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Age-related reduction of hemispheric lateralisation for spatial attention: An EEG study

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ABSTRACT

A group-level visuospatial attention bias towards the left side of space (*pseudoneglect*) is consistently observed in young adults, which is likely to be a consequence of right parieto-occipital dominance for spatial attention. Conversely, healthy older adults demonstrate a rightward shift of this behavioural bias, hinting that an age-related reduction of lateralised neural activity may occur within visuospatial attention networks. We compared young (aged 18–25) and older (aged 60–80) adults on a computerised line bisection (*landmark*) task whilst recording event-related potentials (ERPs). Full-scalp cluster mass permutation tests identified a larger right parieto-occipital response for long lines compared to short in young adults (confirming Benwell et al., 2014a) which was not present in the older group. To specifically investigate age-related differences in hemispheric lateralisation, cluster mass permutation tests were then performed on a *lateralised* EEG dataset (RH-LH electrodes). A period of right lateralisation was identified in response to long lines in young adults, which was not present for short lines. No lateralised clusters were present for either long or short lines in older adults. Additionally, a reduced P300 component amplitude was observed for older adults relative to young. We therefore report here, for the first time, an age-related and stimulus-driven reduction of right hemispheric control of spatial attention in older adults. Future studies will need to determine whether this is representative of the normal aging process or an early indicator of neurodegeneration.

Introduction

Young adults tend to systematically overestimate the size, luminance, number and spatial frequency of objects within the left side of space relative to the right ('pseudoneglect') (Bowers and Heilman, 1980). This leftward attention bias likely arises as a result of a *right* posterior-parietal dominance for visuospatial processing in young adults which results in a net asymmetry of activity between the right (RH) and left (LH) parietal cortices when performing spatial judgements. Specifically, the right dorsal fronto-parietal network is implicated in tasks requiring line midpoint judgements, such as the line bisection and landmark tasks (a computerised version of the line bisection task involving pre-bisected horizontal lines) (Benwell et al., 2014a, 2014b; Çiçek et al., 2009; Fink et al., 2000a; 2000b; 2001; 2002; Foxe et al., 2003; Galati et al., 2000; Longo et al., 2015; Weiss et al., 2000; 2003).

In terms of the timing of the right-lateralisation of activity within the parieto-occipital cortex during landmark task performance, a distinct time course has been reported using electroencephalography (EEG) (the 'line bisection effect': Foxe et al., 2003), which broadly consists of three phases after stimulus onset: Compared to a control landmark task that required a non-spatial decision, Foxe et al. (2003) found a net right-lateralized negativity relative to the control during an early phase (~165–190 ms) involving the right lateral occipital cortex and the right temporo-parietal occipital junction (TPJ). The second phase (~190–240 ms) also comprised this right parietal cortex negativity, with additional involvement of the superior right central parietal cortex. Finally, the peak landmark task effect was observed at ~310 ms where the right central parietal negativity dominated. Using a similar task, and comparing posterior regions of interest (ROI) across the two cerebral hemispheres, Longo et al. (2015) found no strong right-lateralisation differences (landmark vs control) within an early time window (170–190 ms) but found a significant effect of hemisphere in the 190–240 ms window, with a larger negativity in the right vs left parieto-occipital electrodes. Finally, we have also recently reported an increased right central parietal negativity for the landmark task vs a control in a window of 231–500 ms, with a peak bisection effect at 280 ms (Benwell et al., 2014a). Therefore, when compared to a non-

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spatial control task, line bisection performance consistently elicits a larger negativity in the right parieto-occipital region, which probably reflects the engagement of lateralised attention networks localised to the right hemisphere for this task.

In addition to the 'line bisection effect', we have shown a further right parieto-occipital activation that is stimulus-dependent (the 'line length effect'). In Benwell et al. (2014a) we compared long vs short landmark lines in young adults, and found that the two line lengths were maximally differentiated in the right TPJ (electrode PO4) at 140 ms post-stimulus, regardless of the task being performed (i.e. landmark versus control). Specifically, there was a larger right-lateralised negativity for long vs short lines in the right parieto-occipital cortex that corresponded to the P1-N1 component window and this was associated with a group-level leftward behavioural bias (pseudoneglect) for long but not short lines (Benwell et al., 2014a, 2014b). These distinct behavioural and neuroimaging differences between line lengths reveal a behaviourally relevant hemispheric asymmetry in young people in terms of right hemispheric involvement. Therefore, any behavioural changes observed in older adults, for either line length, are likely to also represent hemispheric asymmetry changes in this group.

In older adults, evidence for changes in spatial attention processing as assessed by the landmark/ line bisection task has been provided by many studies reporting a reduction (and sometimes directional reversal) in pseudoneglect for this group relative to young participants (Learmonth et al., 2015a; Benwell et al., 2014b; Failla et al., 2003; Fujii et al., 1995; Fukatsu et al., 1990; Nagamatsu et al., 2009; 2011; 2013; Schmitz and Peigneux, 2011; Stam and Bakker, 1990, but see Brooks et al., 2016, for maintained pseudoneglect into older age). This intriguing finding might be indicative of a reduction of right-hemisphere dominance for spatial attention with advancing age, or perhaps even a shift towards an asymmetry favouring the *left* hemisphere.

This age-related rightward shift in spatial attention is consistent with a number of models that describe a widespread reorganisation of brain function in later life. The principal differences between these models lie in the extent to which the left and right hemispheres are considered to increase and decrease in engagement throughout the lifespan. Although none of these models specifically describe the changes that occur within the spatial attention domain (indeed, many were developed from observations regarding episodic and working memory (Bäckman et al., 1997; Cabeza et al., 1997, 2004; Grady et al., 2002; Madden et al., 1999; Morcom et al., 2003; Reuter-Lorenz et al., 2000)), we can extrapolate from these models to predict both the EEG and behavioural outcomes that might be expected in the present experiment. Firstly, the "right hemi-aging model" claims that cognitive functions which draw upon right hemisphere resources deteriorate faster than those confined to the left hemisphere (e.g. language in the left hemisphere, attention in the right) (Brown and Jaffe, 1975; Dolcos et al., 2002; Goldstein and Shelly, 1981). Following this reasoning, we would predict to observe distinct differences in EEG signals in older adults compared to young, showing either a reduced hemispheric asymmetry or indeed reversed (i.e. stronger left vs right hemispheric activation), depending on the extent of this right hemisphere deterioration. If these cortical changes then go on to influence behavioural bias, then we would expect to observe either an elimination of spatial bias or a distinct rightward bias in the right hemi-aging model scenario. The related model of "hemispheric asymmetry reduction in older adults" (HAROLD model) (Cabeza, 2002; Cabeza et al., 1997; 2002; 2004; Huang et al., 2012; Reuter Lorenz et al., 2000) proposes that cognitive functions that are highly lateralised to one cerebral hemisphere in young adults become generally less lateralised in older adults. This bilateral recruitment may be a compensatory mechanism to support maintained cognitive performance in the elderly, given that PET and fMRI studies have shown a more pronounced bilateral recruitment in difficult tasks (Cabeza, 2002; Cabeza et al., 1997, 2002; Huang et al., 2012; Reuter-Lorenz et al., 2000). This model would predict that older adults exhibit an eliminated hemispheric asymmetry compared to young adults as a result of reduced lateralisation, but would not allow for a shift entirely into rightward space as per the right hemi-aging model. In this scenario, we would expect to observe no lateralised EEG and behavioural bias for the older group. Finally, the "compensation-related utilization of neural circuits hypothesis" (CRUNCH model) (Reuter-Lorenz and Cappell, 2008) proposes that older adults recruit "different" neural pathways (i.e. pathways that are not used by young adults) to undertake difficult tasks as their neural resources diminish, although these additional resources are not necessarily drawn from the contralateral cerebral hemisphere. It has been proposed as a more general, but related, version of the HAROLD model (Berlingeri et al., 2013) in which the age-related changes that occur do not necessarily lead to a reduction of hemispheric asymmetry. In this scenario our EEG results should show a clear increase of activity in older adults compared to young, but these changes could occur at any location within the cortex. However, given that this model is not specific about the location of such changes, it does not allow for predictions in terms of behavioural bias.

