Experimental Gerontology 124 (2019) 110630

Contents lists available at ScienceDirect

Experimental Gerontology

journal homepage: www.elsevier.com/locate/expgero

Preserved left and upper visual field advantages in older adults' orienting of attention

Hadas Erel[a], Tamar Ronen[a], Guy Freedman[b], Leon Y. Deouell[c], Daniel A. Levy[a,*]

[a] Baruch Ivcher School of Psychology, The Interdisciplinary Center Herzliya, Israel
[b] University of Texas at Austin, Austin, TX, USA
[c] Department of Psychology, Edmond and Lily Safra Center for Brain Sciences, The Hebrew University of Jerusalem, Israel

ARTICLE INFO

Editor: Christian Humpel

Keywords:
Attention
Orienting
Laterality
Visual search pseudoneglect

ABSTRACT

Lateralization of the distribution of attentional function in the brain is asserted to lead to asymmetry in attentional allocation. This is expressed in the phenomenon of pseudoneglect, in which line and object bisection judgments indicate left visual field (and presumably right hemisphere) dominance. Several studies indicate that this asymmetry is not found in old age, which is taken as an indication of decline in attentional function with aging. We examined this assertion using a more comprehensive assay of attentional asymmetry. We contrasted the spatial distribution of older and younger adults' visual attention using the Starry Night Task, a speeded visual search task in which targets must be located across a wide spatial distribution against a dynamic background of distracters. As expected, compared to younger adults, older adults' response times were longer overall. However, we found that older adults exhibited a graded left visual field advantage, even more distinctly than did younger adults. Additionally, older adults exhibited a graded upper visual field advantage equivalent to that of younger adults. These results indicate that aging may not necessarily compromise basic patterns of distribution of spatial attention. They do not support claims of aging-related loss of attentional lateralization.

1. Introduction

Among the cognitive abilities essential for mental functioning which may be affected by aging are those that comprise the realm of attention (Erel and Levy, 2016). Attention may be seen as a family of cognitive processes, embodied in several neural networks (Petersen and Posner, 2012). Among these cognitive processes is the ability to orient one's visual attention in space. This ability to selectively attend a location in space engenders perceptual augmentation, leading to faster and more accurate detection and discrimination of stimuli appearing in that location (Erel and Levy, 2016). It is commonly assumed that the mechanisms of orientation of visual attention are not symmetrically distributed across the two cerebral hemispheres (Corbetta and Shulman, 2002; Reuter-Lorenz et al., 1990; Schmitz and Peigneux, 2011). This notion is supported by evidence from both clinical and healthy populations. Patients suffering from inferior parietal or temporo-parietal damage typically develop hemispatial neglect syndrome. This syndrome entails difficulty in reporting or responding to stimuli in spatial areas contralateral to the site of the lesion (Karnath, 2015). The tendency for hemispatial neglect symptoms to occur more frequently and severely after right hemisphere (RH) as compared to left hemisphere (LH) damage is considered an indication of the lateralization of visual attention processes to the right hemisphere (Benwell et al., 2014; Schmitz and Peigneux, 2011; Driver and Mattingley, 1998; Halligan et al., 2003; Harvey and Rossit, 2012; Vallar, 1998). Building on a plethora of neuroimaging data in healthy subjects as well as in brain damage patients, Corbetta, Shulman, and their colleagues suggested that this bias is due to an asymmetry specifically in a ventral attention network (VAN), responsible for re-orienting attention towards salient, unexpected events (Corbetta et al., 2008; Corbetta and Shulman, 2002). As opposed to the dorsal attention network, which was found to be symmetrically represented in the two hemispheres, the VAN, including its substrates in the inferior parietal lobe/temporo-parietal junction, was found to be dominantly represented in the right hemisphere.

1.1. Pseudoneglect and aging

To the extent that attention is similar to perceptual and motor processes regarding contralaterality of function, such RH dominance might be expected to yield a left visual field attentional advantage. This seems to be borne out in an interesting finding observed in healthy young adults – bias in favor of the left visual field, a phenomenon

* Corresponding author at: Baruch Ivcher School of Psychology, The Interdisciplinary Center Herzliya, Kanfei Nesharim St., Herzliya 46150, Israel.
E-mail address: daniel.levy@idc.ac.il (D.A. Levy).

https://doi.org/10.1016/j.exger.2019.110630
Received 5 February 2019; Received in revised form 4 June 2019; Accepted 6 June 2019
Available online 10 June 2019
0531-5565/ © 2019 Elsevier Inc. All rights reserved.

termed “pseudoneglect” (Bowers and Heilman, 1980; see Brooks et al., 2014; Jewell and McCourt, 2000, for reviews). In pseudoneglect, judgments of centrality in line bisection and haptic centering tasks exhibit skewing towards the left of the target object, indicating that the left side of the object is attentionally overrepresented in mind. This attentional bias is asserted to arise due to RH dominance in spatial attention processing (Schmitz and Peigneux, 2011; Reuter-Lorenz et al., 1990; Fink et al., 2000a, 2000b, 2001; Foxe et al., 2003; Thiebaut de Schotten et al., 2005, 2011; Bultitude and Aimola-Davies, 2006; Ghacibeh et al., 2007; Waberski et al., 2008; Çiçek et al., 2009; Cavézian et al., 2012; Cai et al., 2013; Benwell et al., 2014; Hatin et al., 2012). While pseudoneglect is not as extreme as hemispatial neglect caused by brain damage, it is nevertheless a robust and consistent phenomenon in non-clinical populations (Turnbull and McGeorge, 1998).

Interestingly, several studies testing older adults found a right-side rather than left-side advantage in the performance of visual attention tasks compared to young participants (Schmitz and Peigneux, 2011). These studies imply that the systematic bias towards the left visual field is attenuated, eliminated, or even reversed with age (Benwell et al., 2014; Brooks et al., 2014; Failla et al., 2003; Fujii et al., 1995; Hatin et al., 2012; Nagamatsu et al., 2011; Schmitz and Peigneux, 2011; but see Brooks et al., 2011; Chen et al., 2011; McGeorge et al., 2007). Some accounts of diminished pseudoneglect in aging claim that it is part of a more general process of cognition becoming less lateralized with age (McGregor et al., 2009; Przybyla et al., 2011; Vallesi et al., 2010). The Hemispheric Asymmetry Reduction in Older Adults model (HAROLD; Cabeza, 2002) states that compensation processes, based on recruitment of the non-dominant hemisphere, assist in overcoming age-related cognitive decline. These compensation processes are thought to result in generally reduced hemispheric asymmetry (Cabeza, 2002; Reuter-Lorenz and Cappell, 2008; Li et al., 2009). An alternative account suggests that accelerated aging-related decline in RH neural structures relative to the LH is responsible for weakening of the phenomenon of pseudoneglect in aging (Brown and Jaffe, 1975; Goldstein and Shelly, 1981; Lux et al., 2008; Nagamatsu et al., 2011). More generally, this putative differential degenerative process is seen as leading to a decrease in the RH dominance in attentional processes, and more symmetric visual field processing.

Although the age-related weakening of pseudoneglect is considered a robust phenomenon, it is important to note that several studies do observe pseudoneglect in older people (Brooks et al., 2014). Some studies indicate equal pseudoneglect effects for young and older adults (Coolican et al., 2008; De Agostini et al., 1999; Harvey et al., 1995; Varnava and Halligan, 2007), and others actually indicate increased pseudoneglect in older adults (Brooks et al., 2011). In some cases, these effects were observed only when they interacted with additional factors as line length (De Agostini et al., 1999) and the hand (right/left) used in the task (Varnava and Halligan, 2007).

