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Brightness induction and suprathreshold vision: Effects of age and visual field

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ABSTRACT

A variety of visual capacities show significant age-related alterations. We assessed suprathreshold contrast and brightness perception across the lifespan in a large sample of healthy participants ($N = 155$; 142) ranging in age from 16 to 80 years. Experiment 1 used a quadrature-phase motion cancelation technique (Blakeslee & McCourt, 2008) to measure canceling contrast (in central vision) for induced gratings at two temporal frequencies (1 Hz and 4 Hz) at two test field heights (0.5° or 2° × 38.7°; 0.052 c/d). There was a significant age-related reduction in canceling contrast at 4 Hz, but not at 1 Hz. We find no age-related change in induction magnitude in the 1 Hz condition. We interpret the age-related decline in grating induction magnitude at 4 Hz to reflect a diminished capacity for inhibitory processing at higher temporal frequencies. In Experiment 2 participants adjusted the contrast of a matching grating (0.5° or 2° × 38.7°; 0.052 c/d) to equal that of both real (30% contrast, 0.052 c/d) and induced (McCourt, 1982) standard gratings (100% inducing grating contrast; 0.052 c/d). Matching gratings appeared in the upper visual field (UVF) and test gratings appeared in the lower visual field (LVF), and vice versa, at eccentricities of ±7.5°. Average induction magnitude was invariant with age for both test field heights. There was a significant age-related reduction in perceived contrast of stimuli in the LVF versus UVF for both real and induced gratings.

1. Introduction

An improved understanding of how normal aging quantitatively and qualitatively affects sensation, perception, attention and cognition is crucial to the development of sensitive diagnostic instruments and useful therapeutic interventions aimed at mitigating age-related declines in these abilities and improving the quality of life of an increasingly aging population (Humes et al., 2009, 2013; Owsley, 2011).

There are numerous age-related changes in visual function. With respect to temporal processing, sensitivity to high temporal frequencies declines with age (Elliott, Whitaker, & MacVeigh, 1990; Kim & Meyer, 1994; Kline, 1987; McFarland, Warren, & Karis, 1958; Meyer et al., 1988; Sekuler, Hutman, & Owsley, 1980; Sloane, Owsley, & Jackson, 1988; Tulunay-Keesey, Ver Hoeve, & Terkla-McGrane, 1988; Tyler, 1989; Wright & Drasdo, 1985). The amplitude of the inhibitory phase of the temporal impulse response function is reduced, giving rise to a slower and more prolonged response to a flash of light (Shinomori & Werner, 2003). Simple reaction time to visual stimuli is significantly increased (Kline et al., 1983). At higher levels of processing the ability to recover structure from motion is impaired (Blake, Rizzo, & McEvoy, 2008), including biological motion (Pilz, Bennett, & Sekuler, 2010), and discrimination thresholds for temporal order judgments in both visual and auditory modalities may (Ulbrich et al., 2009) or may not (Fiacconi et al., 2013) be elevated.

With respect to spatial vision there is a decrease in contrast sensitivity at medium to high spatial frequencies (Bennett, Sekuler, & Ozin, 1999; Crassini, Brown, & Bowman, 1988; Derefeldt, Lennerstrand, & Lundh, 1979; Elliott, Whitaker, & MacVeigh, 1990; Habak & Faubert, 2000; Kline, 1987; Kline et al., 1983; Tulunay-Keesey, Ver Hoeve, & Terkla-McGrane, 1988; Wright & Drasdo, 1985) which is primarily optical in origin (Burton, Owsley, & Sloane, 1993). Displacement thresholds (Elliott, Whitaker, & Thompson, 1989) and contrast discrimination thresholds are elevated (Elliott & Werner, 2010; Hardy et al., 2005; Schefrin et al., 1999). Aging is associated with significant alterations in motion perception, where detection (Bennett, Sekuler, & Sekuler, 2007), speed (Bidwell, Holzman, & Chen, 2006; Norman et al., 2003; Scialfa et al.,

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1991; Snowden & Kavanagh, 2006), and direction (Ball & Sekuler, 1986) discrimination thresholds are elevated, displacement thresholds are elevated (Wood & Bullimore, 1995), and the strength of surround suppression, which normally causes duration thresholds for motion direction discrimination to increase with increasing stimulus size (Tadin et al., 2003), is weakened (Betts, Sekuler, & Bennett, 2009, 2012; Betts et al., 2005; Tadin & Blake, 2005). Finally, visuomotor transformations are impaired (Baugh & Marotta, 2009).

At the physiological level age-related changes include increases in response latency and spontaneous neuronal activity, and decreases in information processing rate and stimulus selectivity of neurons in a variety of structures including macaque area V1 (Leventhal et al., 2003; Schmolesky et al., 2000; Wang et al., 2005; Yang et al., 2009; Zhang et al., 2008), macaque area V2 (Wang et al., 2005; Yu et al., 2006), macaque area MT (Liang et al., 2010; Yang et al., 2008, 2009, 2010), and cortical neurons in both cat (Hua et al., 2006; Wang et al., 2014) and rat (Wang et al., 2006). One mechanism hypothesized to underlie such age-related changes in visual processing is a weakening of neuronal inhibition due to diminished GABAergic neurotransmission (Hua et al., 2006; Leventhal et al., 2003; Schmolesky et al., 2000), since electrophoretic application of GABA is capable of restoring stimulus selectivity and improving signal-to-noise ratio in the neurons of aged animals (Leventhal et al., 2003).

Brightness induction is a quintessential example of a phenomenon commonly attributed to inhibitory neural interactions occurring at multiple levels in the visual processing hierarchy (Mach, 1865, in Fiorentini et al., 1990; Heinemann, 1972; Hering, 1964; Jameson & Hurvich, 1989; Kingdom, McCourt, & Blakeslee, 1997; McCourt, 1982; Ratliff, 1965). Certain brightness phenomena such as the spots seen at the intersections of the Hermann Grid, and Mach Bands, have historically been attributed to retinal processing, although recent findings indicate that these effects probably arise at a higher, likely cortical, stage of processing (Geier et al., 2008; Wolfe, 1982). In order to account for more complex induction phenomena such as White's effect (Blakeslee & McCourt, 1999, in press; White, 1979, 1981; White & White, 1985), the Benary Cross (Blakeslee & McCourt, 2001), or the Corrugated Mondrian stimulus (Blakeslee & McCourt, 2001), models of brightness perception need to incorporate spatial filters with orientation selectivity (Blakeslee & McCourt, 1999). Neurons possessing significant orientation selectivity do not occur in the primate visual system until primary visual cortex. Age-related alterations in the magnitude of brightness induction might therefore be a useful biomarker to index the status of inhibitory processes, particularly at striate and extrastriate levels.