Few EEG/MEG studies have specifically investigated age-related changes in spatial attention, instead focusing on mapping attention in healthy young adults and in certain clinical groups (e.g. hemispatial neglect: Di Russo et al., 2008, 2013; Rastelli et al., 2013; Sasaki et al., 2013; Spinelli et al., 1994). Nevertheless, the EEG studies that have been performed in older adults are broadly consistent with the corpus of behavioural evidence showing a reduced preference for left hemispace, and provide an intriguing insight into the aging spatial attention network. In a cued target detection task, Nagamatsu et al. (2011) found that seniors have a specific deficit in the top-down allocation of attention to the left side of space as indexed by the attention directing anterior negativity (ADAN) component (375–430 ms post-cue). Young adults exhibited a larger ADAN amplitude for contralateral targets relative to ipsilateral, which was observed for targets presented in both the left and right visual fields. Seniors, however, only demonstrated this contralateral advantage for targets presented in the right visual field. Targets that were presented in the left hemifield only showed a very minor amplitude increase in the right vs left hemisphere, indicating a possible age-related decline in right-hemisphere function. Importantly, left visual field deficits were also associated with an increased risk of falls (Nagamatsu et al., 2009) indicating that these neural changes may have important consequences for maintained functional performance as we age.

Overall, the consistent reports of right-lateralised EEG activity for the landmark task in young adults, combined with distinct behavioural changes observed for this task in older adults, make this an ideal paradigm in which to formally investigate changes in hemispheric asymmetry in healthy aging. Here were aimed to assess, for the first time, whether an age-related functional reorganisation of neural activity can be observed using EEG during a spatial judgement task. We expected older adults to exhibit a rightward behavioural shift on the landmark task relative to young adults, and we investigated whether this shift would be accompanied by a reduction of right-hemispheric lateralisation during landmark task processing (as measured by event related potentials; ERPs). Secondly, we predicted that the effect of age would interact with line length, anticipating more right vs left hemisphere asymmetry for long lines in young adults relative to short lines (in line with Benwell et al., 2014a) but expected this difference to be less pronounced or absent in the older age group.

Method

Participants

Twenty young adults (10 females, mean age=20.8, SD=2.17, range=18–25) and 20 older adults (10 females, mean age=68.75 , SD=6.29, range=60–80) were recruited. Based on task performance, 2

participants (1 young, 1 older) were excluded after application of the median absolute deviation method of outlier detection for curve width and point of subjective equality (PSE) values, leading to 19 participants per group. Both young and older participants were right-handed and reported normal or corrected-to-normal vision. A total of 6/19 young adults wore glasses or contact lenses (2 for distance, 2 for reading, 2 for both), none reported visual pathology (e.g. glaucoma or cataracts) or neurological history (e.g. stroke). In the older group, 16/19 wore glasses or contacts (2 for distance, 8 for reading and 6 for both). Five reported a previous cataract or glaucoma that had been fully treated, and none reported any neurological problems. The study was approved by the University of Glasgow College of Science and Engineering ethics committee and written, informed consent was obtained from each participant.

Procedure

Participants were seated at a fixed distance of 80cm in front of a computer screen in an electrostatically shielded room with their midsagittal plane aligned with the screen. A short (3 minute) computerised visual screening assessment was administered at the beginning of the session (see *Visual acuity screening*) to ensure adequate vision, before proceeding with EEG preparation and the experiment. Two experiments were then performed in a counterbalanced order between participants. Each experiment lasted about 30 min. One of these experiments will form the subject of a separate publication and is therefore not reported here.

Visual acuity screening

Small black 10×10-pixel squares were briefly presented individually at one of 36 locations (extending to 10.0° above and below fixation, and 12.13° to the left and right) for 150ms. A total of 72 trials (36 locations ×2) were randomly interspersed with an additional 24 'catch' trials, where the screen remained blank, to measure adherence with the task. Participants were requested to press the space bar if a stimulus had been detected and to withhold their response when undetected. None of the participants (all having reported normal or corrected-to-normal vision during recruitment) had to be excluded based on performance in this visual screening test.

Landmark task

We asked participants to perform the landmark task, adapted from McCourt (2001) and Benwell et al. (2014a), while EEG was recorded from 64 channels. The landmark task (also called 'tachistoscopic line bisection' (McCourt and Jewell (1999)) is a two alternative forced-choice version of the line bisection task. As in Benwell et al. (2014a), horizontal lines of 100% Michelson contrast were presented on a uniform grey background (luminance=179, hue=160). Half of the lines were shaded black in the upper left/lower right quadrants and half shaded black in the lower left/upper right (see Fig. 1). Two line lengths were presented: long lines measured 800×14 pixels (14.88°×0.27° visual angle) and short lines 80×14 pixels (1.48°×0.27°). Each line was transected vertically at the veridical centre of the screen (i.e. at the same position as the fixation cross). The length of the left and right sections varied across trials, with 13 different stimuli for each line length (6 where the left side was longer than the right, 6 where the right was longer than the left and 1 where both sides were of equal length). For the long lines, the most asymmetrical (left vs right side) stimuli differed by 120 pixels and the asymmetry reduced in 20-pixel increments until the two sides were of equal length. For the short lines the largest asymmetry was 12 pixels with a reduction of 2 pixels per stimulus.

Each landmark block consisted of 156 trials (13 long lines and 13 short lines presented 6 times each in a random order). A centrally located fixation cross appeared for 1500ms, followed by the landmark stimulus for 150 ms. The fixation cross then reappeared until a response was given. For each trial (including those with sides of equal length), participants were instructed to indicate, using their right index (left) or middle finger (right), which side of the line appeared shorter. To control for potential response bias (Toraldo et al., 2004), half of the participants were instructed to indicate the *longer* side, and half indicated the *shorter* side. Five blocks were presented in total, each lasting approximately 6 min.

Data recording and analyses

Landmark task

Stimuli were presented and manual responses recorded using E-Prime 2.0 (Psychology Software Tools Inc., Pittsburgh, PA) with a Dell Precision T3400 PC and 19.5" Sun Microsystems CRT monitor (with 1280×1024 pixel resolution and 100 Hz refresh rate). The percentage of trials where the left side was perceived as shorter was calculated for each of the 13 stimuli. Psychometric functions were fitted for each individual per line length per block using a cumulative logistic function:

$$f\left(\mu,\ x,\ s\right) = 1 \Big/ \left(1 + \exp\left(\frac{x-\mu}{s}\right)\right)$$

where μ is the point of subjective equality (PSE), i.e. the position along the horizontal landmark line that corresponds to where the individual perceives both halves to be of equal length, x represents the tested bisection mark position and s is the psychometric curve width. The PSE provides a measure of the subjective midpoint of the landmark lines for each block and as such, is used to quantify spatial attention bias, whereas the curve width estimates the precision of these judgements. A narrow (small) curve width value indicates high precision and a wide (large) curve width value low precision. The point of subjective equality (PSE) and curve widths were transformed to represent a percentage of the total line length, rather than an absolute number of pixels.

