kutz, & Gamberini, 1999; Tootell, Switkes, Silverman, & Hamilton, 1988; Van Essen et al., 1984).

It is known that visual experience can influence perceptual asymmetries by sculpting the response properties of cortical neurons (reviewed by Karim & Kojima, 2010). Exploring visual hemifield asymmetries in young children can be highly informative regarding

the developmental pattern by which low-level visual asymmetries arise. In this study, we found that patterns of asymmetry remain stable across developmental and aging stages, since no interaction was found between age group and visual hemifield. However, we did find a main effect of age group within both development and aging. This is in line with the reports of increasing contrast sensitivity measures from childhood to adolescence, reaching adult levels in the late adolescence (Ellemberg, Lewis, Lui, & Maurer, 1999; Leat, Yadav, & Irving, 2009; Patel, Maurer, & Lewis, 2010). Accordingly, we found an effect of age group within development. The improvement of contrast sensitivity from childhood ([8:13[) to adolescence ([13:20[) at intermediate spatial (ISF) and at low spatial and high temporal frequency condition (LSF) was found, but was only statically significant for the last condition suggesting that the maturation rate was not equal for the two conditions. Our results are in line with the notion of different speeds of maturation across visual pathways. Previous visual evoked potential (VEP) studies (Crognale, 2002; Crognale, Kelly, Weiss, & Teller, 1998; Kelly, Borchert, & Teller, 1997) have suggested that the neural pathways that process chromatic information are not mature until around puberty. Meanwhile achromatic reversal responses at low spatial frequencies are mature by about three months of age. These results support previous psychophysical studies (Dobkins, Lia, & Teller, 1997; Dobkins & Teller, 1996), which have focused on the development of specific functions carried out by each of the visual pathways in infants. Accordingly, the contrast sensitivity mechanisms develop first for the perception of contrast in luminance (magnocellular), and after for the perception of contrast in chromaticity (parvocellular). In our study, we have used only achromatic stimuli tuned to two spatiotemporal frequency channels, one which is more parvocellular-biased (ISF) and the other strongly magnocellular-biased (LSF). During development, our behavioral results of contrast sensitivity across the two different spatiotemporal frequency channels revealed an improvement of contrast sensitivity, especially for the LSF condition. Moreover, in the LSF condition, the highest contrast sensitivity values were found in the adolescents ([13:20[y) group (within the development cohort), indicating an earlier maturation of the LSF channel (strongly magnocellular biased). For the ISF condition, the contrast sensitivity reached its maximum only in the young adults ([20:40[y) group (within the aging cohorts). This outcome is in line with the study of Ellemberg et al., (1999), where results suggest that temporal vision matures more rapidly than spatial vision. Accordingly, our results are consistent with previous VEPs and behavioral results.

On the other hand, within the aging groups, the contrast sensitivity was significantly diminished among the older adults ([40:65]) for both spatiotemporal frequency conditions. However, the mean contrast sensitivity loss was higher for the intermediate spatial frequency channel, which has a slight peripheral parvocellular bias (Silva et al., 2008). These results are in accordance with previous aging studies (Elliott & Werner, 2010; Mateus et al., 2013). Further studies are required to elucidate the role of aging processes on such anisotropic properties in the visual domain, namely within ages over 65 years.

Visual asymmetry studies have relevance in the design of psychophysical paradigms, clinical training programs for patients with heterogeneous visual field loss, and those who need to reuse the most functional parts of their retina. In low-vision therapy, adult patients seem to have a tendency to naturally adopt a preferred retinal location in the inferior visual field. We have found that inferior/superior visual hemifield asymmetries were present already in children for both spatiotemporal channels of early contrast sensitivity processing. In this way, the functional differences between the superior and inferior visual fields could benefit rehabilitation training for children who have lost central vision.

Conclusion

In conclusion, our findings showed that interhemispheric (left/right visual hemifield) asymmetries were present early in life during childhood and adulthood, but only for the intermediate spatial frequency channel. The inferior/superior visual hemifield asymmetries, with a direct ecological meaning, emerge early in life and maintain during aging, for both spatiotemporal frequency channels. The left visual hemifield advantage that was found from childhood to adulthood, extends the notion the right hemisphere dominance that is recognized for high-level visual processing also holds true concerning low-level spatial vision.

Keywords: contrast sensitivity, development, aging, visual field, asymmetry

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*MFS and OCA contributed equally to this article.
Commercial relationships: none.
Corresponding authors: Miguel Castelo-Branco; Maria Fatima Silva.
Email: mcbranco@fmed.uc.pt; maria.silva@uc.pt.
Address: Visual Neuroscience Laboratory, Faculty of Medicine, University of Coimbra, Coimbra, Portugal.

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