Grating induction (McCourt, 1982) produces a conspicuous sinusoidal brightness modulation (i.e., a grating) in a horizontal homogeneous test field inserted into a sinewave grating, and is a particularly strong version of brightness induction (Blakeslee & McCourt, 1997) which can be reliably measured using both matching (McCourt & Blakeslee, 1994) and canceling methods (Foley & McCourt, 1985). In addition, a novel quadrature-phase motion cancelation procedure (Blakeslee & McCourt, 2008, 2011, 2013) allows the strength of the inhibitory processes giving rise to grating induction to be measured precisely for any combination of spatial and temporal frequency. Here we report results from two experiments designed to measure age-related changes in grating induction magnitude, and suprathreshold contrast perception more generally. In Experiment 1 we measure the strength of grating induction using an indirect method, a quadrature-phase motion canceling technique. In Experiment 2 we employ a more traditional matching technique to measure the strength of both grating induction and contrast perception for suprathreshold real gratings situated in the upper and lower visual fields.

2. Experiment 1: contrast canceling

Experiment 1 used grating induction cancelation to assess whether age-related changes occur in the strength of the inhibitory processes commonly thought to underlie brightness induction effects. We measured the magnitude of grating induction as a function of age using the quadrature-phase motion cancelation technique of Blakeslee and McCourt (2008, 2011, 2013).

2.1. Method

2.1.1. Participants

Participants numbered 155 (81 female, 74 male), ranging from 16 to 80 years of age. This age range is consistent with that sampled by the majority of recent studies seeking to establish associations between age and visual function. Participants were recruited via local advertisements (newspapers, senior newsletters, fliers at senior centers) as well as through on-campus fliers and e-mail correspondence to students, faculty, staff and alumni of North Dakota State University. Participants received $10/h for their participation. Total time commitment per participant was approximately 1.25 h. Participants completed a demographic screening questionnaire and the Pelli–Robson Contrast Sensitivity Test (Pelli, Robson, & Wilkins, 1988). Inclusion criteria were self-reported good physical and mental health, no known retinal disease, normal (or corrected-to-normal) visual acuity of at least 20/30, and a binocular log-contrast sensitivity score of 1.80 or greater. A detailed breakdown of log-contrast sensitivity by age group for Experiment 1 appears in Table 1(a). Participants used their habitual spectacle/contact lens corrections during testing; 26 participants utilized multifocal lenses. All participants provided informed consent (and parental consent for participants under 18 years of age); the experimental protocol was approved by the NDSU Institutional Review Board and the work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.1.2. Stimuli and apparatus

Stimuli were generated using MATLAB routines to control a Cambridge Research Systems ViSaGe system. Stimuli were presented on a 20″ Mitsubishi DiamondPro (model 2070) CRT display with screen size of 38.7° × 29.5°, screen resolution of 1024 × 768, a screen refresh rate of 140 Hz and mean luminance of 46 cd/m^2. Stimuli were observed from a viewing distance of 57 cm (no chinrest was used, but the experimenter monitored viewing distance throughout the experiment), and responses were collected using left/right buttons on a game controller. The room was dimly lit since the primary lightsource was the display itself, and the walls were matte black.

Fig. 1(a) and (b) illustrates the quadrature phase motion cancelation displays used in Experiment 1. These consisted of sinusoidal inducing gratings (100% Michelson contrast, 0.052 c/d, height = 29.5°, width = 38.7°), counterphasing at either 1.0 Hz or 4.0 Hz, which surrounded horizontal test fields (height = 0.5° or 2.0°) set to the mean display luminance.

There were four stimulus conditions produced by combining the two test field heights (0.5° or 2.0°) with two temporal frequencies (1.0 Hz and 4.0 Hz) at which the inducing gratings were counterphased. Quadrature grating spatial frequency was 0.052 c/d, and possessed a Michelson contrast of 30%.

2.1.3. Procedure

The quadrature phase motion cancelation technique has been described in detail elsewhere (Blakeslee & McCourt, 2008, 2011, 2013), and an annotated video demonstration and explanation of

Table 1
Panels (a) and (b) present log contrast sensitivity data as a function of age bracket for participants in Experiment 1 and Experiment 2, respectively.

Age (Years)	⩽20	21–30	31–40	41–50	51–60	61–70	71–80
Experiment 1							
Panel (a)							
Log contrast sensitivity							
Mean	2.04	2.00	2.07	1.99	2.00	1.96	1.95
Median	1.95	1.95	2.10	1.95	1.95	1.95	1.95
SD	0.130	0.089	0.125	0.100	0.098	0.058	0.00
N	13	47	13	17	31	27	7
Min	1.95	1.95	1.95	1.95	1.95	1.95	1.95
Max	2.25	2.25	2.25	2.25	2.25	2.25	1.95
Experiment 2							
Panel (b)							
Log contrast sensitivity							
Mean	2.05	2.00	2.07	2.00	2.00	1.96	1.95
Median	1.95	1.95	2.10	1.95	1.95	1.95	1.95
SD	0.133	0.092	0.125	0.117	0.099	0.059	0.000
N	12	43	13	12	30	26	6
Min	1.95	1.95	1.95	1.95	1.95	1.95	1.95
Max	2.25	2.25	2.25	2.25	2.25	2.25	1.95

