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Aging changes 3D perception: Evidence for hemispheric rebalancing of lateralized processes

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Abstract

When judging the 3D shape of a shaded image, young observers assume that the light source is placed above and to the left. This leftward bias has been attributed to hemispheric lateralization or experiential factors. Since aging is associated with loss of hemispheric lateralization, in the current study we measured the effect of aging on the assumed light source direction. Older participants exhibited, on average, a decreased left bias compared to young participants, as well as greater within-group variability in the distribution of assumed light source directions. In a separate sample of young and old participants, we replicated the age related effect in the assumed light source direction. Furthermore, in both young and old participants the assumed light source direction and the lateralized bias in a line bisection task were correlated. These findings suggest that diminished hemispheric lateralization, which accompanies aging, may affect the perception of the 3D structure of shaded surfaces. Shape from shading may thus provide a simple behavioral tool to track age related changes in hemispheric organization.

Key words: Aging, Perception, Lateralization, Vision, Shape from Shading

1. Introduction

Observers experience a three dimensional world through two dimensional retinal images. Nevertheless, the geometry of visual surfaces can be effortlessly recovered from pictorial cues, available in monocular, stationary images. Shading is one such cue, which aids the internal reconstruction of the 3D shape of solid surfaces by exploiting the fact that the parts of a surface facing the light source are brighter than those facing other directions (Horn 1975). When judging the shape of shaded objects, observers exhibit two perceptual biases (Mamassian, Landy, & Maloney, 2001), which reflect unconscious assumptions about the likely state of the world. The first is that surfaces are more likely to be perceived as convex than concave (Ramachandran, 1988a). The second is that the light-source is located above, possibly reflecting the fact that the illuminant is usually placed above the observer (Ramachandran, 1988b). Surprisingly, human observers seem to assume that the light source is not coming directly from above, but rather, from a direction displaced to the left of the zenith (Adams, 2007; Elias & Robinson, 2005; Gerardin, de Montalembert, & Mamassian, 2007; Mamassian & Goutcher, 2001; McManus, Buckman, & Woolley, 2004; Sun & Perona, 1998). While the reason for this left bias has not been conclusively established, two proposals have been put forward. Sun and Perona (1998) thought that it is driven by learned environmental regularities. They suggested that the left bias reflects the preference of individuals to keep the light source on their left, to avoid writing in the shadow cast by their writing hand. This proposal assumes that individuals' experience of the light source leads to different expectations, which in turn, determines the direction of the assumed light source. Adams, Graf, and Ernst (2004) demonstrated directly that even brief perceptual experiences can modify the

assumed light source direction in young adults, lending credence to the claim that the assumed light source direction reflects a learned environmental regularity.

An alternative interpretation of the left bias, which we will focus on in this study, is that it reflects an internal constraint, which does not depend on environmental regularities, but rather on lateralized attentional processes (Mamassian & Goutcher, 2001). There is empirical evidence consistent with the lateralization hypothesis. Neuroimaging data have shown that a right hemisphere lateralized network is recruited during the perception of shaded images, which mainly includes areas along the intra-parietal sulcus (Taira, Nose, Inoue, & Tsutsui, 2001; Gerardin, Kourtzi, & Mamassian, 2010). Direct evidence for the idea that hemispheric lateralization may determine the light source bias comes mainly from neuropsychological and electrophysiological studies. Attentional impairments associated with right hemisphere lesions were found to change the assumed direction of the light source (de Montalembert, Auclair, & Mamassian, 2010), as well as other directional biases which characterize visual processing in healthy individuals (Campbell, 1978; David, 1989; Luh, Rueckert, & Levy, 1991; Bowers & Heilman, 1980; Bradshaw, Nettleton, Nathan, & Wilson, 1985). Specifically, de Montalembert et al. (2010) measured the assumed light source direction in patients with right hemisphere strokes and healthy aged-matched controls. Patients with right cortical lesions showed a rightward light source bias. It was inferred that lateralized, fronto-temporo-parietal networks support the left bias in healthy individuals. Moreover, electrophysiological data have indicated that scalp potentials evoked by both periodic and impulsive shaded stimuli are right lateralized in young, healthy participants and, more importantly, that individual differences in the degree of lateralization correlate

with individual differences in the assumed light source direction (Mamassian, Jentzsch, Bacon, & Schweinberger, 2003).

Given the converging evidence for hemispheric lateralization being a crucial factor to the assumed light source bias, the question naturally arises whether the direction of the assumed light source correlates with changes in hemispheric lateralization encountered during the lifespan.

Aging is known to affect basic visual functions, such as visual acuity and contrast sensitivity (e.g. Owsley, Sekuler, & Siemsen, 1983). More relevant to the current study, is the finding that depth perception is also diminished in aging. For example, older adults have a diminished ability to perceive depth from binocular disparity and recover 3D shape from motion (Bell, Wolf, & Bernholz, 1972; Norman, Dawson, & Butler, 2000; Mateus, et al., 2013; Norman et al., 2013). Norman and Wiesemann (2007) reported that aging affected shape from shading, having found that older participants were less accurate than young when judging the local surface orientation of a shaded stimulus.

A significant body of imaging data has shown that aging is associated with dedifferentiation of neural processes. That is, brain regions that respond preferentially to certain tasks or stimuli in young participants become less selective with aging (see Goh, 2011 for review). This is evident both in regions involved in high cognitive functions, such as working memory (Reuter-Lorenz et al., 2000), as well as in regions involved in perceptual processes, such as face (Grady, McIntosh, Horwitz, & Rapoport, 2000) and object recognition (Park et al., 2004).