A possible explanation for these inconsistencies might relate to the paradigms used for measuring pseudoneglect. Of the various methods employed, line bisection is the most frequently reported (Jewell and McCourt, 2000). In this task, young adults tend to show general bias to the left of veridical center when asked to bisect horizontal lines. In contrast, older adults may exhibit a rightward bias in this task (Fujii et al., 1995; Fukatsu et al., 1990; Stam and Bakker, 1990). Similar age effects are evident in a non-manual version of the line-bisection task (designed to minimize the influence of motor factors), the Landmark Task, in which participants are asked to estimate which of two segments of a pre-bisected line is shorter (or longer; Milner et al., 1992, 1993; Harvey et al., 1995; Milner and Harvey, 1995). Schmitz and Peigneux (2011) found that while young participants estimated the left side of an equally bisected line to be longer than the right side, older adults gave opposite estimations. Notably, apart from a few exceptions (De Agostini et al., 1999; Harvey et al., 1995; Varnava and Halligan, 2007) these paradigms typically lead to clear age-related reduced or reversed pseudoneglect.

A different pattern of effects is commonly found in representational forms of pseudoneglect (see Brooks et al., 2014, for review). In these paradigms, participants are asked to evaluate mentally represented stimuli, or to bisect objects (wooden or metal rods) with their index finger using touch (with no direct visuospatial processing). In both types of representational tasks, older participants were shown to exhibit pseudoneglect either similar to or larger than younger adults (Brooks et al., 2011; McGeorge et al., 2007).

Apart from the inconsistent aging effects emerging from the standard assays of pseudoneglect, these paradigms have several limitations. First, they incorporate judgment or imagery processes, which may be influenced by age orthogonally to attentional processes. That is, these paradigms do not isolate basic attention-dependent processes such as simple detection (Folk and Hoyer, 1992). Second, they involve judgments made on static representations, and do not reflect the dynamic character of attention in natural environments, in which relevant stimuli occur against an ongoing background of moving objects, changing shadows, and so forth (D'Erme et al., 1992). This is of special importance, as older adults' attention is known to be especially sensitive to distractors (Ball et al., 1988; Sekuler et al., 2000). More generally, while phenomena of pseudoneglect in line bisection-type tasks may reflect the lateralization of spatial orienting, it certainly does not capture the full range of spatial dimensions in which visual attention is expressed. More comprehensive visual detection tasks and measures of lateralization with more ecological degrees of freedom seem to be appropriate for understanding the effects of aging on laterality factors in the orienting of attention.

1.2. Assessing lateralization with a visual search task

To deal with these issues and gain a more comprehensive understanding of age effects on the lateralization of attention, in this study we compared performance of older and younger adults on a version of the Starry Night Test (SNT) (Deouell et al., 2005), a task initially designed for assessing hemispatial neglect. In this task, visual targets appear against a dynamically varying dense background of distractors of a different color, across an entire display screen. This continuous representation of space in the SNT allows testing of performance as a function of both horizontal and vertical dimensions. Some evidence of age differences in the vertical dimension (altitude) has already been presented by Feng et al. (2017). While younger adults showed advantage for detecting a target among distractors when it appeared in the upper visual field (see also Feng and Spence, 2014), older adults did not demonstrate such an advantage. The SNT offers a denser, more distributed array of probe locations than the task employed by Feng and colleagues, and may reveal aspects of performance not assessed by their task, including interactions between horizontal and vertical dimensions. Additionally, the SNT allows for measuring reaction times of target-stimuli detection, allowing a continuous and more sensitive measure of difficulty level than the abovementioned visuospatial assays of laterality.

Notably, targets in the SNT appear against the background of a dynamically changing field of distractors. This enhances the sensitivity of the test, by increasing the competition for attention and offering a more ecologically valid configuration than an empty or static display. The SNT's spatial uncertainty across trials plausibly recruits attentional monitoring resources, and the presence of flickering distractors across the display does not allow participants to respond as soon as any stimulus appears on-screen, rather forcing them to identify the target before responding. At the same time, the SNT does not require judgment or imagery processes. Furthermore, it is a feature-search rather than a conjunction-search type task, such that serial search strategies are not germane to performance (Wolfe, 2007). Thus, the SNT provides a rich characterization of the orienting of attention towards target stimuli across a complex visuospatial array. Indeed, in earlier studies we have demonstrated that the SNT can detect contralesional impairments in performance even in patients who perform normally in paper-and-pencil line bisection or cancellation tests (Deouell et al., 2005; see Bonato and Deouell, 2013, for discussion). We therefore surmised that this task may provide a sensitive assay of age-related changes in the distribution of spatial attention.

We used the SNT to test the prediction that young adults should exhibit a left-side advantage in the speeded detection of visual targets against a dynamic background, and that the left-side advantage should dissipate with aging. We further set out to test the prediction, arising from the report of Feng et al. (2017), that upper visual field advantage is vitiated with aging.

2. Methods

2.1. Participants

Thirty-one healthy older adults (OA; 8 males and 23 females; mean age: 72.3, SD = 5.7; age range: 60–84) and 31 healthy younger adults (YA; 6 males and 25 females; mean age: 24.8, SD = 1.7; age range: 20–33) participated in the experiment. The older adults were volunteers who contacted the lab through flyers or an ad in the newspaper. The OA sample size was comparable to the overall sample size for the OA population administered the SNT in Deouell et al. (2005), on which the current study is based. Older participants were self-reportedly physically healthy with no history of neurological problems (however, they were not asked about specific conditions, such as mild TBI). They were screened for cognitive decline (Mini-mental State Examination (MMSE); Folstein et al., 1975), and tested to verify intact (or corrected) hearing and vision. Participants had a minimum Snellen fraction within clinically normal limits (25/20 for older adults), and a minimum score of 7/8 on the Ishihara color blindness test (see Birch, 1997), reflecting normal color vision. All participants had pure-tone air conduction thresholds within clinically normal limits from 0.25 to 3 kHz in the better ear.

The young adults were undergraduate students who participated for course credit, who self-reported no physical, neurological, psychiatric or visual (including after correction) problems. All participants provided informed consent for a protocol approved by the research ethics committee of Interdisciplinary Center (IDC) Herzliya.

2.2. Stimuli and experimental design

Stimuli were displayed on the background of the blackened screen of a 21.5″ monitor, located ~40 cm from participants' eyes (subtending approximately 38.1° of visual angle). Screen resolution was 640 × 480 pixels. The screen was virtually divided into a Cartesian 7 × 7 grid. The grid itself was not visible. A single target, a bright blue filled square (15 × 15 pixels, subtending approximately 0.08 degrees of visual angle), appeared at a pseudo-randomly distributed latency randomly 500–1800 ms after the beginning of each trial in the center of one of the 49 virtual cells comprising the grid (Fig. 1). The targets appeared against a background of a dynamically varying array of red circle distractors (diameters: 15 pixels, subtending approximately 0.08 degrees of visual angle), which was maintained in the following manner: There were 49 potential distractors, each assigned to one of the cells of the grid. At the start of each trial, each of the distractors could be (randomly) visible ("on") or invisible ("off"). With random intervals of 100–300 ms across the trial, one of the distractors was chosen at random, and its status was toggled (i.e., if it was on, it was turned off, and vice versa). Whenever a distractor was turned on, its location within its cell was chosen randomly. Thus, overall, distractors could appear anywhere on the screen, but the confinement of each distractor to one of the cells provided a relatively uniform distribution on the screen throughout the trial, preventing crowding in one part of the screen. Targets never overlapped a distractor. The overall appearance of the background was that of twinkling, vanishing and appearing red dots. Fig. 1 presents schematic snapshots of five time points along one trial.