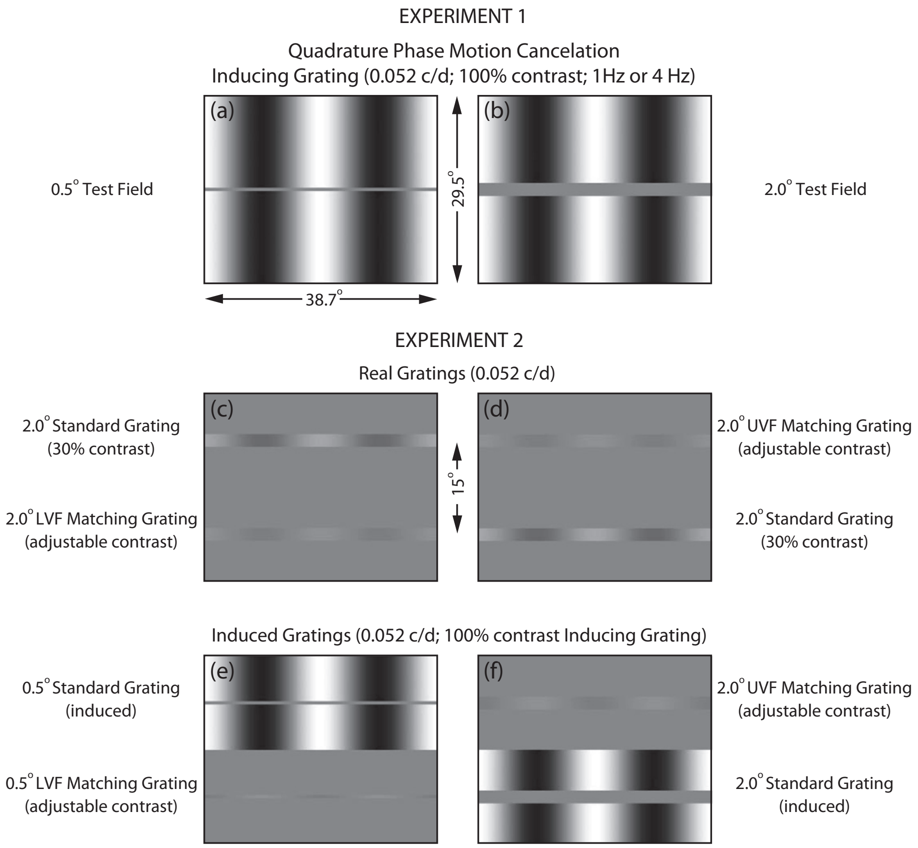

Fig. 1. Stimulus conditions used in Experiment 1 (a and b) and Experiment 2 (c–f). Panels (a) and (b) illustrate the quadrature motion grating induction displays which consisted of sinusoidal inducing gratings (100% Michelson contrast, 0.052 c/d), counterphasing at either 1.0 Hz or 4.0 Hz, which surrounded horizontal test fields (height = 0.5° or 2.0°) set to the mean display luminance (46 cd/m^2). Panels (c) and (d) illustrate the real grating displays which consisted of a sinusoidal standard grating (30% Michelson contrast, 0.052 c/d, height = 2°) situated in the UVF (c) or LVF (d), and an adjustable contrast matching grating (10% or 80% initial contrast, 0.052 c/d, height = 2°) situated in the LVF (c) or UVF (d). Standard and matching grating strip centers were situated ± 7.5° from screen center. Panels (e) and (f) illustrate the grating induction displays which consisted of sinusoidal inducing gratings (100% Michelson contrast, 0.052 c/d) surrounding horizontal homogeneous test fields (0.5° or 2.0°) set to the mean display luminance. The inducing gratings occupied the full extent (14.75°) of the UVF (e) or LVF (f). An adjustable real contrast matching grating (0.5° or 2.0°) was situated in the center of the LVF (e) or UVF (f).

the quadrature phase motion cancelation technique is provided as supplemental material to Blakeslee and McCourt (2011). Briefly, a counterphasing inducing grating, a standing wave, produces a nearly instantaneous phase-reversed counterphasing induced grating, also a standing wave, in the homogeneous test field (Blakeslee & McCourt, 1997, 2008; McCourt, 1982; McCourt & Blakeslee, 1994). Blakeslee and McCourt (2008) showed that induction phase lag was less than 1 ms; for methodological simplicity we treat it here as zero. A counterphasing quadrature grating (0.052 c/d; 0–30% contrast), which is a standing wave in 90° spatial and temporal phase relative to the induced grating, will sum with the counterphasing induced grating to produce a rightward drifting induced + quadrature grating compound, a traveling wave, to which the visual system is extremely sensitive. A second luminance grating, (0.052 c/d), the canceling grating, is added to the test field at variable contrasts. The canceling grating possesses the same spatial and temporal frequency as the induced grating, but is 180° out of spatial phase with it. The canceling grating is added to the test field at contrast levels ranging from 20% to 95% using the method of constant stimuli. When canceling grating contrast is less than induced grating contrast (i.e., when the induced grating is under-canceled) the induced + canceling grating compound possesses the spatial and temporal phase of the induced grating and combines with the quadrature grating to produce a rightward moving traveling wave just as in the case where no canceling grating is present. When canceling grating contrast exceeds induced grating contrast (i.e., when the induced grating is over-canceled) the induced + canceling grating compound possesses the spatial and temporal phase of the canceling grating, and combines with the quadrature grating to produce a leftward moving traveling wave. When canceling grating contrast equals induced grating contrast the contrast of the induced + canceling grating compound is zero (i.e., the induced grating is nulled), and the motion energy of the counterphasing quadrature grating which remains is left/right balanced (i.e., is a standing wave), yielding a 50%:50% proportion of left/right motion judgments in a forced-choice motion direction discrimination task.

The experimental paradigm was a forced-choice motion direction discrimination task. On each trial, which lasted 1500 ms, participants indicated the perceived direction of motion of the pattern within the test field via button press. Ten blocks of 10 trials per canceling contrast were completed by each participant at each test field height/temporal frequency combination. Within each block, trials presenting the various levels of canceling contrast were quasi-randomly interleaved. On each trial quadrature grating contrast was ramped from 0% to 30% over the 1500 ms duration of stimulus presentation. Quadrature grating contrast was ramped because quadrature-pair standing waves sum to produce a pure traveling wave only when the contrasts of the components are equal. Optimal quadrature grating contrast therefore depends on the contrast of each induced-plus-canceling grating compound, which itself depends upon the variable level of canceling grating contrast. Rather than attempting to estimate a singular optimal quadrature grating contrast value we smoothly increased its contrast from 0% to 30% over the duration of each inspection interval, reasoning that observers would experience the optimal quadrature grating contrast (yielding a motion signal with a maximal signal-to-noise ratio) at some point during the inspection interval. Psychometric data for each observer in each experimental condition were fit by a two-parameter – point of subjective equality (PSE) and standard deviation (SD) – cumulative normal function using a maximum-likelihood criterion. The fitted PSE parameter corresponded to the contrast of the canceling grating yielding 50% “right” motion responses and was taken as a measure of grating induction magnitude.

2.1.4. Analysis

Data are analyzed using linear regression; all multiple comparisons are evaluated using Bonferroni correction.

2.2. Results and discussion

Fig. 2(a), (c), (e), and (f) plot percent canceling contrast (C_C) as a function of age in the four experimental conditions. Regression analyses reveal no significant change in canceling contrast with age at either test field height for inducing gratings counterphased at 1 Hz [0.5° test field: $C_C = -0.019\% \times \text{Years} + 83.56\%$; $r_{153} = -0.097$; $p = .229$; $r^2 = 0.009$; 2.0° test field: $C_C = -0.017\% \times \text{Years} + 67.46\%$; $r_{153} = -0.044$; $p = .586$; $r^2 = 0.002$]. Because age does not significantly modulate canceling contrast at 1 Hz, panels (b) and (d) plot frequency histograms of canceling contrast (and Gaussian fits) collapsed across age, where mean canceling contrast for the 0.5° and 2.0° test fields was 82.65% (sd = 3.02%), and 66.35% (sd = 5.81%), respectively. However, a significant age-related decline in canceling contrast was found for inducing gratings counterphased at 4 Hz [0.5° test field: $C_C = -0.093\% \times \text{Years} + 74.85\%$; $r_{153} = -0.396$; $p < .001$; $r^2 = 0.157$; 2.0° test field: $C_C = -0.057\% \times \text{Years} + 48.73\%$; $r_{153} = -0.231$; $p = .004$; $r^2 = 0.053$]. The mean canceling contrast values as well as the falloff in canceling contrast with increasing counterphase frequency and test field height are consistent with those reported by Blakeslee and McCourt (2011).

3. Experiment 2: contrast matching

Experiment 2 used grating induction, in combination with a contrast matching paradigm (as distinct from the induction cancelation paradigm used in Experiment 1) to further assess whether age-related changes occur in the strength of the inhibitory processes commonly thought to underlie brightness induction effects. Observers made contrast matches to both real and induced gratings, which were situated in the upper and lower visual fields.

3.1. Method

3.1.1. Participants

Participants were a subset of those in Experiment 1, and consisted of 142 adults (76 female, 70 male) ranging in age from 16 to 80 years of age. Total time commitment per participant was approximately 1 h. A detailed breakdown of log-contrast sensitivity by age group for Experiment 2 appears in Table 1(b).