EEG acquisition and preprocessing

Data were recorded using a BrainVision EEG system (MR plus) with a 64-channel BrainCap array (62 scalp electrodes and 2 ocular electrodes, placed on the outer canthi to detect blinks and lateral eye movements). Sampling rate was set to 1000 Hz. Preprocessing and subsequent analyses were conducted in Matlab using the EEGLAB toolbox (Delorme and Makeig, 2004) and customised scripts. Raw EEG signals were de-trended, segmented into epochs of 1500 ms duration (500 ms pre-stimulus to 1000 ms post-stimulus onset) and then re-

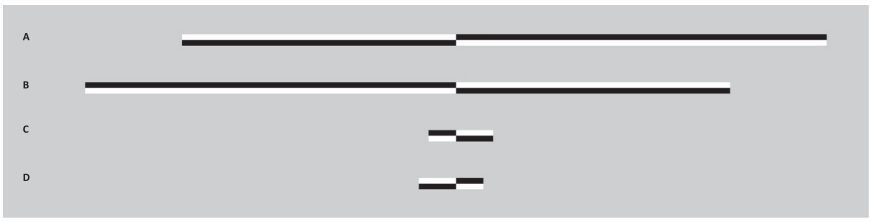

Fig. 1. Example of the landmark task stimuli. Stimulus A: Long line where the left side is shorter by 120 pixels relative to the right. Stimulus B: Long line where the right is shorter by 120 pixels. Stimulus C: Short line where the left is shorter by 12 pixels. Stimulus D: Short line where the right is shorter by 12 pixels.

referenced to an average reference. A finite impulse response filter was applied between 0.3 and 40 Hz. Epochs containing extreme artifacts were identified and removed by visual inspection and channels containing prolonged periods of extreme artefact were rejected. Further artifact elimination was performed using independent component analysis (to remove blink and eye movement artifacts) and previously rejected channels were interpolated using a spherical spline method. The resultant signal was then re-epoched to a 700 ms window (-300 to 400 ms) and finally, baseline corrected. The following mean number of trials per person were included in the statistical analyses: Young adults: Long lines $\bar{x}$=368.74 trials (range=322–387), short $\bar{x}$=370.89 (325–389). Older adults: Long $\bar{x}$=365.68 (285–385), short $\bar{x}$=369 (314–388). The two age groups did not differ in the number of trials included [Age: F(1,36)=0.17, p=0.69; Age×Length F(1,36)=6.37, p=0.59] but slightly more trials were included for short relative to long lines [Length: F(1,36)=6.71, p=0.014].

EEG statistical analyses

EEG data were statistically analysed in the time domain using the Mass Univariate ERP toolbox for Matlab (Groppe et al., 2011a, 2011b). Data were averaged at the single-subject level across all trials of interest, to produce 62 channel waveforms per participant in the full-scalp analysis, and 27 waveforms in the lateralised electrode analysis. Two-tailed cluster mass permutation tests were performed to identify clusters of electrodes and time points which differed between the conditions being compared (Bullmore et al, 1999; Maris and Oostenveld, 2007). Two approaches were used to assess different aspects of our hypotheses:

1. ***Full-scalp cluster analysis****:* i) We first aimed to test the main effect of line length (long vs short lines) across the whole head using repeated-measures t-tests for each of the 62 scalp electrodes and time points in the 0–400 ms window. Neighbouring t-scores corresponding to an uncorrected p-value of < 0.01 were formed into clusters according to their temporal and spatial adjacency (separately for negative and positive t-values). Electrodes were defined as spatial neighbours if they were located within approximately 3.7 cm of each other, which resulted in a mean of 3.55 channels per neighbour (min=1, max=4). The sum of all t-scores within each cluster provided a cluster-level t-score (the 'cluster mass'). The same clustering procedure (and cluster mass extraction) was then performed across 20,000 random permutations of the data in order to build a data driven null hypothesis distribution. At least 1000 permutations are recommended to estimate p-values within $\pm 2\%$ at a 5% alpha level, and 5000 permutations for 1% alpha (Manly, 1997; Groppe et al., 2011a). The relative location of each observed *real* cluster mass t-score within the null hypothesis distribution indicates how probable such a score would be if the null hypothesis were true. An alpha level of 5% was adopted for cluster-level statistics. Within-group cluster tests were then repeated separately for ii) Young and iii) Older adults to assess the line length effect as a function of age. iv) The main effect of Age was then investigated using the same methodology, but using independent-samples t-tests for the between-groups comparison (Young vs Older, both line lengths collapsed). Finally, between-groups cluster tests assessed the effect of age as a function of line length (Young vs Older, separately for v) long and vi) short lines).
2. ***Lateralised electrode cluster analysis****:* In addition to the full-scalp analysis, to answer our principal question of whether differences in hemispheric asymmetry exist between age groups, cluster permutation tests were performed again on the *lateralised* EEG signal. This was generated by pairing each of the 27 electrodes on the left side of the head with its corresponding homologous electrode on the right side (e.g. P1/P2, O1/O2 and excluding the 8 midline electrodes). For each trial per subject, and at each time point in the -300 to 400 ms window, the EEG amplitude from the LH electrode in each pair was subtracted from the amplitude at the RH electrode. This created a lateralised (RH-LH) EEG signal for each of the 27 pairs which was then subjected to cluster mass permutation testing as per the method outlined above.
   i) A series of 4 cluster mass permutation tests were first performed to assess whether either line length or age group was significantly lateralised to one hemisphere at any consecutive time points or electrodes during the 0–400 ms window. This was achieved by performing one-sample t-tests against zero (i.e. the null hypothesis=no lateralisation) during the cluster identification stage, with the subsequent estimation of the null hypothesis distribution proceeding as described above.
   ii) The interaction between line length x age was tested by performing a between-subjects cluster analysis (using same method as above but on the lateralised EEG data) on a long vs short line difference wave, created by subtracting the mean EEG signal in the short lines from the long lines for each participant. This interaction was followed by two within-subjects cluster tests to identify lateralised differences in the line length effect as a function of age (long vs short, separately for iii) Young and iv) Older adults) and between-subjects cluster tests to assessed the effect of age as a function of line length (Young vs Older, separately for v) long and vi) short lines).

Results

Visual acuity screening

Both age groups were highly accurate for stimulus detection, with a 96.13% overall hit rate (Fig. 2). Although young adults were slightly more accurate overall ($\bar{x}$=98.25%) when compared to the older group ($\bar{x}$=94.01%) [t(36)=2.9, p=0.006], the majority of detection errors in the older group occurred in the extreme periphery and not in the vicinity of the landmark lines. When these peripheral trials were excluded (and only the space in which the landmark lines were positioned was analysed), both age groups performed with similar accuracy [t(36)=0.23, p=0.82]. Only 0.38% of catch trials returned false positives (young: 0.22%, older: 0.55%) [t(36)= -1.03, p=0.31].

Behavioural results: landmark task

One-sample t-tests on the PSE values for each block highlighted a significant, but transient, spatial bias in young adults towards the left side of space for long lines at the beginning of the experiment [Block 1: t(18)= -2.48, p=0.023], that is consistent with pseudoneglect. There was however no significant bias when all 5 blocks were averaged together, and no bias was evident for short lines in the younger age group in any block. Older adults displayed no group-level spatial bias for either long or short lines during any of the experimental blocks (see Fig. 3A, illustrating PSE performance over all blocks). The corresponding 2×2×5 (*length×age×block*) mixed ANOVA found no significant PSE differences between young and older adults [AGE: F(1,36)=0.645, p=0.427, ηp^2=0.018], no differences between long and short lines [LENGTH: F(1,36)=0.676, p=0.416, ηp^2=0.018], no main effect of block [BLOCK: F(1,144)=0.932, p=0.477, ηp^2=0.025] and no interactions between factors.

The psychometric function curve widths (Fig. 3B) were also subjected to a 2×2×5 (*length×age×block)* mixed ANOVA, showing greater precision for long relative to short lines [LENGTH: F(1,36) =24.39, $p < 0.001$, ηp^2=0.4]. There were no age-related differences in task precision [AGE: F(1,36)=1.56, p=0.22, ηp^2=0.042], no main effect of block [BLOCK: F(1,144)=1.27, p=0.28, ηp^2=0.034] and no significant interactions.

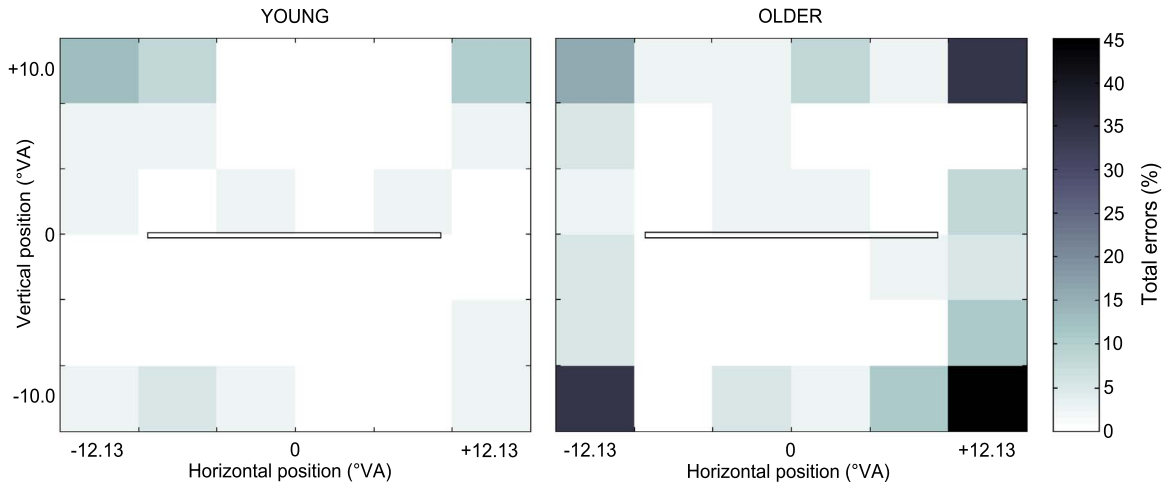

Fig. 2. Heat maps of the total percentage errors for each stimulus location, as assessed by the visual screening task. Shown here in degrees of visual angle relative to the central fixation cross. The maximum display range of the landmark stimuli (long lines) is overlaid.