Importantly, aging is also accompanied by a reduction in hemispheric asymmetry (Cabeza, 2002). For instance, older participants show bilateral hemispheric activations in verbal working memory tasks, which are strongly

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lateralized to the left hemisphere in younger participants (Cabeza et al., 1997; Reuter-Lorenz et al., 2000). Reuter-Lorenz, Stanczak, and Miller (1999) compared old and young participants on a number of letter matching tasks of varying complexity. Letters were presented in the same or opposite visual fields. Older participants performed more quickly and accurately with bilateral presentations regardless of task difficulty, whereas young participants only benefitted from bilateral presentation during the most complex tasks. This result was interpreted as providing evidence for increased bi-hemispheric recruitment in old adults. Moreover, distribution of attention may become less lateralized in aging, as suggested by the observation that the left visual field advantage demonstrated by young adults in line bisection tasks (see Jewell & McCourt, 2000 for review) and judgment of chimeric faces (Failla, Sheppard, & Bradshaw, 2003), is diminished in older adults. Interestingly, anatomical and functional connectivity between homologous areas of the two hemispheres and between dorsal attentional and sensory areas of the same hemisphere are diminished in healthy aging (Andrews-Hanna et al., 2007). Note that age related changes in functional connectivity do not necessarily imply changes in lateralization, but they suggest that attentional, top-down modulations of sensory processes may be specifically liable to age related changes. While neuroimaging data have demonstrated loss of lateralization in healthy aging and in patients with focal brain lesions (e.g. Lotze et al., 2006), behavioral correlates of this loss of lateralization have been limited.

The current study measured the ability to judge shape from shading in young and older adults, to assess the effect of aging, and in particular the diminished hemispheric lateralization, on depth perception. We reasoned that if aging results in diminished hemispheric lateralization and the assumed light source bias depends on

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lateralized brain processes, then one should observe a smaller left bias in the assumed light source in old compared to young participants. Alternatively, if either aging does not affect lateralization or the assumed light source direction does not reflect lateralized brain processes, then there should be no difference between young and old adults in the direction of the assumed light source. Finally, neural changes associated with aging, such as dedifferentiation, may also result in decreased sensitivity to shading information.

2. Experiment 1

2.1 Participants

Twenty-two undergraduate students (three left handed) from Bangor University (mean age = 21.92; $SD = 3.63$; range = 18-33) were recruited and received course credit for their participation. Twenty-four healthy older participants (one left handed), without known neurological impairments, were recruited through the Bangor University, School of Psychology's Panel (mean age 70.36; $SD = 5.61$; range = 62-81) and were paid for their time. We did not formally check visual acuity, but all participants reported having normal or corrected to normal vision and were able to read and sign the consent form without assistance. The experimental protocol was approved by Bangor University's ethical committee and complied with the declaration of Helsinki. Participants gave written informed consent prior to any experimental procedure.

2.2 Apparatus and Stimuli

Participants were tested in a dimly lit room. A LaCie Electron 22blue CRT monitor was used to present the stimuli. The screen resolution was set at 1024x768 pixels. A chin rest was used to ensure that participants maintained a constant distance of 60cm from the screen.

We used “honeycomb” stimuli (Andrews, Aisenberg, d’Avossa & Sapir, 2013). The basic stimulus comprises seven hexagonal tiles, which cover a visual angle of 14.3° and are overlaid on a uniform grey background. Bright and dark edges create the impression of a relief lit from one side (see Figure 1). The stimulus orientation varied over 24 levels, obtained by rotating the stimulus in steps of 15° in the image plane. Figure 1A shows the stimulus with a 0° orientation and figure 1B shows the 180° rotated stimulus. The orientation of the stimulus axes of symmetry is collinear with the two possible directions of the light source. If the observer decides that the light source is on the side closer to the stimulus bright edges, the stimulus will be perceived as convex, while if the observer places the light source on the side closer to the stimulus dark edges the stimulus will be perceived as concave. For example, if the assumed light source is above the stimulus, then the central hexagon in figure 1A should be consistently perceived as convex, while the one shown in figure 1B as concave. However, the same stimulus, rotated 90° , should result in a maximally ambiguous percept, since the light source is equally likely to be placed on the left and the right side of the stimulus.

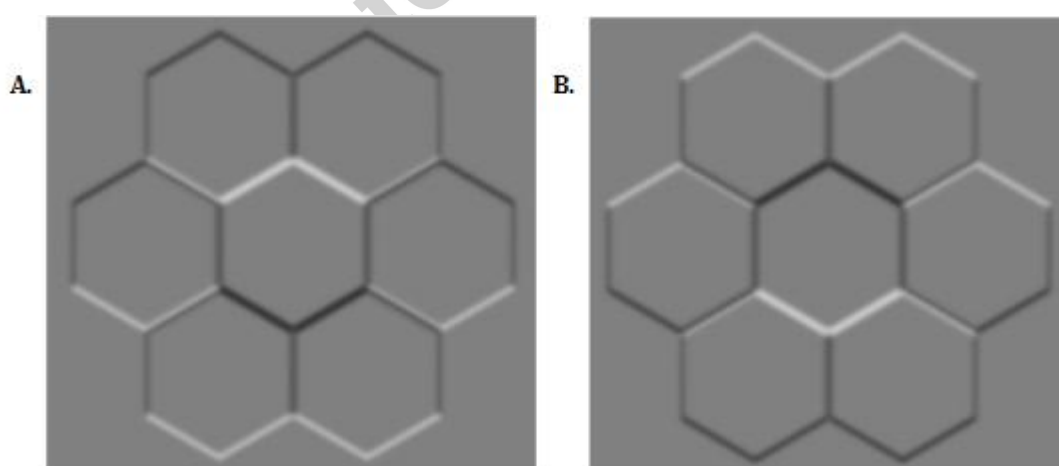


Figure 1: Honeycomb stimulus. A, stimulus with a shading pattern consistent with a central convex hexagon and the light source at the zenith. *B*, The same stimulus rotated 180° .

2.3 Procedure

Participants completed one practice block containing 15 trials. This was followed by experimental blocks of 120 trials. Each orientation was presented five times within a block, and the order of presentation was randomized. Older participants completed two blocks, while young participants completed four. Only responses from the first two blocks were analyzed.

A trial began with a central presentation of the honeycomb. Participants reported verbally whether the central hexagon appeared raised above or receded behind the surrounding hexagons. The experimenter, who could not view the stimulus display screen, pressed the corresponding key. Stimuli were visible until the experimenter pressed the key. If no response was made for 3.0s, the screen went blank for 300ms and then a prompt “is it in or out?” appeared on the screen. The next trial started immediately after the experimenter’s response.