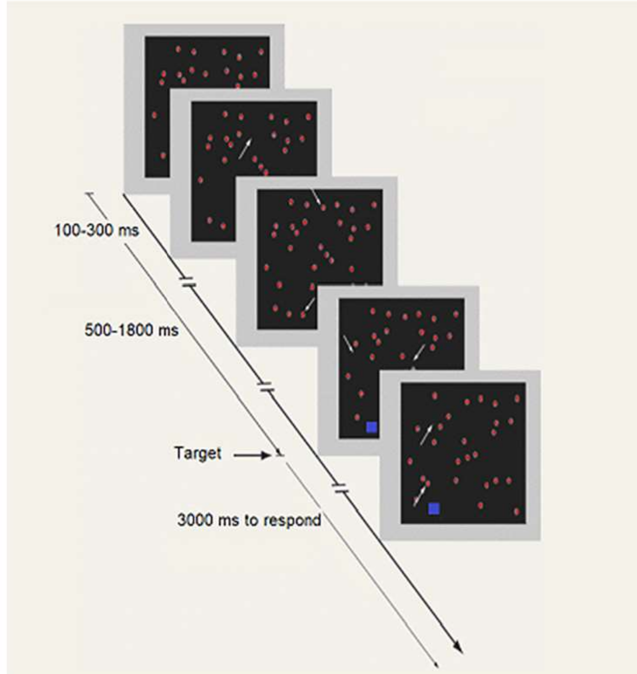

Fig. 1. Schematic portrayal of Starry Night Test displays. The blue square target appears against a dynamically varying "twinkling" background of red circle distractors. Participants are asked to make a speeded response by keypress to the appearance of a target.

The participants were tested in an empty, quiet room with no distractions. A monitor was placed on a table before which participants were comfortably seated, and behind the table was an empty white wall. Participants were instructed to perform the detection task by responding to the blue square as fast as possible. They responded by pressing the letter B on the keyboard with the index finger of their dominant hand. The participants were instructed not to move their finger from the position of the response key at any time. The stimuli remained on the screen until the participant responded or until 3 s had elapsed. Three discernable tones (about 60 dB SPL) indicated whether there had been an accurate target detection, a target missed, or a false alarm (i.e., a premature button press, before target appearance).

2.3. Procedure

Each participant completed a health form and signed a consent form. The experiment took place in a quiet room where participants sat facing the center of a screen. Following instructions, the test consisted of 10 blocks of 49 trials. However, the number of false alarms throughout the first 10 blocks was registered by the experimental program, and that number of make-up trials added to an additional 11th block. The subjects were given a break between each block, and when they were ready to proceed, they pressed the spacebar to continue. Overall, each test lasted approximately 30 min.

2.4. Analyses

Using Stata Release 15 (Stata Data Analysis and Statistical Software, College Station, Texas), we estimated a linear mixed-effects model, in which observations (trials) are nested within subjects. We examined only fixed effects (i.e., we did not include any independent variable in the random part of the model) because we were only interested in taking into account variance that originated at the subject level, rather than allowing the coefficients themselves to vary. The dependent variable was reaction time (RT). Due to the very few errors made (in both age groups) we did not analyze accuracy as a dependent measure.

A multilevel model allowed us to account for the nested structure, separating variance that may originate at the participant level from variance that originates at the task level. Each position on the screen was represented by 4 regressors: the horizontal side of the screen (right/left); the absolute distance from the center on the horizontal axis; the vertical half of the screen (up/down); the absolute distance from the center on the vertical axis. Hence, the independent variables included three categorical variables: age group (young/old), horizontal side (right/left), and vertical half (up/down); and two continuous variables: horizontal distance from screen center and vertical distance from screen center. The variables of (1) distance from center along the horizontal axis, (2) side of screen, (3) distance from center along the vertical axis and (4) top/bottom of screen vary for each observation (trial). The variable of age group varies only at the subject level.

3. Results

The RT analysis was conducted on accurate trials only. Trials with an RT deviating from each subject's mean RT by > 3 absolute deviations (1.4% of all trials) were excluded from further analysis.

Raw RT distributions for YA and OA are portrayed in Fig. 2. As is immediately apparent, overall RTs were faster in YA than in OA. To take these general age-related slowing effects (Salthouse, 2000) into account, statistical analyses were performed on log-transformed RTs. Differences calculated on the logarithmic metric reflect proportional change, enabling clearer examination of whether spatial offsets similarly affect detection among younger and older adults.

In our initial analysis, we examined the relationships between laterality, verticality, distance from center for each dimension, and age. The five-way interaction between these independent variables did not reach significance (i.e., no clear difference was found between the age groups as function of jointly different horizontal and vertical positions [side and distance] on the screen). We therefore proceeded to examine our specific comparisons of interest, comparing older and younger participants' performance across the horizontal and vertical meridians separately. Notably, the results of these analyses were highly similar to the results of models including two factors that were not of a priori theoretical interest in this study: gender and handedness (assessed based on participants' self-report). Those factors did not make significant contributions when modelled, indicating that they had no significant effect on response times (see Appendix for those models). Therefore, in the following we report the results of the analyses conducted without those factors.

3.1. Age effects across the horizontal meridian

Full response time profiles for both age groups across the horizontal meridian are presented in Fig. 3. The three-way interaction between age group (young/old), horizontal side (right/left) and horizontal distance was significant, $z = 2.54$, $p = 0.01$. The analyses in this model revealed several significant effects: an age group main effect ($z = -5.28$, $p < 0.0001$), indicating that older participants had longer RTs compared with younger participants; a horizontal distance effect ($z = 22.62$, $p < 0.0001$), indicating longer RTs for targets of greater horizontal distance from the center; a two-way interaction between age group and horizontal distance ($z = -7.31$, $p < 0.0001$), indicating that the horizontal distance from the center had greater impact on older compared to younger participants; and a two-way interaction between horizontal side and horizontal distance ($z = -1.96$, $p = 0.05$), indicating that the horizontal distance from the center had greater impact on the right side compared to the left side of presentation. Interestingly, there was no main effect of horizontal side of presentation ($z = 0.58$, $p = 0.56$) and a marginal two-way interaction between age group and horizontal side of presentation ($z = -1.74$, $p = 0.08$). A follow-up analysis of the 3-way interaction revealed that the two-way interaction between horizontal side and horizontal distance was significant for older adults, ($z = -1.96$, $p = 0.05$) but not for younger adults ($z = 1.63$, $p = 0.10$). Thus, the asymmetric influence of distance from the center – RTs increasing with eccentricity more on the right than on the left side of presentation – was only evident for older adults.

3.2. Age effects across the vertical meridian

The second comparison focused on the interaction between age group (young/old), vertical half (up/down), and vertical distance from the center of the screen (Fig. 4). The three-way interaction was not significant ($z = 1.21$, $p = 0.26$). The analysis in this model revealed an age group main effect ($z = -5.25$, $p < 0.0001$), indicating that older