EEG: Line length effect

Cluster mass permutation tests for the main effect of line length (long minus short, data of young and older adults collapsed) revealed 2 temporally distinct positive clusters in the frontal electrodes that spanned both cerebral hemispheres (occurring between 67 and 304 ms and 270–400 ms respectively), indicating a significantly larger frontal positivity for long compared to short lines (Fig. 4A). These were accompanied by 2 simultaneous negative clusters: within the posterior electrodes bilaterally at 64–241 ms, and within the right posterior region at 263–400 ms. The peak of the line length effect (in terms of t-value) was localised over the right parieto-occipital cortex (electrode PO4) at 139 ms post-stimulus (t=-8.13). This closely replicates our previous finding (Benwell et al., 2014a) where the peak line length effect was identified at 140 ms over PO4 in a sample of young adults. Long lines therefore elicited a larger parieto-occipital negativity relative to short lines, which was most prominent in the right hemisphere during the P1-N1 complex. This analysis was repeated separately for the young and older groups to identify any age-related differences in the line length effect.

Line length effect: young

Two positive clusters were identified in the bilateral frontal electrodes. The first was in a short time period between 111–172 ms and the second within a longer window of 245–374 ms, with the peak positivity occurring at 149 ms (t=7.1) at electrode FC1 (Fig. 4B). There was a single negative cluster in the 113–178 ms window over the posterior electrodes bilaterally, though with the maximum t-value (observed at 141 ms) peaking over right parieto-occipital sites (electrode PO4).

Line length effect: older

One positive cluster was identified within a sustained time period of 96–246 ms, with a peak t-value at 191 ms (t=6.12) over the right temporo-parietal cortex (electrode TP9: Fig. 4C). One negative cluster was identified, again within a distributed window of 75–227 ms but with less apparent asymmetry (t=-5.56) occurring at 84 ms over the central posterior region (CPz).

Age main effect: young vs. older

Between-groups cluster mass permutation testing found one significant cluster in the frontal electrodes across both hemispheres corresponding with the P300 component window, where young adults had a more negative frontal amplitude compared to older participants (193–400 ms, peak t=-5.11 at electrode F7 at 363 ms) (Fig. 4D). A second significant cluster was identified during a similar time period (180–400 ms) in the posterior electrodes, mostly bilaterally represented, where the amplitude was more positive for young adults (peak t=4.0 at electrode P7, 313 ms).

Age-related changes in the P300 component

Age differences in the topography of the P300 component have

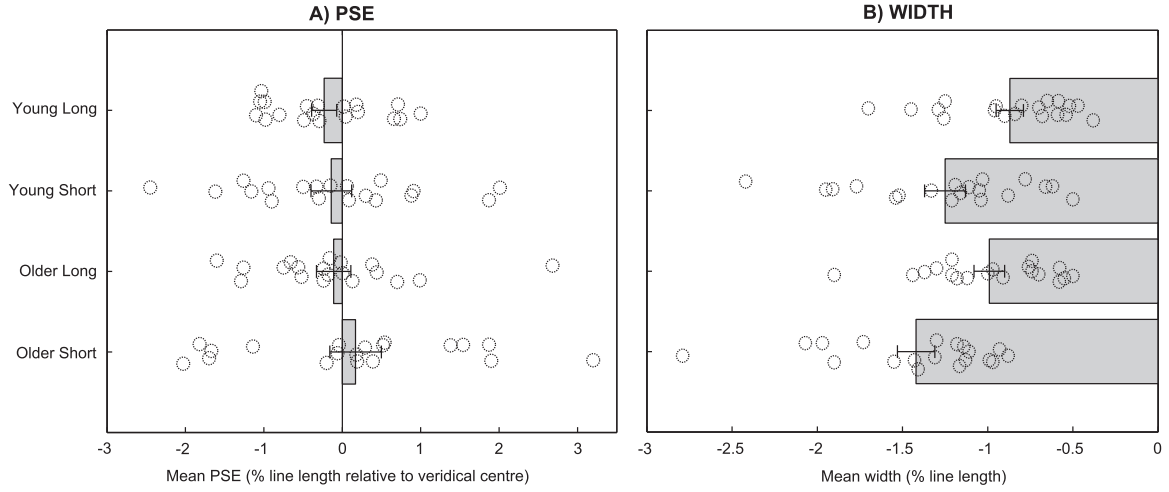

Fig. 3. Group-averaged A) PSEs and B) curve widths over all blocks. Mean values for each subject are overlaid.