2.4 Analysis

A multivariate logistic regression was used to estimate the effects of stimulus orientation, θ , on the probability that a participant would judge the central hexagon as convex, $p(C)$, that is:

$$p(C|\theta) = \frac{1}{1 + e^{-f(\theta)}}$$

We assumed that response probability varied as a sinusoidal function of the stimulus orientation. Therefore, the regressors included a constant term and the sine and cosine of the stimulus orientation:

$$f(\theta) = \alpha_0 + \alpha_1 \cos \theta + \alpha_2 \sin \theta$$

To determine whether a participant’s reports were significantly modulated by the orientation of the stimulus, we computed the log-likelihoods of two logistic

models. The first was the one above, while the second only contained the constant term. The ratio of the two log-likelihoods has an approximately chi squared distribution, with two degrees of freedoms (Hosmer, Lemeshow, & Sturdivant. 2013). Only participants whose logistic fits had a significance value of 0.01 or less were included in the group level analysis. This procedure was employed to remove estimates from participants whose responses were not modulated by the orientation of the stimulus, because in these participants the estimation of the assumed light source is particularly noisy and therefore prone to large errors.

The assumed light source direction, O , which corresponds to the phase of the sinusoidal modulation, can then be computed using the logistic fits (see above) and the following formula:

$$\hat{O} = \tan^{-1} \left(\frac{\alpha_2}{\alpha_1} \right)$$

This procedure allowed us to estimate the assumed light source direction with a precision that was not limited by the orientation step.

The sensitivity to shading information was estimated by computing the proportion of convex judgements predicted by the fitted logistic model when the orientation of the stimulus was aligned with the estimated direction of the assumed light source or anti-aligned, namely, 180° rotated. The first was the stimulus orientation that resulted in the largest proportion of convex responses or ‘hits’, $p(H)$, while the second resulted in the lowest proportion of convex responses or ‘false alarms’, $p(F)$ and were calculated thus:

$$p(H) = \frac{1}{1 + e^{-\left(\alpha_0 + \sqrt{\alpha_1^2 + \alpha_2^2}\right)}}$$

$$p(F) = \frac{1}{1 + e^{-\left(\alpha_0 - \sqrt{\alpha_1^2 + \alpha_2^2}\right)}}$$

The sensitivity, d' and the convexity bias, B , namely the tendency to report the stimulus as convex regardless of its orientation, were computed from the z -scores of the hit and false alarm rates:

$$d' = z[p(H)] - z[p(F)]$$

$$B = \frac{z[p(H)] + z[p(F)]}{2}$$

Group level descriptive statistics for the direction of the assumed light source data were computed using the circular mean and the circular standard deviation (Berens, 2009). Hypothesis testing of between group differences of both means and standard deviations was carried out by unpaired, two tailed bootstrapped comparisons. Bootstrapped p -values were based on 100,000 pseudo-samples. Between group comparisons of the sensitivity and the convexity bias were carried out using unpaired two tailed t -tests. Finally, the relation between the assumed light source direction and sensitivity in old participants was computed using a circular to linear correlation (Berens, 2009)

3. Results and Discussion

Two young and three older participants were excluded from the group analysis because their responses were not significantly modulated by the stimulus orientation (see Methods). The final sample included 20 young and 21 older adults. Figure 2 shows the light bias of each participant as a function of the participants' age, while Figure 3 shows representative individual results for two young and two old participants. The young participants had a significant leftward bias (group average circular mean = -24.84° , 95% CI: -32.13° - -17.54°). Conversely, the older group had a leftward bias which did not deviate significantly from the zenith (group average mean = -6.11° , 95% CI= -16.81° - 4.25°). An unpaired, two tailed bootstrapped

comparison indicated that the bias differs significantly between the young and old participants ($p=.003$). The between group difference accounted for 16% of the overall variance in the joined data distribution.

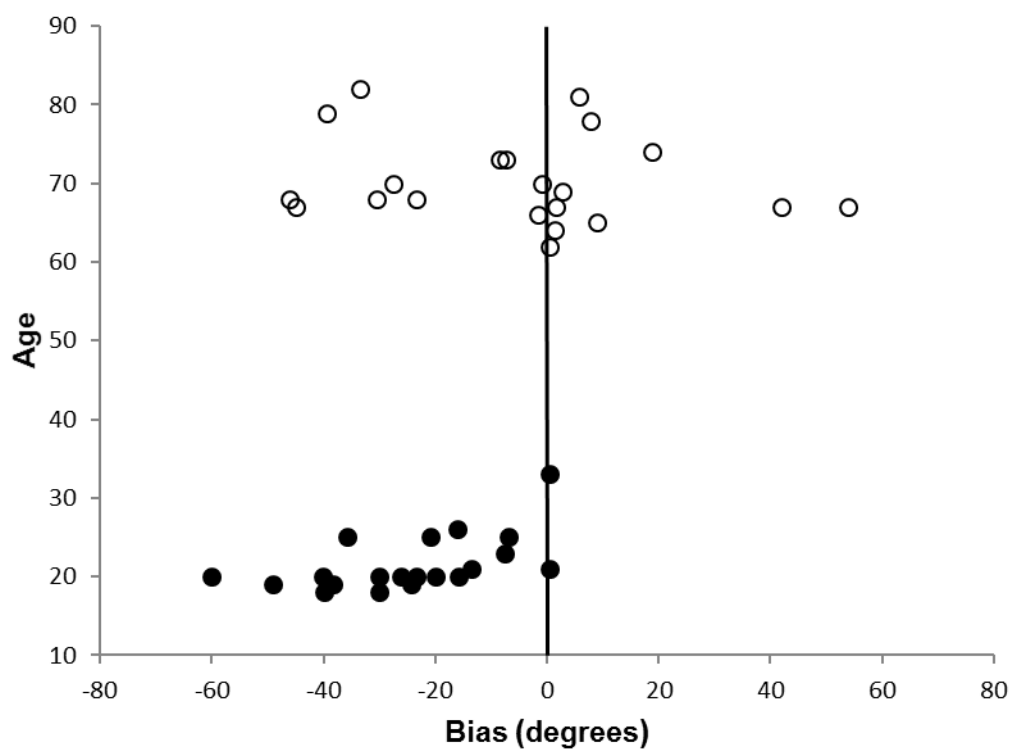


Figure 2: Graph displays the age and the assumed light source direction of each participant. Filled circles indicate participants in the young group; empty circles represent the older participants. The reference line at zero degrees is the zenith. Negative values represent biases to the left.