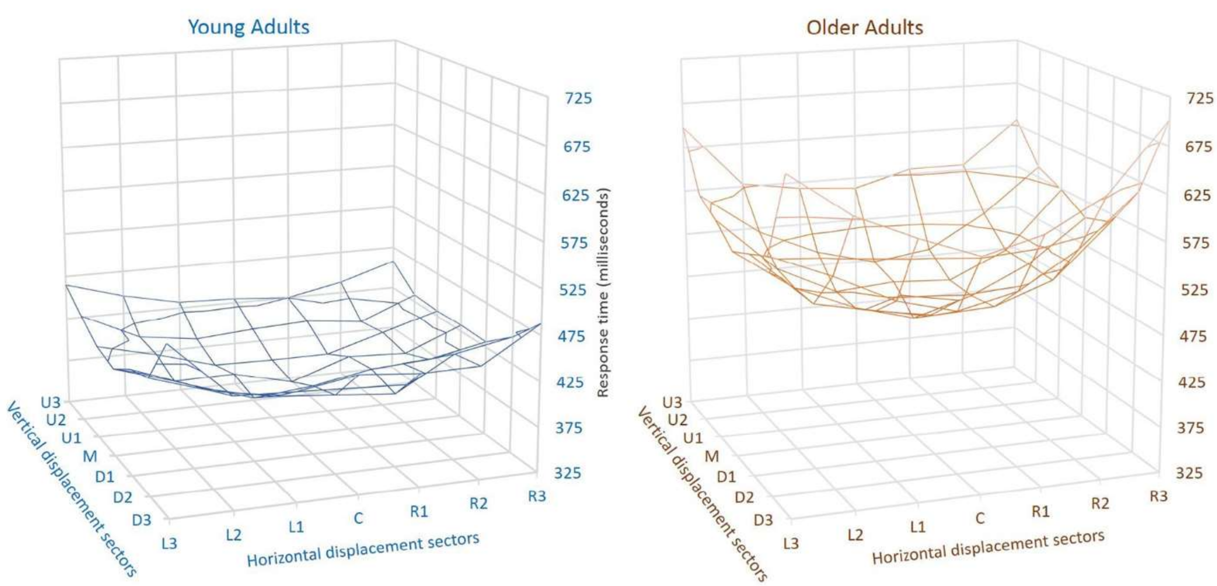

Fig. 2. Synoptic overview of response times for younger and older adult participant groups. Each vertex indicates the mean RT of trials with targets presented in one of 49 sectors (following the 7 × 7 grid used to distribute distractor flicker, as described in the text).

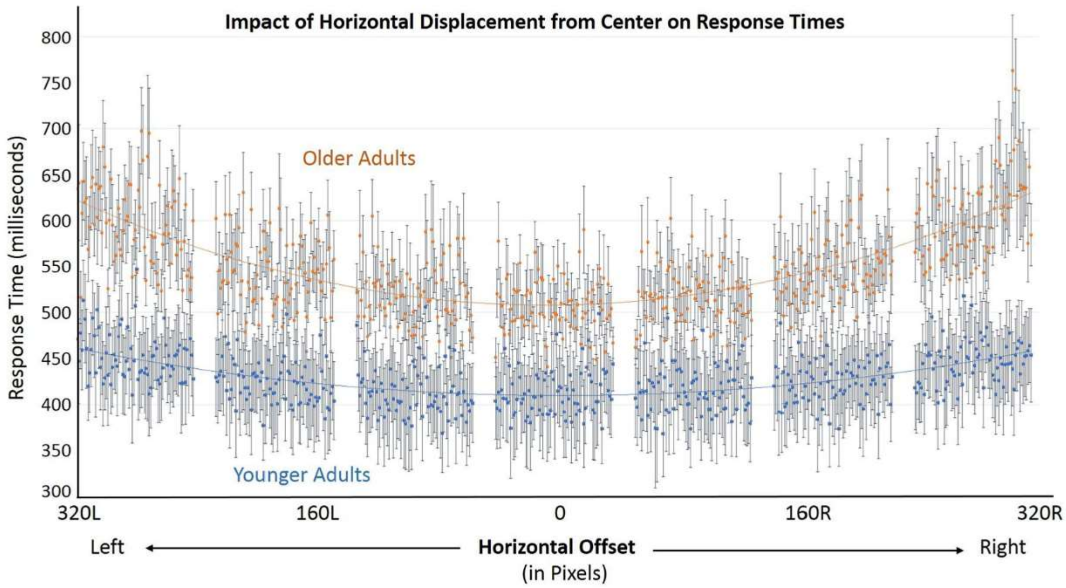

Fig. 3. Distribution of mean response times across horizontal displacements, averaged over all vertical displacements for each horizontal line. Stimuli were presented at 542 of 640 theoretically possible horizontal pixel lines. The mean number of observations across participants at each pixel line was 27.8 (SD = 5.1) for the younger adults and 27.1 (SD = 5.3) for the older adults. Error bars indicate SEM. Second-order polynomial trendlines are fitted to the data points.

participants had longer RTs compared with younger participants; a vertical distance effect ($z = 27.95$, $p < 0.0001$), indicating longer RTs for targets of greater vertical distance from the center; a two-way interaction between age group and vertical distance ($z = -7.84$, $p < 0.0001$), indicating that the vertical distance from the center had greater impact on older compared to younger participants; and a two-way interaction between vertical half and vertical distance ($z = -6.62$, $p < 0.0001$), indicating that the vertical distance from the center had greater impact on the bottom compared to the top side of the screen. As in the horizontal meridian comparisons, there was no vertical half main effect ($z = 0.12$, $p = 0.91$) and no two-way interaction between age group and vertical half of the presentation ($z = 0.08$, $p = 0.94$). In summary, the age groups did not differ in the displacement-mediated upper-visual field RT advantage in target detection.

4. Discussion

In the current study, we assessed age effects on the efficacy of orienting of spatial attention across horizontal and vertical dimensions in a dense visual array. We found evidence for a displacement-mediated left visual field advantage in older adults, even though it was not observed for younger adults. Additionally, we found an equivalent displacement-mediated upper visual field advantage for both age groups.

In this study, we assessed lateralization of visual attention using a detection task in which probes could appear, and distractors were dispersed, in a continuous distribution across a wide swath of the visual field, with no gaze restrictions. Apart from assessing binary lateralization, this task allowed us to measure attentional performance as function of location within each visual field, i.e., the side of the screen and

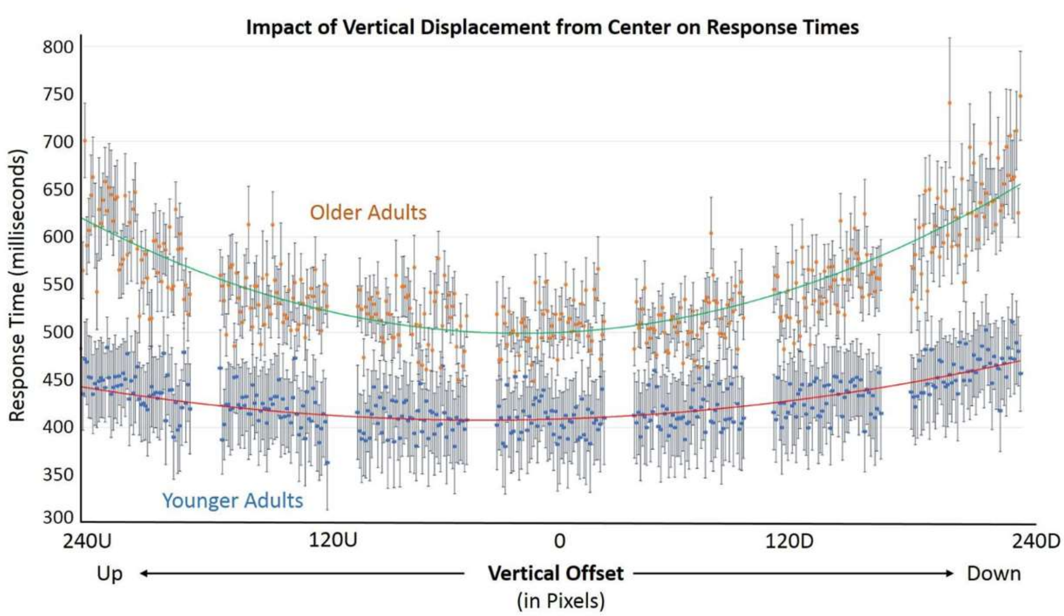

Fig. 4. Distribution of mean response times across vertical displacements, averaged over all horizontal displacements for each vertical line. Stimuli were presented at 382 of 480 theoretically possible vertical pixel lines. The mean number of observations across participants at each pixel line was 39.4 (SD = 6.0) for the younger adults and 38.4 (SD = 6.5) for the older adults. Error bars indicate SEM. Second-order polynomial trendlines are fitted to the data points.

distance from the center, as well as the interaction between them. It further enabled us to collect parallel measurements for the vertical and horizontal meridians of the visual field in the same test. Our findings indicate that older adults' performance was slower when moving from the center towards the right side than towards the left side of the visual field. This interaction between the side of the screen and the distance from the center was evident only for older adults. If all peripheral locations yielded relatively longer response times for older adults, it could be argued that aging-related overall loss of peripheral visual acuity, or the extent of the spatial coverage of selective attention in a single fixation (e.g., Ball et al., 1988; Clay et al., 2005) might be responsible for the findings. However, although the overall stronger effect of eccentricity in the older participants could be the result of some compromise in peripheral visual acuity or oculomotor effects, these factors cannot immediately explain the interaction of the distance factor with both side and altitude.