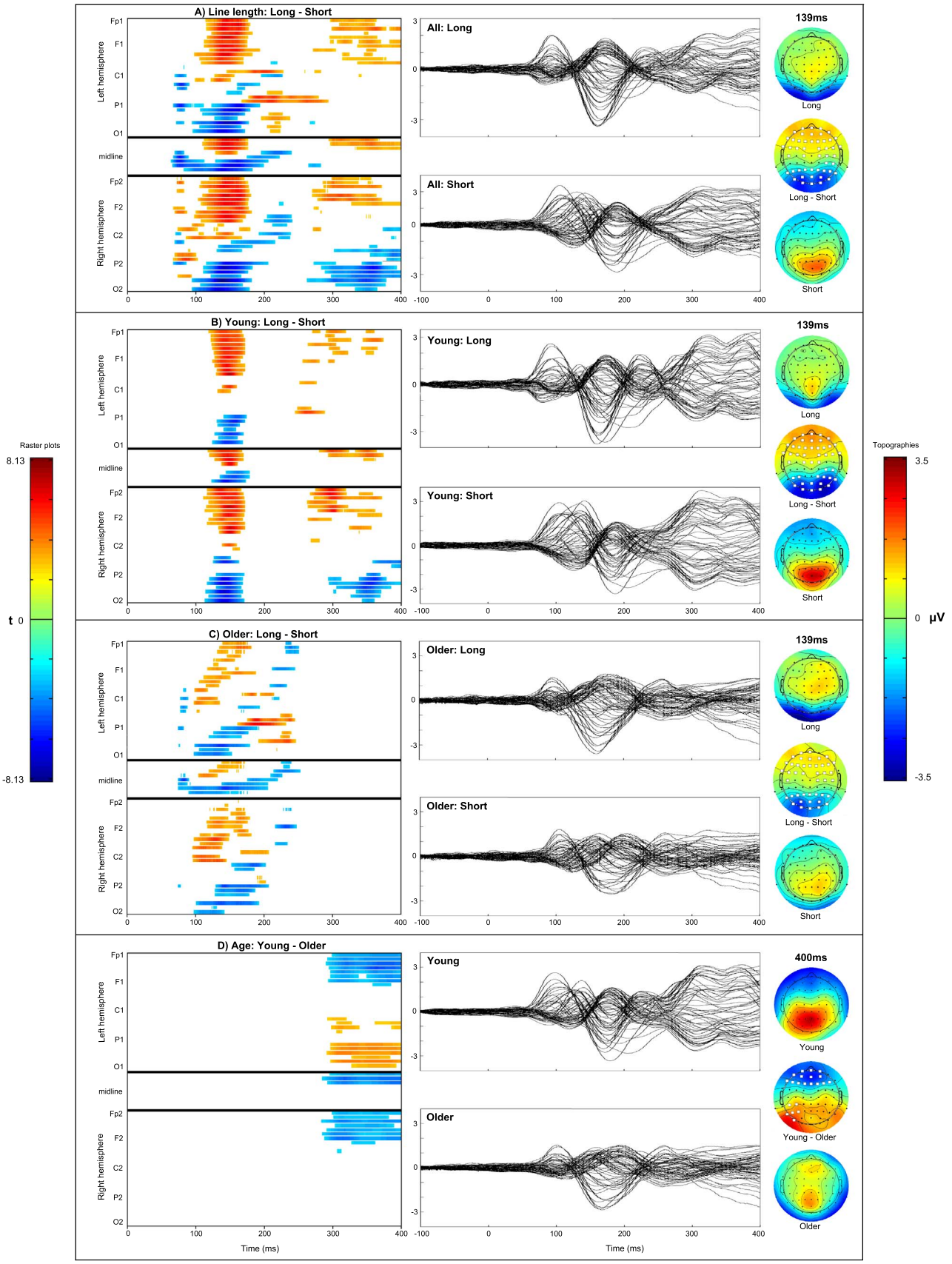

Fig. 4. Raster plots highlighting the significant t-values after cluster correction. For the line length effect (long minus short lines): A) All subjects (Young and Older), B) Young adults only and C) Older adults only. Butterfly plots show the grand average voltage waveforms for the 62 channels (trials averaged within each subject, then averaged across subjects). The topographies for A-C show the voltage distribution at the peak long-short difference time point of 139 ms. The main effect of age (young minus older) is shown in D and the topographic maps show the scalp distribution at 400 ms. Significant electrodes are highlighted in white.

previously been well described, with many reports of the peak P300 amplitude (located at posterior electrodes in young adults), shifting to a more anterior topography in older adults (O'Connell et al., 2012; Fjell and Walhovd, 2004; Friedman, 2003; Polich, 1997; West et al., 2010). To investigate age-related changes in this dataset, the peak amplitude was first identified for each subject within two separate regions of interest (frontal and posterior) within the 280–400 ms window. As per O'Connell et al. (2012) the frontal ROI comprised electrodes F3, Fz and F4 and the posterior ROI P3, Pz and P4. A 2×2×2 (length×ROI×age) ANOVA revealed a small main effect of Age [$F(1,36)=4.16$, $p=0.049$, $\eta p^2=0.1$] where amplitude was generally more positive in young vs older adults. The P300 was also more positive overall in the posterior ROI relative to the frontal ROI [$F(1,36)=16.92$, $p < 0.001$, $\eta p^2=0.32$] and was more positive for short lines compared to long [Length: $F(1,36)=5.46$, $p=0.025$, $\eta p^2=0.13$]. Importantly, there was an Age×ROI interaction [$F(1,36)=13.31$, $p=0.001$, $\eta p^2 =0.27$], with subsequent paired t-tests revealing a large positivity in the posterior relative to frontal ROI in young adults [$t(18)= -4.6$, $p < 0.001$]. There was no amplitude difference between the frontal and posterior ROIs for older adults [$t(18)= -0.44$, $p=0.67$]. Independent samples t-tests between the two age groups found significant age-related differences in both the frontal ROI [$t(36)= -2.84$, $p=0.007$] (more positive for older adults) and in the posterior ROI [$t(36)= 3.68$, $p=0.001$] (more positive for young adults).

Hemispheric lateralisation

Our main motivation for performing this study was to investigate whether any differences exist in the hemispheric contributions (i.e. right vs left hemisphere) to spatial attention judgements in young vs older adults. Given that the peak negative t-value for the line length effect (section *EEG: line length effect*) was located at the right parieto-occipital (PO4) electrode in young adults, but was located in the midline (CPz) for older adults, this hints that the right parietal cortex may contribute proportionally more than the left in the young adults, and that this hemispheric asymmetry may be less pronounced in the older group. In order to formally test this hypothesis, the cluster mass permutation tests were performed once again, but using the *lateralised* EEG signal derived from the RH-LH electrode pairs (see *EEG statistical analyses* for method).

Identifying hemispheric asymmetries

One-sample cluster mass permutation tests were performed using the lateralised EEG signal, separately for the two line lengths and age groups (Fig. 5). One cluster ($p=0.078$) was identified in young adults for long lines between 185–239 ms, involving the electrode pairs FC1/2, FT7/8, C1/2, C3/4, C5/6, T7/8, CP1/2, CP3/4, TP7/8, indicating a small right hemisphere asymmetry for longer lines. Unexpectedly, this cluster did not involve the asymmetrical activation of any posterior parietal or occipital electrodes but did involve the more anterior, centro-parietal electrodes. There were no significantly lateralised clusters for short lines in the young group (all clusters $p > 0.28$). Neither the long nor short lines were lateralised at any time point for the older group (long $p > 0.16$, short $p > 0.33$).

Hemispheric lateralisation as a function of age

Within-subject cluster testing for the main effect of line length identified no lateralised cluster differences between long and short lines (all $p > 0.12$, Fig. 6A). Between-group comparisons for the main effect of age (Fig. 6B) identified one lateralised cluster ($p=0.051$) occurring at stimulus onset (0–81 ms) involving frontal, fronto-central and central electrode pairs F3/4, F5/6, F7/8, FC1/2, FC3/4, FC5/6 and C3/4. This cluster was slightly more positive in the LH vs RH for young adults during this early window. Fig. 6B indicates that this effect is likely to have been present during the baseline period, although statistical tests were performed on the 0–400 ms window only. The length×age interaction was then tested using between-group (young vs older) comparisons of the long-short difference wave (Fig. 6C), which revealed a significant cluster during the 201–230 ms window ($p=0.041$), involving electrode pairs F7/8, FC1/2, FC3/4, FC5/6, FT7/8, C1/2, C3/4, C5/6, T7/8, CP1/2, CP3/4 and CP5/6. There was a more pronounced right-lateralisation of the long-short difference in young adults compared to the older group at this time.

To follow up this interaction, a separate within-group cluster test for the line length effect in the young group found one cluster ($p=0.0068$) involving electrode pairs AF3/4, F3/4, F5/6, F7/8, FC1/2, FC3/4, FC5/6, FT7/8, C1/2, C3/4, C5/6, T7/8, CP1/2, CP3/4, CP5/6 and P1/2, indicative of right-lateralisation during the 198–237 ms window (the N1-P2 component transition period) (Fig. 6D), which was more pronounced for long lines compared to short. It is important to note that most of the electrodes involved in this cluster of electrode asymmetry are not over posterior parietal or parieto-occipital sites (aside from the CP1/2, CP3/4, CP5/6 and P1/2 pairs), and that this cluster was identified at a later window than expected given the results of the full-scalp cluster tests (peak long-short difference at PO4, 139 ms). There was no long vs short difference in the older group (Fig. 6E). Finally, separate between-groups (young vs older) comparisons for long and for short lines did not reveal any significant differences (Long $p > 0.24$, Short $p > 0.11$).

To summarise these results, we found that long lines differentially engaged the RH more than the LH in young adults, and that this hemispheric asymmetry in favour of the RH was significantly more pronounced for long lines relative to short in the younger group. There was no lateralised activity for either line length in older adults.

Brain-behaviour correlation

We then performed a series of correlations between behavioural bias (PSE) and EEG lateralisation in Block 1, where the behavioural bias was strongest. This was achieved by selecting the cluster that was identified above as showing a significant difference between long and short lines in young adults. The 16 electrode pairs involved in the cluster were averaged for each individual (mean of AF3/4, F3/4, F5/6, F7/8, FC1/2, FC3/4, FC5/6, FT7/8, C1/2, C3/4, C5/6, T7/8, CP1/2, CP3/4, CP5/6 and P1/2), and the lateralised EEG signal at 220 ms was selected (i.e. the midpoint during the significant 198–237 ms cluster period). Spearman's rho correlations identified a significant, if weak, relationship for long lines in young adults, where a larger right (vs left) hemisphere negativity correlated with larger leftward spatial bias (PSE) (Spearman's rho=-0.47, $p=0.041$). No significant correlations were identified for short lines in young adults ($r=-0.21$, $p=0.38$), or for either line length in older adults (long $r=0.16$, $p=0.52$; short $r=-0.26$, $p=0.29$).