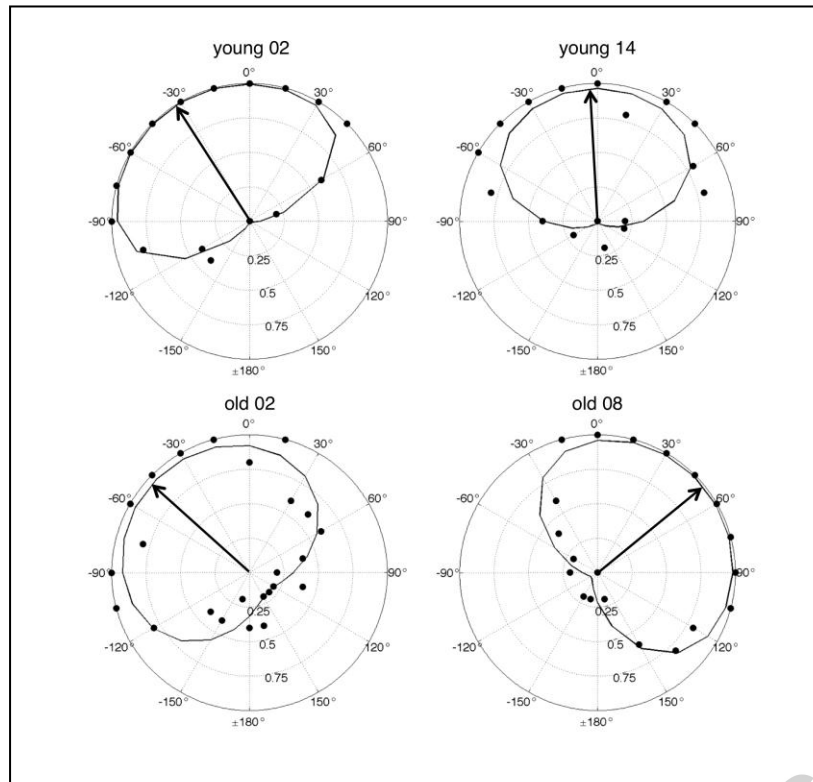


Figure 3: Representative data for two young (upper plots) and two old (lower plots) participants. The data points in the polar plots show the proportion of trials in which a participant reported a convex central hexagon for each stimulus orientation. Stimulus orientation varied in steps of 15°. The solid lines are the best logistic fits and the arrows are the estimated directions of the assumed light source.

The distribution of light source directions was wider in the old than young participants. The circular standard deviation of the older group's distribution was 24.09° (95% CI= 16.70°-31.10°) while the standard deviation of the young participants distribution was 15.38° (95% CI= 10.61°-19.05°). The bootstrapped, two tailed difference was significant, $p=.033$, suggesting greater inter-individual variations in the direction of the assumed light source in the old than young participants' group.

Next, we examined the sensitivity to shading information and convexity biases. Measures of sensitivity and bias were obtained from the logistic fits (see

Methods). The older participants were less sensitive to shading than the young, their d' being on average 3.21 (95% CI= 2.58- 3.85) while the young participants' d' was 4.42 (95% CI= 3.51 - 5.33). The difference, however, did not reach significance ($t(39)= 1.98, p= .053$). The Cohen's effect size had an intermediate value ($d = .62$) and the between group difference accounted for 9% of the overall variance. In the older group the correlation between sensitivity and the assumed light source directions was not significant ($r = -0.18, p= .71$), suggesting that the participants with low sensitivity to shading were not necessarily those with the least leftward bias. The older group also showed a tendency to report the central hexagon as concave rather than convex. The group average convexity bias for the old was -0.79 and for the young 0.09; however, the difference was not significant ($t(39)= 1.94, p=.06$). The Cohen's effect size had an intermediate value ($d = .61$) and the between group difference accounted for 9% of the overall variance.

In summary, we found age related differences in the assumed light source direction and sensitivity to shading information. Whereas young participants showed a consistent left bias, older participants showed a smaller bias on average, as well as greater inter-individual variability. Additionally, older participants were less sensitive to shading information than young adults.

4. Experiment 2

To test the hypothesis that the diminished light source bias in older adults reflects reduced hemispheric lateralization, we correlated, in a new sample of older participants and a group of young controls, the assumed light source direction with the lateralized performance on a line bisection task (Bowers & Heilman, 1980). The latter is thought to measure hemispheric lateralization in the deployment of attention.

Healthy young participants overestimate the length of the left side of a horizontal line, and therefore bisect it to the left of its true midpoint. In a meta-analytical review, Jewell and McCourt (2000) confirmed that healthy young participants have a consistent left line bisection bias. This bias correlates with functional and anatomical measures of hemispheric lateralization. For instance, fMRI data have indicated that line bisection activates a right lateralized attentional network (Çiçek, Deouell, & Knight, 2009). Additionally, inter-individual differences in line bisection bias correlate with hemispheric differences in the volume of fronto-parietal white matter tracts (De Schotten, et al., 2011). Finally, inactivating areas of the right attentional network causes a rightward shift in line bisection (de Schotten, et al., 2005). Finally, the left line bisection bias is known to be diminished in older adults, a finding that has been interpreted in terms of reduced hemispheric lateralization (e.g., Benwell, Thut, Grant, & Harvey, 2014; Failla et al., 2003; Schmitz & Peigneux, 2011).

4.1 Participants

Fourteen naive healthy older participants (all right handed; mean age 69.28; SD = 4.48; range = 63-79), and 20 young adults (one left handed, mean age 21.85; SD = 2.45; range = 19-30), were recruited through the Bangor University, School of Psychology Community Panel and were paid for their time. All participants reported having normal or corrected to normal vision.

4.2 Measurements and Procedure

Participants were tested with the 'honeycomb' stimulus, in exactly the same way as in the previous experiment. In addition, participants completed a line bisection task. Participants were presented with 13 black horizontal lines on 13 separate white A4 papers. Lines were 1mm thick. There were five 20mm long lines, five 100mm

long lines, and three 200mm long lines. Lines were positioned on either left, center or right of the A4 sheet. The edge of the peripheral lines was 20mm from the closest paper margin. Each A4 sheet was placed in front of the participants at their midline. Participants were asked to mark the center of each line using their right dominant hand. No time limit was applied. The distance from the true center was measured to the closest .5mm, with left deviations scored as negative values, and right deviations as positive values. The mean deviation was calculated for the three long lines (200mm), in keeping with established practice (McCourt & Jewell, 1999).