Notably, the SNT is not the only paradigm that indicate pseudoneglect in a task that requires detection of a stimulus among an array of distractors. Cancellation tasks are typically initiated with a left-side item when tested in right-handed participants. This was interpreted as an indication for a leftward-bias related to pseudoneglect and the hemispheric control of attention (Gigliotta et al., 2017). Leftward bias is also evident in search tasks in which targets on the left side of the display are commonly identified faster than targets on the right side of the display (Bartolomeo et al., 1994; Azouvi et al., 2006).

The older adults' left visual field advantage observed in the SNT task is in line with the lateralization observed when testing representational neglect, in which older adults show similar or even increased lateralization when compared to younger adults (Brooks et al., 2011; McGeorge et al., 2007). However, the SNT paradigm does not involve imagery processes, and effects are expressed in a simple detection task, suggesting that not only representational but also some attentional orienting processes are lateralized. An interesting question raised by these results regards the difference in the processes required for line bisection and the landmark task compared to those required for the SNT paradigm. Specifically, it is clear that general theories of laterality dynamics in aging, such as RH decline (Nagamatsu et al., 2011) and HAROLD (Cabeza, 2002) cannot explain the opposite age-related lateralization changes observed in these paradigms. Furthermore, the findings of stronger left-side representation as expressed in pseudoneglect tendencies in line bisection tasks would seem to predict that there would be a left side RT benefit for young adults, which we did not observe. We should note that this absence of lateralization in the SNT for healthy participants is compatible with our prior findings (Deouell et al., 2005).

Quite likely, line bisection and target detection depend on different cognitive, perceptual, and motor processes. Indeed, in patients with unilateral spatial neglect, factor analysis of a variety of non-computerized tests clearly separated line bisection from target detection (cancellation) tasks, and mapped deficits in these tasks to different neural networks. Specifically, Verdon et al. (2010) argue that line bisection, calling for online representation of an object and its spatial extent, relies strongly on posterior parietal cortex, whereas more exploratory tasks, especially with distractors (like the SNT), rely more on prefrontal cortex (although not exclusively in either case).

Taken together, these explanations for paradigm inconsistencies may provide preliminary insights into findings regarding the age-related visuospatial dimensionality differences found in this study. It is possible that the SNT's specific characteristics and requirements, such as its representation of a broad swath of space, employment of willful exploration, speeded responses, and dealing with interference, interact with age-related changes in executive control (e.g., avoiding distraction, guiding exploration) and lateralization of attention.

4.1. Reading direction and sex effects

An issue of relevance for this study is the extent to which reading direction affects perceptual or attentional asymmetries (Chung et al., 2017). The fact that the current study was conducted with the participation of Israelis whose primary reading direction was right-to-left is of possible relevance to the findings. Since the comparison of horizontal offset effects was conducted between older and younger Israeli adults of comparable educational backgrounds, the reading direction effects should be equivalent across groups. However, we cannot categorically rule out the contribution of differential multi-lingual reading history and habits in the older adult group to the greater left-side RT advantage that they displayed. Furthermore, the right-to-left reading practice of the younger adults might be a factor in their lack of left-side advantage in their performance in the SNT.

Another factor that might conceivably have impacted on the reported findings is the possible influence of the menstrual cycle on functional hemispheric lateralization (Hausmann, 2017). As there were more female than male participants in both younger and older age groups, this sex effect may contribute to the difference between age groups. We therefore conducted additional analyses to rule out an interaction between age group (young/old), horizontal side (right/left)/ vertical side (top/bottom), and sex, both with and without the factor of distance from center of display. These analysis (reported in the Appendix) indicated no significant interactions with sex, suggesting that at least in this sample the age-lateralization effects were independent of participants' sex.

4.2. Vertical asymmetries of attention

We note that the factors listed above may not relate solely to lateralization, as similar asymmetry patterns were found in the vertical direction. Participants slowed their responses as vertical distance from the center increased, an effect that was larger for the lower compared to the upper side of the visual field. This interaction was equivalent for younger and older adults. It is interesting to compare the current findings regarding preserved upper visual field advantage in older adults with the results of an ecological object search paradigm employed in a recent study by Brennan et al. (2017). In that study, children, young adults and older adults opened the door of a room and searched for a target object placed within a cluttered display case. Interestingly, for both the youngest children group (mean age 6 y) and the healthy older adult group (mean age 75 y), search time was longer for targets placed in the right visual field. In contrast, longer search times were found for the upper visual field than for the lower field only for the older adults. For healthy young adults (mean age 22 y) there were no target detection time differences as a function of either horizontal or vertical dimensions. Brennan and colleagues note that in their ecological task that involved walking and opening a door, the lower visual field advantage they observed among older adults might be a function of stooped posture or the need to look more closely where one is walking. Given that our task did not require those activities, our results might be more directly reflective of core attentional processes. It is also possible that the use of bifocal or multifocal glasses for vision correction might have affected the relative ease of detection in lower visual space. However, this would have had a greater impact on older participants, and the effects in this study were not found to be age-dependent.

The results of the SNT may also be compared with findings about age differences in asymmetries between upper and lower visual fields in target detection reported by Feng et al. (2017). As opposed to younger adults who showed advantage for detecting a target among distractors when it appeared in the upper visual field (as in Feng and Spence, 2014), older adults were not found to demonstrate such an advantage. This contrasts with our findings in which older adults exhibited an upper visual field advantage. There are several possible reasons for the discrepancy between the results of the two studies. One is that the SNT employs a denser, more distributed array of probe locations than the task employed by Feng and colleagues. Greater distractor clutter differentially impairs older adults' visual processing in discrimination tasks (McCarley et al., 2012), and the visually rich and busy background of the SNT may have taxed older adults' processing abilities to the point that subtle visual field differences become apparent.

Feng et al. (2017) propose that the upper visual field advantage which they observed in younger adults might result from two possible processes: processing of the target, or better filtering of distractor noise. While the longer RTs for older adults indicate that they are generally less efficient than younger adults in either or both of those processes, in the current study they still exhibit the same left visual field and upper visual field advantages that may be observed in this paradigm or in other paradigms for young adults, even when the distractors are dynamic.