3.1.2. Stimuli and apparatus

Fig. 1(c–f) illustrates the stimulus displays used in Experiment 2. Stimuli were generated, displayed, and viewed as in Experiment 1. Contrast adjustments were made using a Cambridge Research Systems CB7 rotary response device. On half the trials (adjustable) matching gratings were situated in the upper visual field (UVF) and standard gratings appeared in the lower visual field (LVF); on half the trials this arrangement was reversed. The order in which the two conditions were administered was counterbalanced across subjects.

3.1.2.1. Real gratings. The real grating displays consisted of static sinusoidal standard gratings (30% Michelson contrast, 0.052 c/d, height = 2°, width = 38.7°) situated in the UVF (Fig. 1c) or LVF (Fig. 1d) and an adjustable contrast static matching grating (10% or 80% initial contrast, 0.052 c/d, height = 2°, width = 38.7°) situated in the opposite visual field. Standard and matching grating strips were situated ±7.5° from screen center.

3.1.2.2. Induced gratings. The grating induction display consisted of static sinusoidal inducing gratings (100% Michelson contrast, 0.052 c/d) surrounding horizontal homogeneous test fields (height = 0.5° or 2.0°, width = 38.7°) set to the mean display luminance. The inducing gratings occupied the full extent (14.75°) of the UVF (Fig. 1e) or LVF (Fig. 1f). An adjustable real contrast static matching grating (height = 0.5° or 2.0°, width = 38.7°) was situated in the center of the opposite visual field.

3.1.3. Procedure

Participants adjusted the contrast of matching gratings to equal that of both real and induced (McCourt, 1982) standard gratings under free viewing conditions. Real and induced gratings were

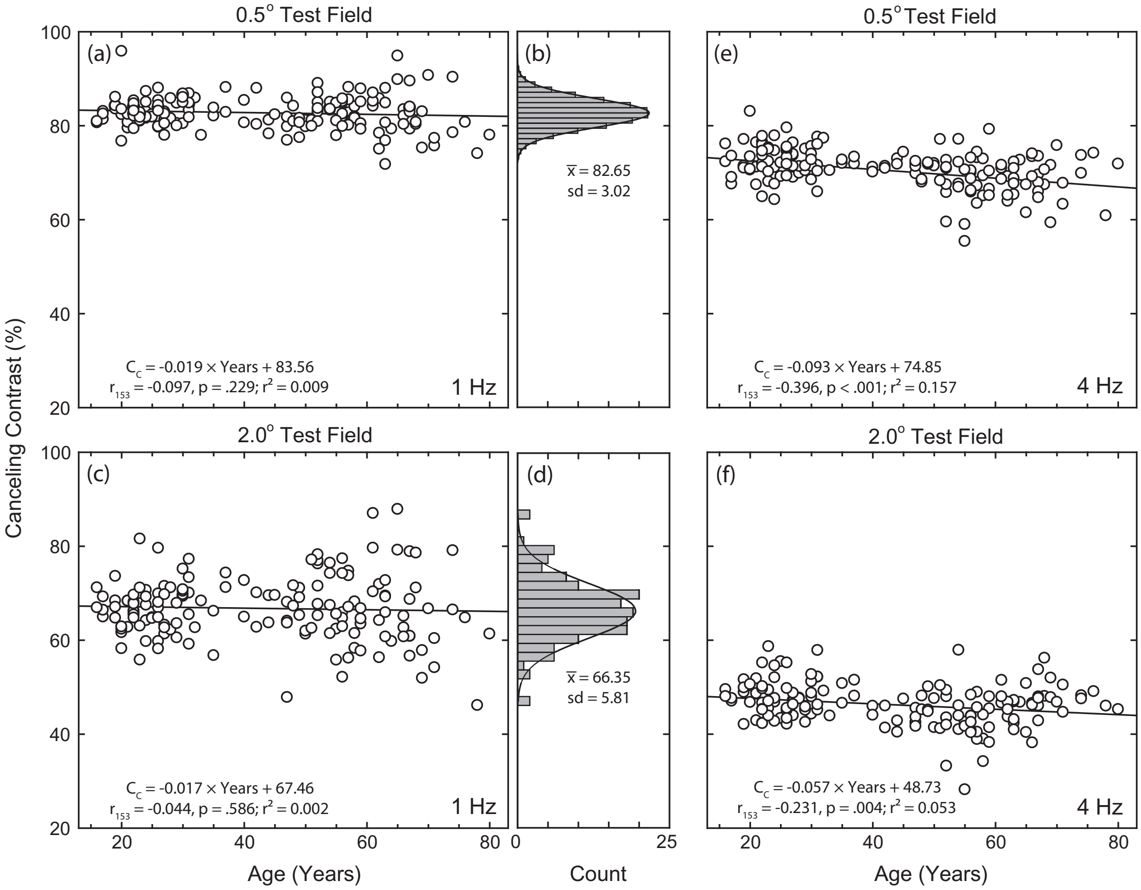

Fig. 2. Panels (a), (c), (e), and (f) plot percent canceling contrast as a function of age in the four experimental conditions. There was no significant change in canceling contrast with age at either test field height for inducing gratings counterphased at 1 Hz [0.5° test field: $C_C = -0.019\% \times \text{Years} + 83.56\%$; $r_{153} = -0.097$; $p = .229$; $r^2 = 0.009$; 2.0° test field: $C_C = -0.017\% \times \text{Years} + 67.46\%$; $r_{153} = -0.044$; $p = .586$; $r^2 = 0.002$]. Because age does not significantly modulate canceling contrast at 1 Hz, panels (b) and (d) plot frequency histograms of canceling contrast (and Gaussian fits) collapsed across age, where mean percent canceling contrast for the 0.5° and 2.0° test fields was 82.65% (sd = 3.02%), and 66.35% (sd = 5.81%), respectively. A significant age-related decline in canceling contrast was found for inducing gratings counterphased at 4°Hz [0.5° test field: $C_C = -0.093\% \times \text{Years} + 74.85\%$; $r_{153} = -0.396$; $p < .001$; $r^2 = 0.157$; 2.0° test field: $C_C = -0.057\% \times \text{Years} + 48.73\%$; $r_{153} = -0.231$; $p = .004$; $r^2 = 0.053$].

matched in separate blocks of trials. Each block of induced grating trials consisted of quasi-randomly interleaved presentations of the two test field heights in one of the two matching grating conditions (UVF, LVF). The order in which blocks of trials with matching gratings in the two visual fields were presented was counterbalanced across participants. Participants made five matches in each of the six experimental conditions. The dependent measure was mean matching grating contrast. Stimuli were observed from a viewing distance of 57 cm (no chinrest was used, but the experimenter monitored viewing distance throughout the experiment). The room was dimly lit since the primary lightsource was the display itself, and the walls were matte black. Stimuli remained on screen until matches were made, and no time limit was imposed on the duration of trials.

3.1.4. Analysis

As in Experiment 1 data are analyzed using linear regression; all multiple comparisons are evaluated using Bonferroni correction.