Control analysis

Finally, we performed a 'traditional' ERP peak analysis of the P1, N1, P2 and N2pc components within two posterior regions of interest (ROI) in the left and right hemispheres. The ROIs comprised: Left ROI=electrodes P1, P3, P5, P7, PO3, PO7 & O1 and Right ROI=electrodes P2, P4, P6, P8, PO4, PO8 & O2. The peak amplitude and latency of each component were identified on a subject-by-subject basis (averaged across all relevant trials for each participant), within the following windows: P1 (50–150 ms), N1 (120–220 ms), P2 (190–260 ms), N2pc (190–260 ms) (Fig. 7). The raw mean latencies and amplitudes are appended as Supplementary data.

Peak amplitude

A series of 2×2×2 ANOVAs were performed on the peak amplitudes of each component, to assess the effects of Age (young vs older), Line length (long vs short lines) and ROI (left vs right hemisphere). In summary, we found significant main effects of Length and Age for P1 (a

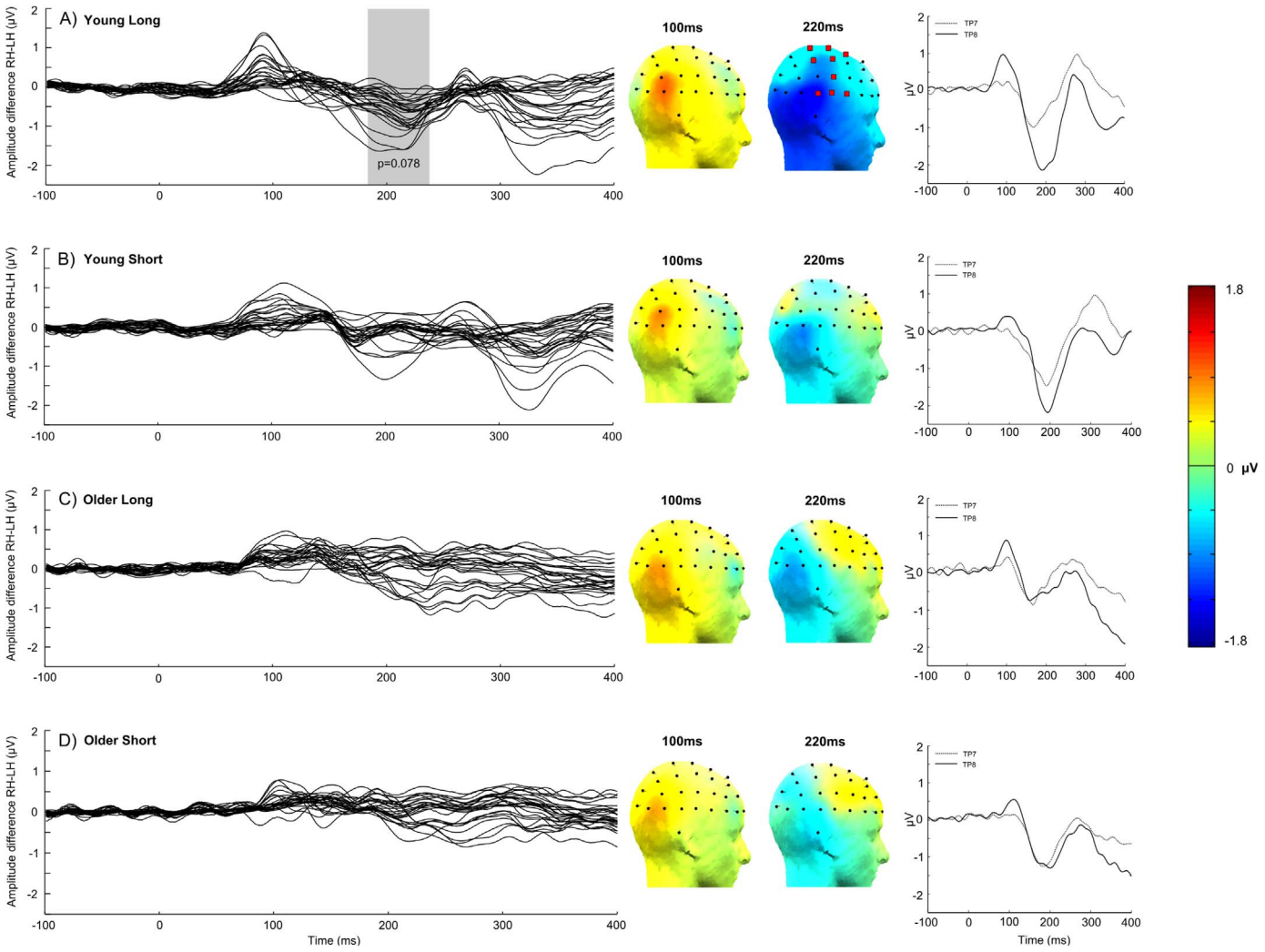

Fig. 5. Butterfly plots showing the lateralised (RH-LH) grand average EEG waveforms for the 27 electrode pairs, separately for the two line lengths and age groups. The amplitude difference at each time point in the -100 to 400 ms window is shown (RH electrode minus its homologous LH electrode pair). Half-scalp topographies are then plotted for the RH-LH difference at 100 ms and at 220 ms post-stimulus. Here, warm colours represent a larger RH vs LH amplitude during the positive-going time points (e.g P1, ~100 ms). At the negative-going time points (e.g N1, ~200 ms), cool colours represent a larger RH vs LH amplitude. Cluster analysis identified a RH lateralisation for long lines in the young group during the 185–239 ms window (shaded in Fig. 5A). The electrodes involved in the cluster are highlighted in red on the sagittal topography plot. The waveforms for TP7 and TP8 (identified in the cluster shown in 5A) are then shown separately in the panels on the right.

larger P1 amplitude for short lines vs long [$F(1,36)=6.64$, $p=0.014$, $\eta p^2=0.16$], and for young adults vs older [$F(1,36)=11.86$, $p=0.001$, $\eta p^2=0.25$]), and a Length×Hemisphere interaction (larger P1 amplitude for short lines vs long lines in the left ROI [$F(1,36)=9.70$, $p=0.004$, $\eta p^2=0.21$]). We found a significant effect of Length for N1 (larger N1 amplitude for long lines vs short [$F(1,36)=22.47$, $p < 0.001$, $\eta p^2=0.38$]), but no significant effects for P2 and N2pc. Importantly, in terms of peak amplitudes, we did not find any interaction of Age with Length and Hemisphere (Age×Length×Hemisphere: max $F=1.67$, min $p=0.21$) nor of Age with Hemisphere (Age×Hemisphere: max $F=1.12$, min $p=0.3$) for any component tested, indicating that the traditional analysis of peak amplitude did not capture the change of hemispheric lateralisation with age.

Peak latency

The ANOVAs were then repeated for the component peak latencies. In summary, there were earlier P1 and N1 peaks for long lines vs short [P1: $F(1,36)=41.05$, $p < 0.001$, $\eta p^2=0.53$; N1: $F(1,36)=66.73$, $p < 0.001$, $\eta p^2=0.65$], and no significant effects of P2 or N2pc. In addition, the interactions of interest were also non-significant for analyses of peak latencies of any component tested (Age×Length×Hemisphere: max $F=0.97$, min $p=0.21$; Age x Hemisphere: max $F=1.19$, min $p=0.28$), ruling out that the results of our cluster analysis can be explained by differences in the latencies of components between age groups.

Overall, the above analyses therefore suggest that the lateralised electrode cluster analysis approach provides useful additional information about lateralisation during the transition periods between component peaks, that would not have been gained from a 'traditional' ERP analysis. Importantly, the control analysis also confirmed that the between-group differences in lateralisation are unlikely to be related to age-related changes in the latency of component peaks.