The broader context of the vertical displacement effects herein observed is the range of findings concerning lower vs. upper visual field advantages in general (Christman and Niebauer, 1997; Thomas and Elias, 2010). It has been reported that motion is better processed in the lower visual field, inter alia in judgments of direction discrimination (Amenedo et al., 2007) and segmentation (Lakha and Humphreys, 2005). Lower visual field advantage has also been reported for spatial resolution and contrast sensitivity (e.g., He et al., 1996), and most relevantly for the current study, in tasks of target detection and discrimination (e.g., Abrams et al., 2012). Our finding of an upper visual field advantage in the current task, as well as the report of Feng et al. (2017) noted above, are at variance with those findings. Beyond overall upper visual field advantage, even when examining performance in our task for the central locations on the vertical meridian (column "C" in Fig. 1), RTs for upper peripheral locations were faster than for lower peripheral locations for both older and young adults, unlike the vertical meridian specificity findings of Carrasco et al. (2004). However, it should be noted that most of the studies reporting lower visual field advantage employed discrimination tasks (e.g., Kristjánsson and Sigurdardottir, 2008), whereas the current study used a simple detection task. Similarly, He et al. (1996) found a lower visual field advantage for orientation discrimination in a crowded display and in a conjunction detection task but not for a feature detection task. Earlier studies (summarized by Christman and Niebauer, 1997) had similarly indicated upper visual field advantage in feature search tasks. Rezec and Dobkins (2004) investigated detection, but measured discrimination thresholds for briefly presented stimuli rather than response times to detection. More generally, many of the aspects of vision for which lower visual field advantage have been documented, such as crowding, gap resolution, and Vernier acuity have been attributed to primary visual factors (Greenwood et al., 2017) or to the shape of the visual field (Fortenbaugh et al., 2015), rather than to attentional advantages. Thus, there are subtle differences between the SNT (and the task used by Feng et al., 2017) in which upper visual field advantage was found, and prior findings of lower visual field advantage. The complexity of the pattern of attentional advantages across the visual field is exemplified in the study of Loughnane et al. (2015), who employed a task requiring the detection by young adults of transient targets appearing among a dynamic checkerboard background. They report that RTs were faster to left hemifield targets in the lower visual field, but the opposite trend was observed for targets in the upper field. This interaction was not observed in studies testing line bisection (Drain and Reuter-Lorenz, 1996; Nicholls et al., 2004) and objects mid-point evaluation (Churches et al., 2017). In these studies, the strength of the bias in one dimension was not related to the bias in the orthogonal dimension. As in our study, this independence was also observed within the same stimulus presented on varying horizontal and vertical locations in the visual field (Churches et al., 2017). This inconsistency demonstrates again the influence of the paradigm used on the results pattern. Interestingly, in the case of interaction between horizontal and vertical attentional bias, our results resemble those of line-bisection, and no interaction was observed in our study. The determinants of the conditions under which upper and lower visual fields enjoy attentional advantages require further elaboration, and age effects may differ depending on the task used to assess the effects of vertical displacement on attentional performance.

4.3. Conclusion

The current study demonstrates the sensitivity of age-related changes in attention to the specific paradigm used to assess them. We have essayed some explanations of the discrepancies between our observations of older adults' preserved visual field asymmetries and prior findings suggesting that older adults do not display such asymmetries. Finding the most appropriate balance between ecologically valid tests (such as those employed by Brennan et al., 2017) and more precisely constructed tests with the sensitivity to detect subtle effects (such as the Starry Night Test) is a desideratum for further studies of attention in aging.

Funding

This work was supported by the Chief Scientist Office of the Ministry of Health, Israel, (grant no. 3-9542) to D.A.L.

Appendix A. Regression models with added factors of sex and handedness

Model 1: Outliers removed, log-values, horizontal interaction.

Variable	B	SE	z	p
Fixed effects:				
Distance from center (horizontal axis)	0.0006	0.0000	22.6178	0.0000
Age group: young vs. old	−0.1753	0.0336	−5.2094	0.0000
Side of screen: left vs. right	0.0039	0.0067	0.5846	0.5588
Age × distance (horizontal axis)	−0.0003	0.0000	−7.3146	0.0000
Side × distance (horizontal axis)	−0.0001	0.0000	−1.9604	0.0499
Age × side	−0.0165	0.0095	−1.7414	0.0816
Age × side × sex	−0.0156	0.0237	−0.6585	0.5102
Age × side × distance (horizontal axis)	0.0001	0.0001	2.5383	0.0111
Age × side × distance (horizontal axis) × sex	0.0001	0.0001	1.0934	0.2742
Distance from center (vertical axis)	0.0007	0.0000	38.9447	0.0000
Altitude on screen: top vs. bottom	−0.0327	0.0024	−13.8514	0.0000
Handedness: left vs. right	0.0804	0.0466	1.7265	0.0843
Sex: male vs. female	−0.0026	0.0405	−0.0635	0.9494
Intercept	6.0810	0.0270	225.3842	0.0000
Random effects:				
SD (intercept)	0.1286	0.0120		

SD (residuals)	0.2017	0.0008	
Subjects			62
Tasks			29,281

Contrasts: comparing side × distance by age group

Variable	B	SE	z	p
Older	−0.0007	0.0003	−1.96	0.050
Young	0.0005	0.0004	1.63	0.104

Model 2: Outliers removed, log-values, vertical interaction.

Variable	B	SE	z	p
Fixed effects:				
Distance from center (vertical axis)	0.0010	0.0000	27.9513	0.0000
Age group: young vs. old	−0.1743	0.0337	−5.1763	0.0000
Altitude on screen: top vs. bottom	0.0008	0.0067	0.1183	0.9059
Age × distance (vertical axis)	−0.0004	0.0001	−7.8357	0.0000
Altitude × distance (vertical axis)	−0.0003	0.0000	−6.6162	0.0000
Age × altitude	0.0007	0.0094	0.0768	0.9388
Age × altitude × sex	0.0111	0.0236	0.4684	0.6395
Age × altitude × distance (vertical axis)	0.0001	0.0001	1.1217	0.2620
Age × altitude × sex × distance (vertical axis)	−0.0002	0.0002	−0.9443	0.3450
Distance from center (horizontal axis)	0.0005	0.0000	37.0641	0.0000
Side of screen: left vs. right	−0.0053	0.0024	−2.2367	0.0253
Handedness: left vs. right	0.0803	0.0466	1.7248	0.0846
Sex: male vs. female	−0.0025	0.0405	−0.0606	0.9517
Intercept	6.0623	0.0270	224.6083	0.0000
Random effects:				
SD (intercept)	0.1287	0.0120		
SD (residuals)	0.2013	0.0008		
Subjects			62	
Tasks			29,281	

References

Abrams, J., Nizam, A., Carrasco, M., 2012. Isoeccentric locations are not equivalent: the extent of the vertical meridian asymmetry. Vis. Res. 52 (1), 70–78.

Amenedo, E., Pazo-Alvarez, P., Cadaveira, F., 2007. Vertical asymmetries in pre-attentive detection of changes in motion direction. Int. J. Psychophysiol. 64, 184–189.

Azouvi, P., Bartolomeo, P., Beis, J.M., Perennou, D., Pradat-Diehl, P., Rousseaux, M., 2006. A battery of tests for the quantitative assessment of unilateral neglect. Restor. Neurol. Neurosci. 24 (4–6), 273–285.

Ball, K.K., Beard, B.L., Roenker, D.L., Miller, R.L., Griggs, D.S., 1988. Age and visual search: expanding the useful field of view. J. Opt. Soc. Am. A 5, 2210–2219.

Bartolomeo, P., D'erme, P., Gainotti, G., 1994. The relationship between visuospatial and representational neglect. Neurology 44 (9), 1710–1714.

Benwell, C.S., Thut, G., Grant, A., Harvey, M., 2014. A rightward shift in the visuospatial attention vector with healthy aging. Front. Aging Neurosci. 6, 113.

Birch, J., 1997. Efficiency of the Ishihara test for identifying red-green colour deficiency. Ophthalmic Physiol. Opt. 17, 403–408.

Bonato, M., Deouell, L.Y., 2013. Hemispatial neglect: computer-based testing allows more sensitive quantification of attentional disorders and recovery and might lead to better evaluation of rehabilitation. Front. Hum. Neurosci. 7, 162.

Bowers, D., Heilman, K.M., 1980. Pseudoneglect: effects of hemispace on a tactile line bisection task. Neuropsychologia 18, 491–498.