4.3 Results

Two older participants were excluded from the analysis because their shape judgement was not significantly modulated by the stimulus orientation (see Experiment 1- Analysis). One older participant completed one block only, due to equipment malfunction.

In the 12 older participants, the circular mean of the light source direction was -2.92° (95% CI= $-18.3^\circ - 12.45^\circ$) and the mean line bisection bias was $-.1075\text{cm}$ (95% CI= $-.3703 - .1553$). In the young participants, the mean light source direction was -17.25° (95% CI= $-23.34^\circ - -12.16^\circ$), and the line bisection bias was $-.2615\text{cm}$ (95% CI= $-0.4226 - -0.1004$). Unpaired, two tail bootstrapped comparison indicated that the assumed light source direction differed significantly between the groups ($p=.047$), while no significant age related differences were found in the line bisection bias ($p=.28$). There was a significant correlation between the assumed light source direction and line bisection across all participants, ($r = .554, p<.001$), suggesting shared directional biases in the shape from shading and line bisection tasks. This correlation was significant in the older participants group ($r = .616, p=.016$) as well as

the young ($r = .448, p = .024$) (see Figure 4). A model II geometric mean regression (Ricker, 1973) was used to estimate the relation between the two measured variables. It indicated that in older individuals there is a $5.78^\circ (\pm 1.57^\circ)$ leftward deviation in the assumed light source direction for every 1.0mm leftward change in the line bisection bias. The results of the regression indicate that in young individuals there is a $3.7^\circ (\pm 0.84^\circ)$ deviation to the left in the light source direction for every 1.0mm deviation to the left in the line bisection task. An unpaired, two-tailed bootstrapped comparison indicated that the slopes of the light direction vs line bias are not significantly different between young and old ($p = 0.13$).

Inter-individual differences in the direction of the assumed light source were greater in old than young participants. The circular standard deviation of the older group's distribution was 23.18° (95% CI = 14.37 - 28.17), while the standard deviation of the young participants' distribution was 12.96° (95% CI = 9.91 - 14.90). The bootstrapped two tailed difference was significant ($p = .02$).

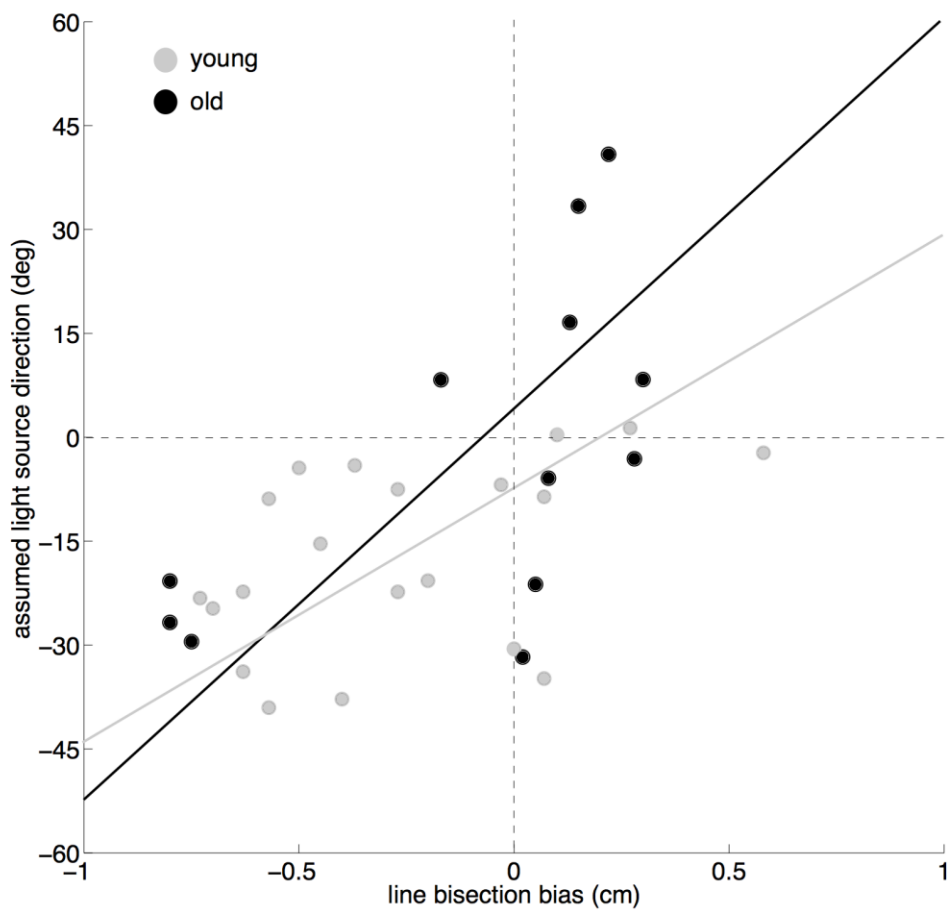


Figure 4: Assumed light source directions are displayed as a function of the line bisection bias. Each data point represents one participant. Grey circles represent young participants, black circles represent older participant. Zeros are the direction corresponding to straight above the observer and the line mid-point, respectively. Positive values represent rightward biases, while negative values represent leftward biases.

5. General Discussion

In the current study, we measured the effect of aging on the assumed light source direction. We reasoned that if the bias in the direction of the assumed light source is due to hemispheric lateralization, and aging leads to a loss of hemispheric lateralization, then older adults should show a smaller bias than young adults. In two separate experiments, we found group level differences between old and young participants in the distribution of the assumed light source directions. These included a decreased left bias of the assumed light source, as well as increased within group variability in older adults. While young adults' reports of 3D shape indicated that they placed the light source about 20° to the left of the zenith, old adults showed no significant bias at the group level. Though the assumed light source direction was never measured to assess changes in hemispheric lateralization in aging, our finding is consistent with one previous observation. In a study measuring the light source bias in stroke patients, de Montalembert et al. (2010) also tested healthy, age matched participants. Interestingly, this group of older individuals showed a mean bias of only 5° to the left, which was less than the 22° left bias found in a separate study, using the same stimulus, in young university students (Gerardin et al., 2010). The finding that old participants have a lesser bias than young participants supports our prediction. Specifically, if the estimation of shape from shading relies on lateralized representations of the assumed light source position in young adults, and aging results in diminished lateralization, one should expect to find a smaller left bias in older adults.