3.2. Results and discussion

3.2.1. Real gratings

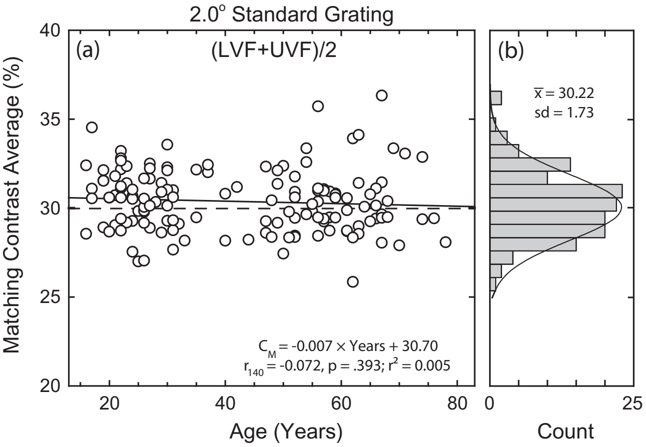

Fig. 3. Panel (a) plots mean matching grating contrast, averaged across matching grating visual field, versus age in the real grating condition. There is no significant change in average matching contrast with age [$C_M = -0.007\% \times \text{Years} + 30.70\%$; $r_{140} = -0.072$; $p = .393$; $r^2 = 0.005$]. Panel (b) plots a frequency histogram of average matching contrast (and Gaussian fit) collapsed across age, where mean matching contrast to the 30% contrast standard grating was 30.22% (sd = 1.73%).

Fig. 3 plots mean matching grating contrast, averaged across matching grating visual field, versus age in the real grating condition. Panel (a) shows that regression analysis revealed no significant change in matching contrast (C_M) with age [$C_M = -0.007\% \times \text{Years} + 30.70\%$; $r_{140} = -0.072$; $p = .393$; $r^2 = 0.005$]. Because age does not significantly modulate matching contrast, panel (b) plots a frequency histogram of matching contrast (and Gaussian fit) collapsed across age, where mean matching contrast to the 30% contrast standard grating was 30.22% (sd = 1.73%). These data illustrate that, as reported in an earlier study employing the same technique (McCourt & Blakeslee, 1994), observers are capable of making highly accurate contrast matches.

Fig. 4 plots mean matching grating contrast, differenced across matching grating visual field, versus age in the real grating condition. Regression analysis revealed a significant age-related change in matching contrast across the upper and lower visual fields [$C_M = 0.048\% \times \text{Years} - 1.50\%$; $r_{140} = 0.449$; $p < .001$; $r^2 = 0.202$], where a relative LVF advantage of 1% in perceived suprathreshold contrast segues to a LVF deficiency of 2% as age increases.

3.2.2. Induced gratings

Fig. 5 plots mean matching grating contrast, averaged across matching grating visual field, versus age in the induced grating condition. Panels (a) and (c) show matches in the 0.5° and 2.0° test field height conditions, respectively. For neither test field height condition was there a significant age-related change in matching contrast [0.5°: $C_M = 0.074\% \times \text{Years} + 32.55\%$; $r_{140} = 0.171$; $p = .042$ (n.s.); $r^2 = 0.029$; 2.0°: $C_M = 0.019\% \times \text{Years} + 23.65\%$; $r_{140} = 0.040$; $p = .635$; $r^2 = 0.002$]. Because there was no significant effect of age, panels (b) and (d) plot frequency histograms of matching contrast (and Gaussian fit) collapsed across age, where mean matching contrast in the 0.5° test field condition was 36.03% (sd = 7.56%), and mean matching contrast in the 2.0° test field condition was 24.23% (sd = 8.33%). That observers are highly accurate in their matches to real gratings lends credibility to the match values for induced gratings. The mean matching contrasts of 36.03% and 24.23% are in good agreement with previous estimates of grating induction magnitude (McCourt & Blakeslee, 1994).

Fig. 6 plots mean matching grating contrast, differenced across matching grating visual field, versus age in the induced grating condition. Panels (a) and (b) show that regression analysis revealed significant age-related changes in matching contrast across the upper and lower visual fields for the 0.5° [$C_M = 0.072\% \times \text{Years} - 3.69\%$; $r_{140} = 0.350$; $p < .001$; $r^2 = 0.123$] and 2.0° [$C_M = 0.042\% \times \text{Years} - 0.30\%$; $r_{140} = 0.218$; $p = .009$; $r^2 = 0.048$] test field height conditions, respectively. As was the case for real gratings (Fig. 4), increasing age is associated with a progressive relative deficit of around 2% in the perceived suprathreshold contrast of gratings situated in the LVF.

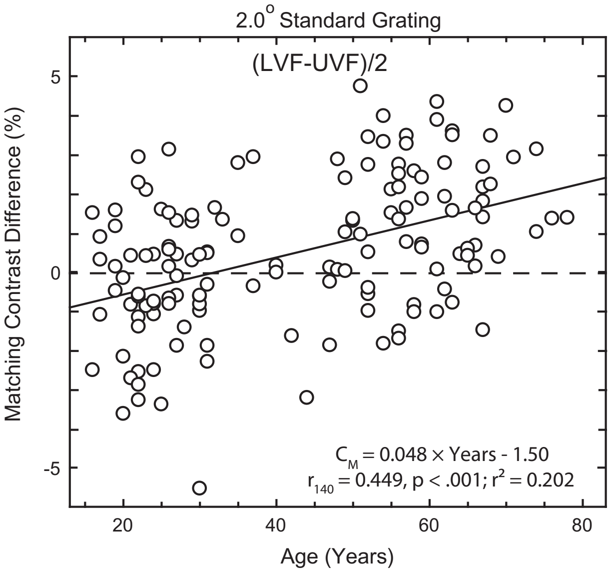

Fig. 4. Mean matching grating contrast, differenced across matching grating visual field, versus age in the real grating condition. There is a significant age-related change in matching contrast across the upper and lower visual fields [$C_M = 0.048\% \times \text{Years} - 1.50\%$; $r_{140} = 0.449$; $p < .001$; $r^2 = 0.202$], where a relative LVF advantage of 1% in perceived suprathreshold contrast at age 16 segues to a relative LVF deficiency of 2% by age 80.