Discussion

The purpose of this study was to assess age-related changes in the cortical distribution of neural activity for spatial attention tasks. Here we present evidence of a stimulus- (i.e. line length) dependent, asymmetric engagement of the right hemisphere in young adults, accompanied by a baseline leftward spatial bias for long lines that is representative of pseudoneglect. For the first time, we provide evidence of reduced hemispheric lateralisation in an older age group for visuospatial processing, which we hypothesise may be a contributing factor to the age-related attenuation of spatial attention biases (Benwell

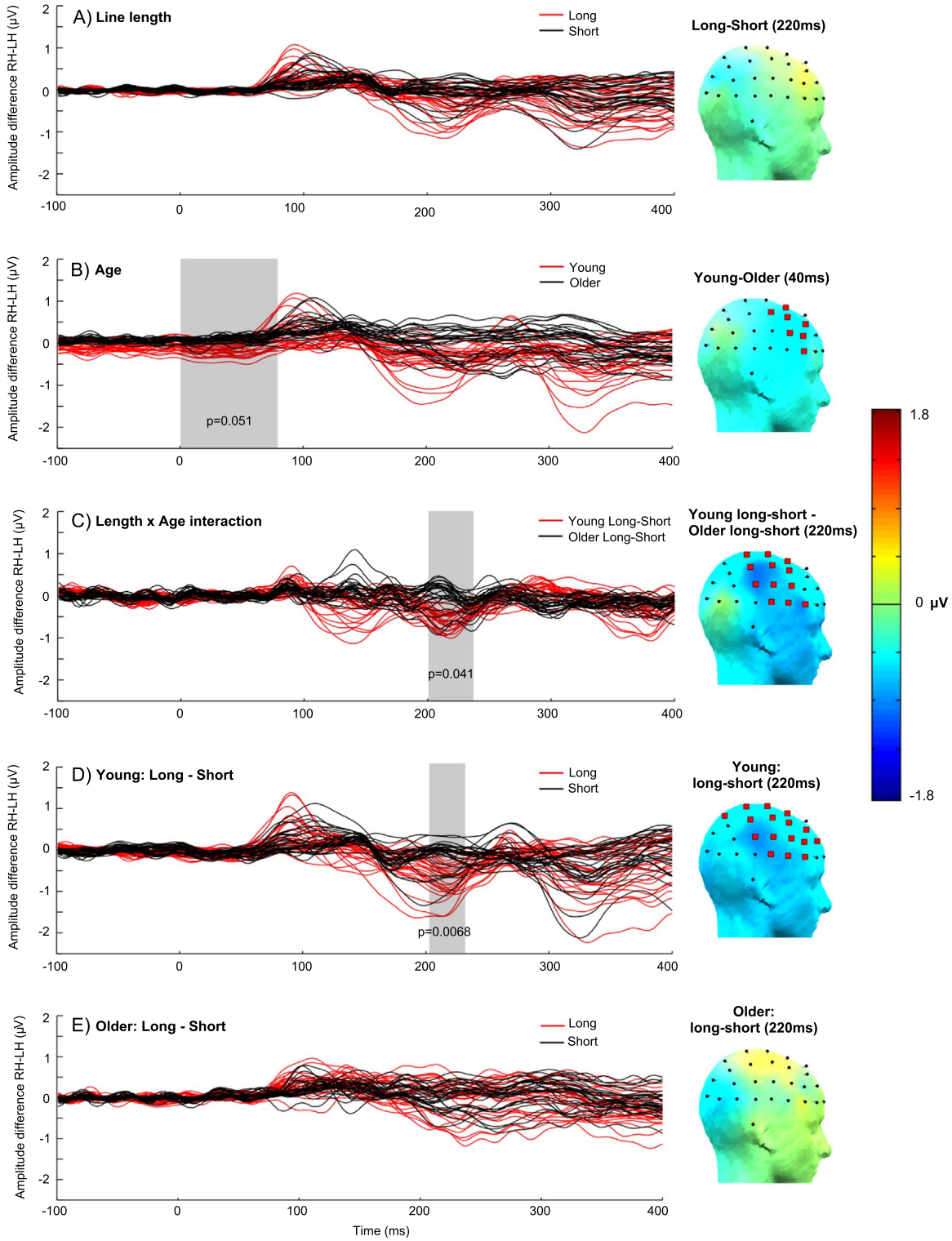

Fig. 6. Butterfly plots showing the lateralised (RH-LH) grand average EEG waveforms for the 27 electrode pairs: A) the main effect of line length, B) the main effect of age and C) the line length×age interaction (young vs older comparison of the long-short difference wave). The within-group line length effect (long vs short) comparisons are then shown separately for D) Young and E) Older adults.

et al., 2014b; Failla et al., 2003; Fujii et al., 1995; Fukatsu et al., 1990; Learmonth et al., 2015a; Nagamatsu et al., 2009; 2011; 2013; Schmitz and Peigneux, 2011; Stam and Bakker, 1990).

Right-lateralisation for spatial attention in young adults

Our behavioural results from the landmark task show that young adults exhibited a significant leftward behavioural bias (pseudoneglect) at baseline for long lines, that was absent for short lines. This was accompanied by an asymmetry of cortical activity in the lateralised (half-scalp) EEG cluster analysis favouring the right hemisphere in the 185–239 ms window which, akin to the behavioural bias, was absent for short lines. Interestingly, the electrodes involved in the asymmetric cluster were located predominately around the central gyrus, only

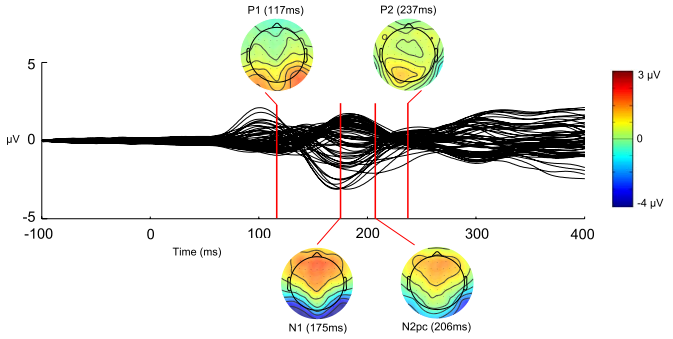

Fig. 7. Grand average 62-channel butterfly plot illustrating the scalp topographies of the mean component peaks (P1, N1, P2 and N2pc).

extending posteriorly as far as the centro-parietal electrodes, but not indicating any strong posterior parietal or occipital lateralisation per se.

Although this asymmetry for long lines in the young group only showed a trend (p=0.078) in the one-sample t-test analysis compared to zero (i.e. a null hypothesis of no significant lateralisation), there was a clear lateralisation difference when long and short lines were compared directly. Long lines elicited a stronger right-lateralisation relative to short lines in the young group. Similar to the one-sample cluster analysis, this long-short difference also mainly involved a lateralisation of the central and centro-parietal electrodes rather than the posterior parietal and occipital channels, as predicted. These results were somewhat unexpected in terms of both the topography and the latency of the lateralised line length effect, given that the results of the full-scalp cluster analysis identified the maximum long vs short line difference in the young group to be earlier (at 141 ms, during the P1-N1 complex) and distributed more posteriorly over the right parieto-occipital cortex (PO4), although electrodes of both hemispheres tended to show responses at this time point. Although we have successfully replicated the line length effect from our previous study (Benwell et al., 2014a), here we show that the peak *lateralisation* difference for long vs short lines in young adults actually occurs slightly later (198–237 ms, N1-P2 complex) and involves the asymmetrical activation of more anterior electrodes. Collectively, our data suggests a two stage time course of the line length effect during landmark task performance which differs in terms of topography and lateralisation (posterior, less lateralised followed by more central, right lateralised).