To test the hypothesis that the reduced left bias in older adults reflects a diminished hemispheric lateralization, we measured the assumed light source direction and line bisection performance in a separate sample of young and old

participants. Line bisection biases are thought to reflect lateralized attentional processes (Jewell & McCourt, 2000; Çiçek et al., 2009; De Schotten et al., 2011; de Schotten et al., 2005). Previous studies have reported that aging results in a decreased leftward line bisection bias (e.g., Schmitz & Peigneux, 2011; Benwell et al., 2014), a finding that has been interpreted to reflect age related changes in hemispheric lateralization. We found a significant correlation between the direction of the assumed light source and line bisection in both young and older adults. In older adults 38% of the light source direction group variance was accounted by individual differences in line bisection biases, while in the young only 20% of the variance was accounted by line bisection biases. Nevertheless, in both groups the relation between the two variables was significant and not differ significantly between the groups. This suggests that lateralized processes that underlie individual differences in the line bisection task affect the assumed light source direction. Moreover, it suggests that age related changes in hemispheric lateralization contribute substantially to increased individual differences in the assumed light source direction found in older participants.

Our data leave open the possibility that other factors, beyond hemispheric lateralization, may modulate the effects of aging on the assumed light source direction. Specifically, we found that older participants with a left deviation in line bisection showed a leftward assumed light source bias, whereas those with a rightward deviation in line bisection exhibited a broad range of assumed light source directions. This suggests that age related changes in the assumed light source direction may require more than age related changes in attentional biases associated with hemispheric lateralization.

For example, old adults may be exposed to different environmental regularities than young adults and therefore shift their assumed light source direction to reflect the conditions prevalent in their own visual environment. Additionally, age related changes in reading habits may impact attentional biases, and by extension, the assumed light source direction. We recently showed that the direction in which participants read and write in their native language does correlate with the assumed light source bias (Andrews et al., 2013), being smaller in Hebrew than English readers, a finding that has since been replicated (Smith, Szelest, Friedrich, & Elias, 2015).

It has been suggested that 3D shape perception depends on the interaction between top-down signals generated in parietal regions, which may maintain a representation of the observer's expectations, and bottom-up sensory signals in visual regions (Taira et al., 2001; Yuille & Kersten, 2006). Neuroimaging data have confirmed that shape from shading relies on the interaction between early visual areas and intraparietal sulcus regions and that the light source direction may be represented early in the computation of shape from shading (Gerardin et al., 2010). While the functional connectivity between early visual regions is spared in aging, the connectivity between regions along the intraparietal sulcus and early visual regions is diminished in old compared to young adults (Andrews-Hanna et al., 2007). Thus, one could speculate that shape from shading may be particularly vulnerable to the effects of aging. Shape from shading tasks could provide a simple way to assess changes in visual processes during aging.

Older participants also showed a wider distribution of assumed light source directions. This is not surprising since performance variability, both within and between individuals, is increased in aging (Hedden & Gabrieli, 2004), suggesting that

cerebral functions may deteriorate at a different pace in different individuals. In addition, we expected that older participants would demonstrate lower sensitivity to shading information than young adults, as previous studies using binocular and motion cues found that older adults have diminished depth perception compared to young adults (Bell et al., 1972; Norman et al., 2000; Mateus et al., 2013; Norman et al., 2013). Moreover, Norman and Wiesemann (2007) found that older adults were less precise than young adults judging the local surface orientation of a shaded object. When additional depth cues were provided, aging effects were no longer found, suggesting that shading may be specifically vulnerable to aging. In the current study older adults showed lower sensitivity than young adults, however the between group difference did not reach significance.

Is it possible that the changes we observed in older participants are due to low level sensory factors? It is certainly conceivable that aging related changes in visual acuity may result in decreased sensitivity to shading information. However, that low-level sensory impairments may result in changes in the direction of the assumed light source is not particularly plausible. Increasing levels of blurring of shaded stimuli do not change the direction of the assumed light source in young participants, unless blurring results in stimuli that are no longer perceived as 3D (Gerardin et al., 2007). Moreover, the correlation between shading sensitivity and the assumed light source bias in our group of older participants was small and not significant, suggesting that the older participants with the smallest leftward bias were not necessarily those who were least sensitive to shading information. More generally, visual acuity, including contrast sensitivity, and motion and depth perception, has been found to decrease with age. Older participants show a decreased sensitivity to gratings at high spatial frequencies (e.g., Owsley et al., 1983). It is also well established that aging is

associated with reduced ability to perceive depth from binocular disparity and recover the 3D structure from motion (Bell et al., 1972; Norman et al., 2000; Mateus et al., 2013; Norman et al., 2013). Not all of the perceptual changes found in aging can be attributed to low-level changes in sensory factors (Owsley, 2011 for review; Spear, 1993). Interestingly, while tactile sensation has been found to decrease in aging (Amaied, Vargiolu, Bergheau, & Zahouani, 2015), 3D tactile perception remains intact (Norman et al., 2011), supporting the viewpoint that impairments in 3D perception in aging largely reflect high-level perceptual, rather than low-level sensory deficits.

6. Conclusions

In summary, we found changes in the perception of shape from shading in old compared to young participants. Additionally we found that individual differences in the assumed light source direction were correlated with lateralized biases in a line bisection task. We propose that these findings reflect the reorganization of lateralized processes for depth perception in aging. The shape from shading task may provide a simple behavioral tool to track age related changes in the lateralized organization of brain functions.