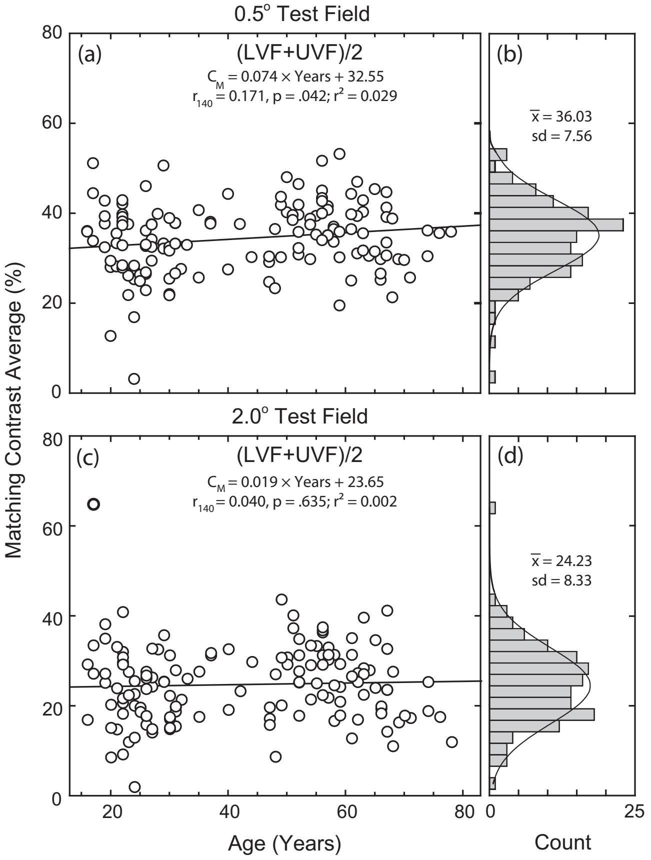

Fig. 5. Mean matching grating contrast, averaged across matching grating visual field, versus age in the induced grating condition. Panels (a) and (c) show matches in the 0.5° and 2.0° test field height conditions, respectively. There is no significant age-related change in matching contrast in either test field condition [0.5°: $C_M = 0.074\% \times \text{Years} + 32.55\%$; $r_{140} = 0.171$; $p = .042$; $r^2 = 0.029$; 2.0°: $C_M = 0.019\% \times \text{Years} + 23.65\%$; $r_{140} = 0.040$; $p = .635$; $r^2 = 0.002$]. Panels (b) and (d) plot frequency histograms of matching contrast (and Gaussian fits) collapsed across age in the 0.5° and 2.0° test field conditions, respectively.

4. General discussion

4.1. Aging and inhibition

Using a canceling measure (Experiment 1) we found no significant age-related change in the strength of grating induction at either the 0.5° or 2.0° test field height at the low inducing grating counterphase modulation frequency (1 Hz). Using a matching measure (Experiment 2) we likewise found no age-related change in induction in either the 0.5° or 2.0° test field height condition, nor was there any significant age-related change in average matching contrast for real gratings in the real suprathreshold contrast condition. Tulunay-Keesey, Ver Hoeve, and Terkla-McGrane (1988) similarly found no effect of age on suprathreshold contrast matching.

In the canceling condition, since the inhibitory processes which give rise to grating induction are strongest at low temporal frequencies (Blakeslee & McCourt, 2011), the lack of age-related changes in induction magnitude in the 1 Hz condition is inconsistent with the idea that there is a generalized age-related weakening of inhibitory processing (Betts, Sekuler, & Bennett, 2009, 2012;

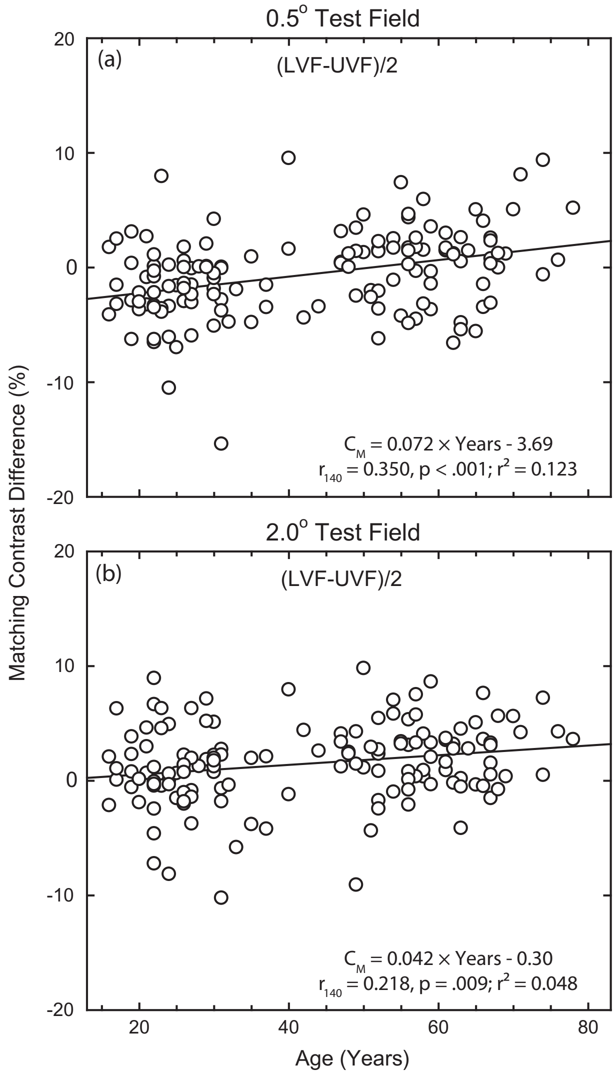

Fig. 6. Mean matching grating contrast, differenced across matching grating visual field, versus age in the induced grating condition. Panels (a) and (b) show matches in the 0.5° and 2.0° test field height conditions, respectively. Significant age-related changes in UVF versus LVF matching contrast occur in the 0.5° [$C_M = 0.072\% \times$ Years $- 3.69\%$; $r_{140} = 0.350$; $p < .001$; $r^2 = 0.123$] and 2.0° [$C_M = 0.042\% \times$ Years $- 0.30\%$; $r_{140} = 0.218$; $p = .009$; $r^2 = 0.048$] test field height conditions, respectively.

Betts et al., 2005; Hua et al., 2006; Leventhal et al., 2003; Schmolesky et al., 2000; Tadin & Blake, 2005). Also inconsistent with the hypothesis that aging might entail a generalized weakening of inhibitory cortical processes are recent findings by Delahunt, Hardy, and Werner (2008) and by Govenlock et al. (2009, 2010), who report that psychophysically-derived spatial frequency and orientation channel bandwidths are comparable in young and older subjects, and by Karas and McKendrick (2009, 2012), who report that the magnitude of contrast–contrast (Chubb, Sperling, & Solomon, 1989), a contrast-domain (second-order) induction phenomenon thought, like luminance-domain (first-order) brightness induction, to index the strength of inhibition (McCourt, 2005), actually increases with increasing age. Hence, we interpret the age-related decline in grating induction magnitude we find only at the higher counterphase frequency (4 Hz) to reflect a diminished capacity for inhibitory processing at higher temporal frequencies (Elliott, Whitaker, & MacVeigh, 1990; Kim & Meyer, 1994; McFarland, Warren, & Karis, 1958; Meyer et al., 1988; Sekuler, Hutman, & Owsley, 1980; Sloane, Owsley, & Jackson, 1988; Tulunay-Keesey, Ver Hoeve, & Terkla-McGrane, 1988; Tyler, 1989).