Brennan, A.A., Bruderer, A.J., Liu-Ambrose, T., Handy, T.C., Enns, J.T., 2017. Lifespan changes in attention revisited: everyday visual search. Can. J. Exp. Psychol. 71 (2), 160–171.

Brooks, J.L., Logie, R.H., McIntosh, R., Della Sala, S., 2011. Representational pseudoneglect in an auditory-driven spatial working memory task. Q. J. Exp. Psychol. 64, 2168–2180.

Brooks, J.L., Della Sala, S., Darling, S., 2014. Representational pseudoneglect: a review. Neuropsychol. Rev. 24, 148–165.

Brown, J.W., Jaffe, J., 1975. Hypothesis on cerebral dominance. Neuropsychologia 13, 107–110.

Bultitude, J., Aimola-Davies, A.M., 2006. Putting attention on the line: investigating the activation-orientation hypothesis of pseudoneglect. Neuropsychologia 44, 1849–1858.

Cabeza, R., 2002. Hemispheric asymmetry reduction in older adults: the HAROLD model. Psychol. Aging 17, 85–100.

Cai, Q., Van der Haegen, L., Brysbaert, M., 2013. Complementary hemispheric specialization for language production and visuospatial attention. In: Proceedings of the National Academy of Sciences of the United States of America. vol. 110. pp. 322–330.

Carrasco, M., Giordano, A.M., McElree, B., 2004. Temporal performance fields: visual and attentional factors. Vis. Res. 44 (12), 1351–1365.

Cavézian, C., Valadao, D., Hurwitz, M., Saoud, M., Danckert, J., 2012. Finding Centre: ocular and fMRI investigations of bisection and landmark task performance. Brain Res. 1437, 89–103.

Chen, P., Goedert, K.M., Murray, E., Kelly, K., Ahmeti, S., Barrett, A.M., 2011. Spatial bias and right hemisphere function: sex-specific changes with aging. J. Int. Neuropsychol. Soc. 17, 455–462.

Christman, S.D., Niebauer, C.L., 1997. The relation between left-right and upper-lower visual field asymmetries (or: What goes up goes right, while what's left lays low). In: Christman, S.D. (Ed.), Cerebral Asymmetries in Sensory and Perceptual Processing. Elsevier Science B.V, Amsterdam, pp. 263–296.

Chung, H.K., Liu, J.Y., Hsiao, J.H., 2017. How does reading direction modulate perceptual asymmetry effects? Q. J. Exp. Psychol. 70 (8), 1559–1574.

Churches, O., Loetscher, T., Thomas, N.A., Nicholls, M.E., 2017. Perceptual biases in the horizontal and vertical dimensions are driven by separate cognitive mechanisms. Q. J. Exp. Psychol. 70, 444–460.

Çiçek, M., Deouell, L.Y., Knight, R.T., 2009. Brain activity during landmark and line bisection tasks. Front. Hum. Neurosci. 3, 7.

Clay, O.J., Wadley, V.G., Edwards, J.D., Roth, D.L., Roenker, D.L., Ball, K.K., 2005. Cumulative meta-analysis of the relationship between useful field of view and driving performance in older adults: current and future implications. Optom. Vis. Sci. 82 (8), 724–731.

Coolican, J., Eskes, G.A., McMullen, P.A., Lecky, E., 2008. Perceptual biases in processing facial identity and emotion. Brain Cogn. 66 (2), 176–187.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3 (3), 201–215.

Corbetta, M., Patel, G., Shulman, G.L., 2008. The reorienting system of the human brain: from environment to theory of mind. Neuron 58 (3), 306–324.

De Agostini, M., Curt, F., Tzortzis, C., Dellatolas, G., 1999. Comparing left and right hand in line bisection at different ages. Dev. Neuropsychol. 15 (3), 379–394.

Deouell, L.Y., Sacher, Y., Soroker, N., 2005. Assessment of spatial attention after brain damage with a dynamic reaction time test. J. Int. Neuropsychol. Soc. 11 (6), 697–707.

D'Erme, P., Robertson, I., Bartolomeo, P., Daniele, A., Gainotti, G., 1992. Early rightwards orienting of attention on simple reaction time performance in patients with left-sided neglect. Neuropsychologia 30, 989–1000.

Drain, M., Reuter-Lorenz, P.A., 1996. Vertical orienting control: evidence for attentional bias and" neglect" in the intact brain. J. Exp. Psychol. Gen. 125, 139–158.

Driver, J., Mattingley, J.B., 1998. Parietal neglect and visual awareness. Nat. Neurosci. 1, 17–22.

Erel, H., Levy, D.A., 2016. Orienting of visual attention in aging. Neurosci. Biobehav. Rev.