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References

- Adams, W. J. (2007). A common light-prior for visual search, shape, and reflectance judgments. *Journal of Vision* 7(11), 11.
doi: 10.1523/JNEUROSCI.4564-05.2006
- Adams, W. J., Graf, E. & Ernst, M. (2004). Experience can change the 'light-from-above' prior. *Nature Neuroscience*, 7 (10), 1057-1058. doi:10.1038/nn1312
- Amaied, E., Vargiolu, R., Bergheau, J. M., & Zahouani, H. (2015). Aging effect on tactile perception: Experimental and modelling studies. *Wear*, 332, 715-724.
doi:10.1016/j.wear.2015.02.030
- Andrews, B., Aisenberg, D., d'Avossa, G., & Sapiro, A. (2013). Cross-cultural effects on the assumed light source direction: evidence from English and Hebrew readers. *Journal of vision*, 13(13), 2-2. 10.1167/13.13.2
- Andrews-Hanna, J. R., Snyder, A. Z., Vincent, J. L., Lustig, C., Head, D., Raichle, M. E., & Buckner, R. L. (2007). Disruption of large-scale brain systems in advanced aging. *Neuron*, 56(5), 924-935. doi:10.1016/j.neuron.2007.10.038
- Bell, B., Wolf, E., & Bernholz, C. D. (1972). Depth perception as a function of age. *The International Journal of Aging and Human Development*, 3(1), 77-81.
doi:10.2190/ORQM-RRNK-A8GN-X99J
- Benwell, C. S., Thut, G., Grant, A., & Harvey, M. (2014). A rightward shift in the visuospatial attention vector with healthy aging. *Frontiers in aging neuroscience*, 6, 113.
- Berens, P. (2009). CircStat: A MATLAB toolbox for circular statistics. *Journal of Statistical Software*, 31(10), 1-21.
- Bowers, D. & Heilman, K. M. (1980). Pseudoneglect: Effects of hemispace on a

tactile line bisection task. *Neuropsychologia*, 18(4), 491-498.

doi:10.1016/0028-3932(80)90151-7

Bradshaw, J. L., Nettleton, N. C., Nathan, G., & Wilson, L. (1985). Bisecting rods and lines: Effects of horizontal and vertical posture on left-side underestimation by normal subjects. *Neuropsychologia*, 23(3), 421-425. doi:10.1016/0028-3932(85)90029-6

Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: The HAROLD model. *Psychology and Aging*, 17(1), 85. doi:10.1037/0882-7974.17.1.85

Cabeza, R., Grady, C. L., Nyberg, L., McIntosh, A. R., Tulving, E., Kapur, S., ... & Craik, F. I. (1997). Age-related differences in neural activity during memory encoding and retrieval: A positron emission tomography study. *The Journal of Neuroscience*, 17(1), 391-400.

Campbell, R. (1978). Asymmetries in interpreting and expressing a posed facial expression. *Cortex*, 14(3), 327-342. doi:10.1016/S0010-9452(78)80061-6

Çiçek, M., Deouell, L. Y., & Knight, R. T. (2009). Brain activity during landmark and line bisection tasks. *Frontiers in human neuroscience*, 3. doi:10.3389/neuro.09.007.2009

David, A. S. (1989). Perceptual asymmetry for happy–sad chimeric faces: Effects of mood. *Neuropsychologia*, 27(10), 1289–1300. doi:10.1016/0028-3932(89)90041-9.

de Montalembert, M., Auclair, L. & Mamassian, P. (2010). Where is the sun for hemi-neglect patients? *Brain and Cognition*, 72(2), 264-270. doi:10.1016/j.bandc.2009.09.011

de Schotten, M. T., Dell'Acqua, F., Forkel, S. J., Simmons, A., Vergani, F., Murphy,

- D. G., & Catani, M. (2011). A lateralized brain network for visuospatial attention. *Nature neuroscience*, *14*(10), 1245-1246. doi:10.1038/nn.2905
- de Schotten, M. T., Urbanski, M., Duffau, H., Volle, E., Lévy, R., Dubois, B., & Bartolomeo, P. (2005). Direct evidence for a parietal-frontal pathway subserving spatial awareness in humans. *Science*, *309*(5744), 2226-2228.
- Elias, L. J. & Robinson, B. M. (2005). Lateral biases in assumptions of lighting position. *Brain and Cognition*, *59*(3), 303–305.
doi:10.1016/j.bandc.2004.08.021
- Failla, C. V., Sheppard, D. M., & Bradshaw, J. L. (2003). Age and responding-hand related changes in performance of neurologically normal subjects on the line-bisection and chimeric-faces tasks. *Brain and cognition*, *52*(3), 353-363.
doi:10.1016/S0278-2626(03)00181-7
- Gerardin, P., de Montalembert, M., & Mamassian, P. (2007). Shape from shading: New perspectives from the polo mint stimulus. *Journal of Vision*, *7*(11), 13.
doi:10.1167/7.11.13
- Gerardin, P., Kourtzi, Z., & Mamassian, P. (2010). Prior knowledge of illumination for 3D perception in the human brain. *Proceedings of the national academy of sciences of the USA*, *107*(37), 16309-16314. doi: 10.1073/pnas.1006285107
- Girshick, A. R., Landy, M. S., & Simoncelli, E. P. (2011). Cardinal rules: visual orientation perception reflects knowledge of environmental statistics. *Nature neuroscience*, *14*(7), 926-932.
- Goh, J. O. (2011). Functional dedifferentiation and altered connectivity in older adults: Neural accounts of cognitive aging. *Aging and disease*, *2*(1), 30.
- Grady, C. L., Randy McIntosh, A., Horwitz, B., & Rapoport, S. I. (2000). Age-related

- changes in the neural correlates of degraded and nondegraded face processing. *Cognitive Neuropsychology*, *17*(1-3), 165-186. doi:10.1080/026432900380553
- Hedden, T., & Gabrieli, J. D. (2004). Insights into the ageing mind: A view from cognitive neuroscience. *Nature reviews neuroscience*, *5*(2), 87-96. doi:10.1038/nrn1323
- Horn, B. K. P. (1975). Obtaining Shape from Shading Information. In P. H. Winston (Ed.), *The Psychology of Computer Vision* (115-156). New York, NY: McGraw-Hill.
- Hosmer Jr, D. W., Lemeshow, S., & Sturdivant, R. X. (2013). *Applied logistic regression* (Vol. 398). Hoboken, NJ: John Wiley & Sons.
- Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia*, *38*(1), 93-110. doi:10.1016/S0028-3932(99)00045-7
- Knill, D. C. & Kersten, D. (1990). Learning a near-optimal estimator for surface shape from shading . *Computer Vision, Graphics, and Image Processing*, *50*(1), 75-100. doi:10.1016/0734-189X(90)90068-7
- Lehky, S. R. & Sejnowski, T. J. (1988). Network model of shape from shading: Neural function arrives from both receptive and projective fields. *Nature*, *333*, 452-454.
- Lotze, M., Markert, J., Sauseng, P., Hoppe, J., Plewnia, C., & Gerloff, C. (2006). The role of multiple contralesional motor areas for complex hand movements after internal capsular lesion. *The Journal of neuroscience*, *26*(22), 6096-6102. doi: 10.1523/JNEUROSCI.4564-05.2006
- Luh, K. E., Rueckert, L. M., & Levy, J. (1991). Perceptual asymmetries for free