4.2. Nomothetic measures of grating induction magnitude

This is the first study documenting the strength and variability of grating induction in a large sample ($N = 155$; 142) of observers. Mean canceling contrasts in the 1 Hz counterphase frequency condition were 82.65% and 66.35% for test field heights of 0.5° and 2.0°, respectively. These mean canceling contrasts are in good agreement with earlier reports on smaller sample sizes (Blakeslee & McCourt, 2011). Canceling contrasts are distributed normally in both cases with standard deviations of 3.02% and 5.81%, respectively. Mean matching contrasts in Experiment 2 were 36.03% and 24.23% for test field heights of 0.5° and 2.0°, respectively. The mean matching contrast in the 0.5° test field height condition is in good agreement with the asymptotic contrast match value of 27.5% reported earlier by McCourt and Blakeslee (1994) for a 0.5° test field at the higher inducing grating spatial frequency of 0.125 c/d. Matching contrasts are distributed normally in both cases with standard deviations of 7.56% and 8.33%, respectively.

Table 2 presents correlations between canceling and average [(LVF + UVF)/2] matching measures of induction magnitude. Note that there are highly significant correlations between four of the six non-identity pairings of the canceling measures. Canceling contrasts across test field height at common temporal frequencies are highly correlated, as are canceling contrasts at common test field heights across inducing temporal frequency. There is, however, no significant correlation between canceling contrasts when neither inducing temporal frequency nor test field height are similar. Finally, none of the canceling contrast measures are significantly correlated with the average [(LVF + UVF)/2] matching contrast. Matching contrasts at the two test field heights are, however, highly significantly correlated.

The significant correlations between canceling contrasts for combinations of inducing temporal frequency and test field height

Table 2
This table presents correlations between canceling and average [(LVF + UVF)/2] matching measures of induction magnitude. There are significant correlations between four of the six non-identity pairings of the canceling measures. There is no significant correlation between canceling contrasts when neither inducing temporal frequency nor test field height are similar. None of the canceling contrast measures are significantly correlated with average matching contrast. Matching contrasts at the two test field heights are strongly correlated.

		Canceling				Matching	
		1 Hz		4 Hz			
		0.5°	2.0°	0.5°	2.0°	0.5°	2.0°
Canceling							
1 Hz							
0.5°	r	1	.505	.238	.095	.022	−.020
	p		**<.001**	**.003**	.238	.792	.814
	N		155	155	155	142	142
2.0°			1	.114	.287	.073	.115
				.159	**<.001**	.387	.173
				155	155	142	142
4 Hz							
0.5°				1	.342	−.100	−.071
					<.001	.236	.403
					155	142	142
2.0°					1	−.094	−.054
						.268	.527
						142	142
Matching							
0.5°						1	.725
							<.001
							142
2.0°							1

Significant correlations are highlighted in bold.

where at least one stimulus dimension (i.e., inducing frequency or test field height) is congruent, combined with the lack of correlation when neither stimulus dimension is similar, suggests that multiple neural mechanisms give rise to brightness induction at different combinations of inducing temporal frequency and test field height. This is consistent with the Oriented Difference of Gaussians (ODOG) model of brightness perception (Blakeslee, Cope, & McCourt, submitted for publication; Blakeslee & McCourt, 1999).

The low degree of correlation found between matching and canceling measures of induction is interesting, but perhaps not surprising given that the canceling data were obtained at temporal modulation frequencies of 1 Hz or 4 Hz, whereas the matching data were obtained using static gratings, and the neural mechanisms responsible for induction under these different conditions will likely differ.

The only other large-scale study of brightness induction ($N = 101$) was conducted by Bosten and Mollon (2010) who, using a matching paradigm, report a mean brightness induction magnitude, for a 3.1° diameter circular test region centered within a 12.4° diameter surround, of approximately 34.4%. In agreement with present findings these authors likewise reported no significant correlation between brightness induction magnitude and participant age, nor was there a significant correlation between the magnitude of brightness induction and the magnitude of another phenomenon commonly thought to reflect the strength of inhibitory visual processes, contrast–contrast (Chubb, Sperling, & Solomon, 1989).

4.3. Age-related changes in the upper versus lower visual field

Perhaps the most intriguing result of the present study was the discovery of differential age-related changes in suprathreshold contrast processing across the upper (UVF) and lower visual field (LVF). Table 3 shows the correlations between the magnitude of the upper and lower visual field differences for the three stimulus conditions: Induced gratings (0.5° and 2.0° test fields) and real gratings (2.0° standard). These correlations are all highly significant, suggesting first that the UVF/LVF differences we observe are robust and repeatable, and that the mechanisms which drive these differences are similar across our three stimulus conditions.

There are a variety of known anatomical and functional asymmetries between the two visual fields; see Skrandies (1987) and Previc (1990) for comprehensive reviews. At a peripheral level there is a greater retinal thickness (Silva et al., 2010) and higher photoreceptor (Osterberg, 1935; Perry & Cowey, 1985) and ganglion cell density (Curcio & Allen, 1990; Stone & Johnston, 1981) in the superior retina (LVF). Component latencies of the electroretinogram (Skrandies, 1987) and visual evoked cortical potentials (Eason, White, & Oden, 1967; Kimura & Tsutsui, 1981; Lehmann & Skrandies, 1979) are shorter to stimulation in the LVF. In monkey the LVF is overrepresented in a number of visual areas such as the lateral geniculate nucleus (Connolly & Van Essen, 1984), area V1 (Van Essen, Newsome, & Maunsell, 1984), area MT (Maunsell & Van Essen, 1987; Van Essen, Maunsell, & Bixby, 1981) and V6A (Galletti et al., 1999). In humans the LVF also enjoys a larger anatomical representation in early retinotopically mapped visual cortex, as well as larger BOLD (Liu, Heeger, & Carrasco, 2006), MEG (Portin et al., 1999), and ERP (Eason, White, & Oden, 1967) responses to visual stimuli. There is enhanced sensitivity to stimuli in the LVF at both threshold (Carrasco, Talgar, & Cameron, 2001; Rijsdik, Kroon, & van der Wildt, 1980; Silva et al., 2008, 2010; Skrandies, 1985b, 1987, 1995) and suprathreshold contrast levels (Fuller, Rodriguez, & Carrasco, 2008; Levine & McAnany, 2005). Attentional contrast enhancement (Fuller, Rodriguez, & Carrasco, 2008) and attentional acuity (He, Cavanagh, & Intrilligator, 1996), as well as illusory contour perception (Rubin, Nakayama, & Shapley, 1996), and letter recognition (Skrandies, 1987) are superior in the LVF. Spatial resolution (Skrandies, 1985b; Talgar & Carrasco, 2002), visual search (Rezec & Dobkins, 2004), visuomotor transformations (Carlsen et al., 2007; Danckert & Goodale, 2001; Khan & Lawrence, 2005), perceptual identification (Carlsen et al., 2007), critical flicker fusion frequency (Landis, 1954; Skrandies, 1985a), double flash discrimination (Skrandies, 1985a), simple reaction time (Ellison & Walsh, 2000; Payne, 1967), pursuit eye movement initiation (Tychsen & Lisberger, 1986), and chromatic (Levine & McAnany, 2005), and motion processing (Lakha & Humphries, 2005; Levine & McAnany, 2005) also show a LVF superiority.

Table 3
This table shows the correlations between the magnitude of the upper and lower visual field differences for the three stimulus conditions. These correlations are all highly significant.

LVF–UVF differences		Induced		Real
		0.5°	2.0°	2.0°
Induced				
0.5°	r	1	.553	.258
	p		**<.001**	**.002**
	N		142	142
2.0°			1	.260
				.002
				142
Real				
2.0°				1

Significant correlations are highlighted in bold.