69, 357–380.
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 Cogn. 52, 353–363.
Feng, J., Spence, I., 2014. Upper visual field advantage in localizing a target among distractors. i-Perception 5, 97–100.
Feng, J., Craik, F.I., Levine, B., Moreno, S., Naglie, G., Choi, H., 2017. Differential age-related changes in localizing a target among distractors across an extended visual field. Eur. J. Ageing 14 (2), 167–177.
Fink, G.R., Marshall, J.C., Shah, N.J., Weiss, P.H., Halligan, P.W., Grosse- Ruyken, M., et al., 2000a. Line bisection judgments implicate right parietal cortex and cerebellum as assessed by fMRI. Neurology 54, 1324–1331.
Fink, G.R., Marshall, J.C., Weiss, P.H., Shah, N.J., Toni, I., Halligan, P.W., Zilles, K., 2000b. 'Where' depends on 'what': a differential functional anatomy for position discrimination in one-versus two-dimensions. Neuropsychologia 38 (13), 1741–1748.
Fink, G.R., Marshall, J.C., Weiss, P.H., Zilles, K., 2001. The neural basis of vertical and horizontal line bisection judgments: an fMRI study of normal volunteers. Neuroimage 14, S59–S67.
Folk, C.L., Hoyer, W.J., 1992. Aging and shifts of visual spatial attention. Psychol. Aging 7, 453–465.
Folstein, M.F., Folstein, S.E., McHugh, P.R., 1975. "Mini-mental state". A practical method for grading the cognitive state of patients for the clinician. J. Psychiatr. Res. 12, 189–198.
Fortenbaugh, F.C., Silver, M.A., Robertson, L.C., 2015. Individual differences in visual field shape modulate the effects of attention on the lower visual field advantage in crowding. J. Vis. 15 (2), 19.
Foxe, J.J., McCourt, M.E., Javitt, D.C., 2003. Right hemisphere control of visuospatial attention: line-bisection judgments evaluated with high-density electrical mapping and source analysis. Neuroimage 19 (3), 710–726.
Fujii, T., Fukatsu, R., Yamadori, A., Kimura, I., 1995. Effect of age on the line bisection test. J. Clin. Exp. Neuropsychol. 17, 941–944.
Fukatsu, R., Fujii, T., Kimura, I., Saso, S.I., Kogure, K., 1990. Effects of hand and spatial conditions on visual line bisection. Tohoku J. Exp. Med. 161 (4), 329–333.
Ghacibeh, G.A., Shenker, J.I., Winter, K.H., Triggs, W.J., Heilman, K.M., 2007. Dissociation of neglect subtypes with transcranial magnetic stimulation. Neurology 69 (11), 1122–1127.
Gigliotta, O., Malkinson, T.S., Miglino, O., Bartolomeo, P., 2017. Artificial Pseudoneglect: Connectional Constraints Leading to the Emergence of Spatial Bias in Neurorobots. bioRxiv, pp. 129171.
Goldstein, G., Shelly, C., 1981. Does the right hemisphere age more rapidly than the left? J. Clin. Exp. Neuropsychol. 3, 65–78.
Greenwood, J.A., Szinte, M., Sayim, B., Cavanagh, P., 2017. Variations in crowding, saccadic precision, and spatial localization reveal the shared topology of spatial vision. Proc. Natl. Acad. Sci. 201615504.
Halligan, P.W., Fink, G.R., Marshall, J.C., Vallar, G., 2003. Spatial cognition: evidence from visual neglect. Trends Cogn. Sci. 7, 125–133.
Harvey, M., Rossit, S., 2012. Visuospatial neglect in action. Neuropsychologia 50, 1018–1028.
Harvey, M., Milner, A.D., Roberts, R.C., 1995. Differential effects of line length on bisection judgements in hemispatial neglect. Cortex 31 (4), 711–722.
Hatin, B., Tottenham, L.S., Oriet, C., 2012. The relationship between collisions and pseudoneglect: is it right? Cortex 48, 997–1008.
Hausmann, M., 2017. Why sex hormones matter for neuroscience: a very short review on sex, sex hormones, and functional brain asymmetries. J. Neurosci. Res. 95 (1–2), 40–49. https://doi.org/10.1002/jnr.23857.
He, S., Cavanagh, P., Intrilligator, J., 1996. Attentional resolution and the locus of visual awareness. Nature 383, 334–337.
Jewell, G., McCourt, M.E., 2000. Pseudoneglect: a review and meta-analysis of performance factors in line bisection tasks. Neuropsychologia 38, 93–110.
Karnath, H.O., 2015. Spatial attention systems in spatial neglect. Neuropsychologia 75, 61–73.
Kristjánsson, A., Sigurdardottir, H.M., 2008. On the benefits of transient attention across the visual field. Perception 37 (5), 747–764.
Lakha, L., Humphreys, G., 2005. Lower visual field advantage for motion segmentation during high competition for selection. Spat. Vis. 18, 447–460.
Li, Z., Moore, A.B., Tyner, C., Hu, X., 2009. Asymmetric connectivity reduction and its relationship to "HAROLD" in aging brain. Brain Res. 1295, 149–158.
Loughnane, G.M., Shanley, J.P., Lalor, E.C., O'Connell, R.G., 2015. Behavioral and electrophysiological evidence of opposing lateral visuospatial asymmetries in the upper and lower visual fields. Cortex 63, 220–231.
Lux, S., Marshall, J.C., Thimm, M., Fink, G.R., 2008. Differential processing of hierarchical visual stimuli in young and older healthy adults: implications for pathology. Cortex 44, 21–28.
McCarley, J.S., Yamani, Y., Kramer, A.F., Mounts, J.R., 2012. Age, clutter, and competitive selection. Psychol. Aging 27 (3), 616–626.
McGeorge, P., Beschin, N., Colnaghi, A., Rusconi, M.L., Della Sala, S., 2007. A lateralized bias in mental imagery: evidence for representational pseudoneglect. Neurosci. Lett. 421, 259–263.
McGregor, K.M., Craggs, J.G., Benjamin, M.L., Crosson, B., White, K.D., 2009. Age-related changes in motor control during unimanual movements. Brain Imaging Behav. 3 (4), 317–331.
Milner, A.D., Harvey, M., 1995. Distortion of size perception in visuospatial neglect. Curr. Biol. 5, 85–89.
Milner, A.D., Brechmann, M., Pagliarini, L., 1992. To halve and to halve not: an analysis of line bisection judgements in normal subjects. Neuropsychologia 30, 515–526.
Milner, A.D., Harvey, M., Roberts, R.C., Forster, S.V., 1993. Line bisection errors in visual neglect: misguided action or size distortion? Neuropsychologia 31, 39–49.
Nagamatsu, L.S., Carolan, P., Liu-Ambrose, T.Y., Handy, T.C., 2011. Age-related changes in the attentional control of visual cortex: a selective problem in the left visual hemifield. Neuropsychologia 49, 1670–1678.
Nicholls, M.E., Hughes, G., Mattingley, J.B., Bradshaw, J.L., 2004. Are object- and space-based attentional biases both important to free-viewing perceptual asymmetries? Exp. Brain Res. 154 (4), 513–520.
Petersen, S.E., Posner, M.I., 2012. The attention system of the human brain: 20 years after. Annu. Rev. Neurosci. 35, 73–89.
Przybyla, A., Haaland, K.Y., Bagesteiro, L.B., Sainburg, R.L., 2011. Motor asymmetry reduction in older adults. Neurosci. Lett. 489 (2), 99–104.
Reuter-Lorenz, P.A., Cappell, K.A., 2008. Neurocognitive aging and the compensation hypothesis. Curr. Dir. Psychol. Sci. 17, 177–182.
Reuter-Lorenz, P.A., Kinsbourne, M., Moscovitch, M., 1990. Hemispheric control of spatial attention. Brain Cogn. 12, 240–266.
Rezec, A.A., Dobkins, K.R., 2004. Attentional weighting: a possible account of visual field asymmetries in visual search? Spat. Vis. 17, 269–293.
Salthouse, T.A., 2000. Aging and measures of processing speed. Biol. Psychol. 54, 35–54.
Schmitz, R., Peigneux, P., 2011. Age-related changes in visual pseudoneglect. Brain Cogn. 76, 382–389.
Sekuler, A.B., Bennett, P.J., Mamelak, M., 2000. Effects of aging on the useful field of view. Exp. Aging Res. 26 (2), 103–120.
Stam, C.J., Bakker, M., 1990. The prevalence of neglect: superiority of neuropsychological over clinical methods of estimation. Clin. Neurol. Neurosurg. 92, 229–235.
Thiebaut de Schotten, M., Urbanski, M., Duffau, H., Volle, E., Levy, R., Dubois, B., et al., 2005. Direct evidence for a parietal-frontal pathway subserving spatial awareness in humans. Science 309, 2226–2228.
Thiebaut de Schotten, M.T., Dell'acqua, F., Forkel, S.J., Simmons, A., Vergani, F., Murphy, D.G.M., Catani, M., 2011. A lateralized brain network for visuospatial attention. Nat. Neurosci. 14, 1245–1246.
Thomas, N.A., Elias, L.J., 2010. Do perceptual asymmetries differ in peripersonal and extrapersonal space? J. Int. Neuropsychol. Soc. 16, 210–214.
Turnbull, O.H., McGeorge, P., 1998. Lateral bumping: a normal-subject analog to the behaviour of patients with hemispatial neglect? Brain Cogn. 37 (1), 31–33.
Vallar, G., 1998. Spatial hemineglect in humans. Trends Cogn. Sci. 2, 87–97.
Vallesi, A., McIntosh, A.R., Kovacevic, N., Chan, S.C.C., Stuss, D.T., 2010. Age effects on the asymmetry of the motor system: evidence from cortical oscillatory activity. Biol. Psychol. 85 (2), 213–218.
Varnava, A., Halligan, P.W., 2007. Influence of age and sex on line bisection: a study of normal performance with implications for visuospatial neglect. Aging Neuropsychol. Cognit. 14, 571–585.
Verdon, V., Schwartz, S., Lovblad, K.-O., Hauert, C.-A., Vuilleumier, P., 2010. Neuroanatomy of hemispatial neglect and its functional components: a study using voxel-based lesion-symptom mapping. Brain 133 (3), 880–894.
Waberski, T.D., Gobbelé, R., Lamberty, K., Buchner, H., Marshall, J.C., Fink, G.R., 2008. Timing of visuo-spatial information processing: electrical source imaging related to line bisection judgements. Neuropsychologia 46, 1201–1210.
Wolfe, J.M., 2007. Guided search 4.0. . In In: Gray, W.D. (Ed.), *Integrated models of cognitive systems* (Cognitive Models and Architectures). Oxford University Press, Oxford, pp. 99–120.