- viewing of several types of chimeric stimuli. *Brain and Cognition*, *16*, 83–103. doi:10.1016/0278-2626(91)90087-O
- Mamassian, P. & Goutcher, R. (2001). Prior knowledge on the illumination position. *Cognition*, *81*, 1-9. doi:10.1016/S0010-0277(01)00116-0
- Mamassian, P., Jentzsch, I., Bacon, B. A., & Schweinberger, S. R. (2003). Neural correlates of shape from shading. *Neuroreport*, *14*(7), 971-975. doi:10.1097/01.wnr.0000069061.85441.f2
- Mamassian, P., Landy, M., & Maloney, L. T. (2001). Bayesian modelling of visual perception. In R. P. N. Rao, B. A. Olshausen & M. S. Lewicki (Eds.), *Probabilistic models of the brain: Perception and neural function* (13-36). Cambridge, MA: MIT Press.
- Mateus, C., Lemos, R., Silva, M. F., Reis, A., Fonseca, P., Oliveiros, B., & Castelo-Branco, M. (2013). Aging of low and high level vision: From chromatic and achromatic contrast sensitivity to local and 3D object motion perception. *PloS one*, *8*(1). doi:10.1371/journal.pone.0055348
- McCourt, M. E. & Jewell, G. (1999). Visuospatial attention in line bisection: Stimulusmodulation of pseudoneglect. *Neuropsychologia* *37*(7), 843–855. doi:10.1016/S0028-3932(98)00140-7
- McManus, C., Buckman, J., & Woolley, E. (2004). Is light in pictures presumed to come from the left side? *Perception*, *33*, 1421-1436. doi:10.1068/p5289
- Norman, J. F., Cheeseman, J. R., Pyles, J., Baxter, M. W., Thomason, K. E., & Calloway, A. B. (2013). The effect of age upon the perception of 3-D shape from motion. *Vision research*, *93*, 54-61. doi:10.1016/j.visres.2013.10.012
- Norman, J. F., Dawson, T. E., & Butler, A. K. (2000). The effects of age upon the

- perception of depth and 3-D shape from differential motion and binocular disparity. *Perception* 29(11), 1335-1360. doi:10.1068/p3111
- Norman, J. F., Kappers, A. M., Beers, A. M., Scott, A. K., Norman, H. F., & Koenderink, J. J. (2011). Aging and the haptic perception of 3D surface shape. *Attention, perception, & psychophysics*, 73(3), 908-918. doi:10.3758/s13414-010-0053-y
- Norman, J. F. & Wiesemann, E. Y. (2007). Aging and the perception of local surface orientation from optical patterns of shading and specular highlights. *Perception and Psychophysics*, 69(1), 23-31. doi:10.3758/BF03194450
- Park, D. C., Polk, T. A., Park, R., Minear, M., Savage, A., & Smith, M. R. (2004). Aging reduces neural specialization in ventral visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 101(35), 13091-13095. doi: 10.1073/pnas.0405148101
- Owsley, C. (2011). Aging and vision. *Vision research*, 51(13), 1610-1622. doi:10.1016/j.visres.2010.10.020
- Owsley, C., Sekuler, R., & Siemsen, D. (1983). Contrast sensitivity throughout adulthood. *Vision research*, 23(7), 689-699. doi:10.1016/0042-6989(83)90210-9
- Ramachandran, V. (1988a). The perception of shape from shading. *Nature*, 331, 163-165. doi:10.1038/331163a0
- Ramachandran, V. (1988b). Perceiving shape from shading. *Scientific American*, 259(2), 76-83.
- Reuter-Lorenz, P.A., Jonides, J., Smith, E., Hartley, A., Miller, A., Marshuetz, C., &

- Koeppe, R. (2000). Age differences in the front lateralization of verbal and spatial working memory revealed by PET. *Journal of Cognitive Neuroscience*, 12(1), 174-187. doi: 10.1162/089892900561814
- Reuter-Lorenz, P. A., Stanczak, L., Miller, A. C. (1999). Neural recruitment and cognitive aging: Two hemispheres are better than one, especially as you age. *Psychological Science*, 10(6), 494-500. doi:10.1111/1467-9280.00195
- Ricker (1973). Linear regressions in Fishery Research. *Journal of the Fisheries Research Board of Canada* . 30, 409-434.
- Schmitz, R., & Peigneux, P. (2011). Age-related changes in visual pseudoneglect. *Brain and cognition*, 76(3), 382-389.
- Smith, A. K., Szelest, I., Friedrich, T. E., & Elias, L. J. (2015). Native reading direction influences lateral biases in the perception of shape from shading. *Laterality: Asymmetries of Body, Brain and Cognition*, 20(4), 418-433. doi:10.1080/1357650X.2014.990975
- Spear, P. D. (1993). Neural bases of visual deficits during aging. *Vision research*, 33(18), 2589-2609. doi:10.1016/0042-6989(93)90218-L
- Sun, J. & Perona, P. (1998). Where is the Sun? *Nature Neuroscience*, 1(3), 183-184. doi:10.1038/630
- Taira, M., Nose, I., Inoue, K., & Tsutsui, K. I. (2001). Cortical areas related to attention to 3D surface structures based on shading: An fMRI study. *Neuroimage*, 14(5), 959-966. doi:10.1006/nimg.2001.0895
- Yuille, A., & Kersten, D. (2006). Vision as Bayesian inference: Analysis by synthesis? *Trends in cognitive sciences*, 10(7), 301-308. doi:10.1016/j.tics.2006.05.002

- When judging the shape of shaded images, we assume the light source to be on the left
- This left bias may reflect lateralized processes, which are diminished in aging
- We found a smaller left bias in old than young participants
- The assumed light source direction was correlated with line bisection biases
- Shape from shading may be used to track hemispheric lateralization

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