Beyond area V1 visual processing bifurcates into two complimentary streams which course ventrally (into temporal cortex) and dorsally (into parietal cortex). While both the UVF and LVF afferents contribute to both streams, the LVF may have a stronger representation within the dorsal stream whereas the UVF may have a stronger association with the ventral stream (Danckert & Goodale, 2001). Moreover, there is a relatively greater contribution of the magnocellular system to the dorsal stream, and of the parvocellular system to the ventral stream. Hence, one conceptualization of the origin of UVF/LVF visual processing differences is that the UVF may be specialized for object identification in far (extrapersonal) space, and rely more strongly on parvocellular input, whereas the LVF may be specialized for visual processing in near (peripersonal) space, and rely more strongly on magnocellular input in support of visuomotor behavior (Previc, 1990).

Our results are broadly consistent with the large body of literature referenced above, since we find that, for young observers, both real and induced suprathreshold gratings possess higher perceived contrast when they are situated in the LVF. Our novel finding is that this LVF advantage progressively weakens with age until, for our oldest observers it is reversed and perceived contrast is significantly lower for stimuli in the LVF. It should be noted that the age-related change in UVF versus LVF sensitivity to suprathreshold contrast is not accompanied by a wholesale reduction in suprathreshold contrast perception, since average matched contrast to both real and induced gratings is relatively constant with age (Experiment 2), and induced contrast measured in central vision is likewise relatively stable with age, at least at low temporal frequencies (Experiment 1).

To the extent that visual processing in the LVF may have a stronger association with the magnocellular system it is possible that the age-related reversal of the typical UVF/LVF anisotropy we find is a consequence of magnocellular dysfunction, which is thought to underlie the psychophysically-defined “transient” channel (Kline & Schieber, 1981; Kline et al., 1983; Sturr, Van Orden, & Taub, 1987). Alternatively, since attention has been proposed to modulate perceived contrast (Carrasco, Ling, & Read, 2004), it is possible that the effects we report accrue from age-related reductions of space-, object-, or feature-based attention within the lower visual field. However, since attentional modulation of perceived contrast occurs primarily at low (perithreshold) contrasts (Schneider, 2006), it is unlikely that this explanation is applicable to the highly suprathreshold (30% contrast) stimuli used in the present experiment.

Cortical cataract formation has been reported to be asymmetrical (Sasaki et al., 2003) owing to exposure to ultraviolet B radiation which induces opacification in older observers localized to the lower nasal quadrant of the lens. Since lens opacity in the lower quadrants will reduce the perceived contrast of peripheral stimuli in the UVF, this phenomenon cannot account for the reduced perceived contrast of stimuli in the LVF reported here.

Finally, there is a significant association between LVF deficits, impairments of locomotion, and increased prevalence of falls in the elderly (Black, Wood, & Lovie-Kitchin, 2011; Lord, 2006; Marigold & Patla, 2008; Timmis, Bennett, & Buckley, 2009). Since seeing takes place primarily at suprathreshold levels of contrast, the age-related reductions in perceived contrast for stimuli in the LVF which we document could certainly contribute to this health risk, particularly for older persons who are at the upper end of the distribution.

4.4. Potential limitations

One potential limitation of the present study is that contrast matches were made under conditions of free viewing, meaning that observers were able to move their eyes to inspect the stimulus array. Thus, the effective eccentricity of the standard and matching gratings might be somewhat less than their physical values (±7.5°). However, many perceptual asymmetries are reliably revealed under free-viewing conditions, such as the left visual field advantages in the perception of chimeric faces (Levy & Heller, 1981; Levy et al., 1983; Luh, Rueckert, & Levy, 1991), in perceived object midpoint (Jewell & McCourt, 2000; McCourt & Jewell, 1999), in perceived object size (Charles, Sahraie, & McGeorge, 2007), as well as in the perceived numerosity and brightness of objects (Nicholls, Bradshaw, & Mattingley, 1999). Thus we may have underestimated the true magnitude of the UVF/LVF asymmetry in suprathreshold contrast perception, and further experiments are warranted in which observers' patterns of fixations will be monitored via eye-tracking, or under instructions to maintain steady fixation. On the other hand, that these UVF/LVF differences in perceived suprathreshold contrast are found under conditions of free viewing is a potential strength, and lends these results heightened ecological validity, since it is under these conditions that normal visual perception occurs.

A second potential limitation is that we did not control for possible reductions in retinal illuminance due to the age-related reduction in pupil size (Winn et al., 1994). However, this concern is lessened by the fact that grating induction magnitude is relatively stable with changes in retinal illumination across the photopic regime (McCourt, 1990), and by previous studies which find that differential pupil size does not constitute a major source of age-related differences in visual processing (Betts, Sekuler, & Bennett, 2007; Betts et al., 2005; Elliott, Whitaker, & Thompson, 1989; Karas & McKendrick, 2009). Finally, reduced retinal illuminance seems an unlikely source of the UVF/LVF asymmetry, and despite potential age-related differences in mean retinal illuminance we find no significant age-related alterations in contrast matching to real or induced gratings, or in induced grating canceling contrast.

A third limitation is that we cannot determine whether the age-related UVF/LVF differences we find are due to a loss of sensitivity in the LVF or to an increase of sensitivity in the UVF (or to some combination of each), because we do not have a neutral matching condition, such as in central vision. However, it seems less likely for sensitivity to increase with age than the opposite.

A fourth potential limitation is that we did not refract our participants to our viewing distance of 57 cm, but instead allowed them to wear their habitual spectacle lenses. This limitation is mitigated by the following considerations.

First, depth of field (DOF) varies inversely with stimulus spatial frequency. DOF for 0.625 c/d gratings (4 mm pupil, white light) is about 3 D (Marcos, Moreno, & Navarro, 1999). Because the spatial frequency of our stimuli is an order of magnitude lower still (0.052 c/d), DOF for our observers will be correspondingly greater, significantly lessening the potential impact of uncorrected refractive error.

Second, the effect of modest refractive error on stimulus contrast is quite small. The point-spread function of the blur circle produced by a 2.5 D lens (assuming an age-corrected 4.5 mm pupil: Winn et al., 1994) is 38.7 min of arc (Hoffman & Banks, 2010; : Eq. (3)). Since the spatial period of our 0.052 c/d sinewave gratings is 1154 min of arc, the transmission efficiency of this system is quite high: 0.9990. This means that defocusing the 30% contrast gratings used in this study by 2.5 D will lower their contrast to 29.97%, a reduction of just 0.03% contrast. It should also be noted that grating induction magnitude is not reduced (actually subtly increased) by blurring the inducing field/test field boundary (McCourt & Blakeslee, 1993). Since the age-related difference in UVF/LVF matching contrast we observe for both real and induced grating stimuli is nearly 3.0%, we conclude that refractive error does not contribute to the UVF/LVF differences in perceived contrast we report.

Third, we reanalyzed our data after excluding the 26 participants who wore multifocal lenses during testing and none of the significant trends we report are affected by their exclusion.

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