It is tempting to compare this time course to the time course of line bisection judgment identified by Foxe et al. (2003), with the caveat that these are based on different comparisons to isolate activity associated with spatial bias in the landmark task (long vs short lines in our case, landmark task vs non-spatial control task in Foxe et al.). Our later window of lateralised activity does align with the second distinct topographic phase of activity occurring between 190 and 240 ms of Foxe et al. This phase involved the emergence of a larger right lateral parieto-occipital and central parietal negativity for the spatial judgement task relative to the non-spatial control. However, this distribution was more posterior than the lateralised cluster observed for long lines compared to short here. Moreover, we found no clusters of asymmetry corresponding to the first phase window (170–190 ms) nor their third phase (240–400 ms), even though their stimuli were almost identically proportioned with respect to our long landmark task lines. Our results also agree with Longo et al. (2015) who found no lateralisation in an early window (170–190 ms) but a significant right-lateralisation of activity for the landmark task compared to a control task. It is possible that the more anterior topography identified here, when compared to the posterior effects of Foxe et al. and Longo et al., may be related to the different control tasks used. In the aforementioned studies, when comparing a spatial task to a non-spatial control, the right parieto-occipital electrodes are identified as showing the maximal effect. However, here we compared two spatial tasks, without a non-spatial control, and we would therefore not necessarily expect to find an identical topography. Indeed, as shown in Fig. 3 of Benwell et al. (2014a), the topography of the landmark task for long lines at 220 ms post-stimulus (i.e. the same condition and latency as identified here), tentatively hints that a similar cluster of right hemisphere lateralised electrodes may have been identified if we had applied the same method of lateralised cluster identification to that dataset. Our data therefore add to these previous studies to now show that this later latency window indexes the largest clustered lateralisation differences between long and short landmark lines for young adults.

Age-related reduction of hemispheric lateralisation

As expected, the lack of hemispheric lateralisation in older adults was accompanied by a lack of behavioural bias for both long and short lines in the landmark task. Although we did find long vs short differences in the full-scalp cluster analysis for older adults, the peak t-value was located over the midline (Cz). Corroborating this, the long vs short cluster analysis performed on the *lateralised* EEG signal found no asymmetric RH vs LH activity differences for either long or short lines in this older age group. We tentatively propose that this reduced EEG lateralisation may correspond with the lack of behavioural bias for older adults observed here. We did not find any significant age differences within this ~200 ms post-stimulus window when the young and older group were directly compared against each other - for either long or short lines - but this could be due to a lack of sensitivity of the cluster analysis method in detecting small, between-group differences that are localised to few electrodes or time points (Groppe et al., 2011a, 2011b).

We did however find evidence of an interaction between age and line length for the lateralised EEG signal in the 201–230 ms window. Specifically, this shows a complex, stimulus-dependent response where young adults exhibit a more pronounced long-short differentiation in the right-hemisphere compared to the older group. We can therefore conclude that at a group level, aging is indeed accompanied by a significant reduction of dynamic RH engagement for spatial attention, although this is only apparent when taking into account the relative difference between stimulus characteristics, in this case line length.

How then can the results of the mass univariate cluster approach be reconciled with the control ERP analysis, which failed to identify an interaction between age, line length and cerebral hemisphere in either the peak amplitude or latencies of the P1, N1, N2pc and P2 components? One possible account is that the mass univariate analysis picked up between-group differences in the slope of the transition between the N1 and P2 peaks, rather than differences within the component peaks per se. However, it is not yet clear what a right-hemispheric lateralisation during this N1-P2 transition period means at a neurophysiological level, nor how changes during this period are relevant to the aging process. Our differential results indicate that the mass univariate approach may be a useful method of identifying clusters of lateralised activity that cannot be identified using the more traditional ERP approach, but the functional significance of this particular result remains unknown and should be investigated in future studies.

Age-related reduction of the parietal P300

The largest between-group difference was found during the P300 component time window (280–400 ms post-stimulus). This was temporally distinct from the main line length effect which occurred earlier at 139 ms. In terms of topography, we found a large positivity with a parietal distribution for young adults (with a corresponding frontal negativity) but there was a significant reduction of both the parietal positivity and the frontal negativity for the older group. Indeed, the topography plot for the older group (Fig. 4D) appears to show a small *positivity* at the anterior electrodes, which could corroborate previous

reports of a posterior-anterior shift in P300 topography for older adults (Fjell and Walhovd, 2004; Friedman, 2003; O'Connell et al., 2012; Polich, 1997; West et al., 2010).

Given that this P300 shift has been observed across a range of different tasks (Kuba et al., 2012; Pfefferbaum et al., 1984; van Dinteren et al., 2014; Walhovd and Fjell, 2003) and that it has been variously associated with decision making, context-updating and stimulus processing (see van Dinteren et al., 2014 for review), this finding may reflect age-related changes for a non-spatial aspect of the landmark task in our study. Yet, most of these studies described above adopted an oddball task paradigm to investigate the P300. It should be noted that the changes in P300 as observed here (and e.g. O'Connell et al., 2012), as opposed to P300 changes in oddball paradigms (Fjell and Walhovd, 2004; West et al., 2010) may reflect different functional components of a similar anatomical origin. The functional significance of both the amplitude reduction and topographic change of the P300 component is still under debate, particularly in relation to whether the recruitment of anterior regions may help to facilitate behavioural performance in older adults, similar to the CRUNCH model (Davis et al., 2008; Grady, 2012). It is worth noting that compared to the young adults, our older group performed the task with no reduction in precision, and therefore this shift could potentially represent a mechanism whereby their performance was maintained, although this remains speculative.

Models of neurocognitive aging

How then might models of cognitive aging explain this change in hemispheric lateralisation as individuals get older? Firstly, we found no strong evidence for the CRUNCH model of a compensatory recruitment of additional neural circuits (Reuter-Lorenz and Cappell, 2008) that might explain the previous behavioural findings of age-related rightward shifts of lateralised spatial attention bias. However we did find tentative evidence of later additional anterior recruitment as indexed by the P300 component described above. Our results indicate that age-related neuro-plastic changes for spatial attention biases are likely to be confined to more subtle, stimulus-driven changes in activation within the left and right hemispheres. Secondly, we expected to observe a *rightward* behavioural bias for short lines in the older group, as per Benwell et al. (2014b), but bias was primarily lacking for this group rather than shifted entirely into the right hemispace. A clear shift into right space, accompanied by an asymmetry of cortical activity favouring the *left* hemisphere for short lines in this group, could conceivably have occurred in case of a strong right hemispheric change, rendering activity *lower* in the right vs left parietal cortex, and thus providing evidence for the right hemi-aging model. However, this model can also accommodate the scenario we observe here of an eliminated (rather than rightward) bias, in which the RH has indeed declined in function but is not (yet) less functional than the LH. We cannot therefore exclude that these findings may be explained, at least in part, by an account of premature right hemisphere aging.

Overall, we conclude that our results align most closely with the hemispheric asymmetry reduction (HAROLD) model of cognitive aging, given that we find both a lack of behavioural bias and a lack of cortical lateralisation in the older group. To date, the bulk of evidence supporting the HAROLD model has been gained from memory studies, which report bilateral activity predominately within the frontal cortex in cognitive aging (Cabeza, 2002). Here we present evidence of a posterior asymmetry reduction, and in doing so add to a handful of studies which find HAROLD-compatible effects for tasks involving posterior regions (e.g. Berlingeri et al., 2010; Benwell et al., 2014b; Collins and Mohr, 2013). Further, as it stands the HAROLD model asserts that asymmetry reduction occurs as a *compensatory mechanism* whose purpose is to sustain cognitive performance within the aging brain in response to increased task difficulty. In support of this, highly-performing older individuals are known to exhibit a more extensive bilateral frontal recruitment in memory tasks compared to their lower-performing counterparts (Berlingeri et al. 2010; Cabeza, 2002; Cabeza et al., 1997, 2002; Huang et al., 2012; Reuter-Lorenz et al., 2000). We show here in the analysis of psychometric curve widths that, contrary to our previous study (Benwell, 2014b), older adults did *not* perform the landmark task with any less precision compared to the young adults for either line length. We cannot exclude the possibility that our sample of older adults simply represents a more 'highly functioning' subset of the general older population in terms of task performance, and that the neural changes we observed here are unrelated to performance requirements. Alternatively it may be the case that their good performance was a direct result of this more bihemispheric recruitment, reflecting the compensatory mechanisms specified by the HAROLD model. In either case, our results indicate that models of neurocognitive aging remain under-specified and are as yet unable to account fully for asymmetry reduction within the spatial attention domain.

Aside from the evidence uncovered by Nagamatsu et al. (2009), who found that older adults with a specific left hemispace visual processing deficit have a higher risk of falls, there is a distinct lack of evidence that a rightward shift exerts any negative influence on, for example spatial navigation in complex environments, safe driving (i.e. maintaining lane position), or general life quality in older age. Put simply, should we be *concerned* if an older adult begins to exhibit a rightward shift of spatial bias, or does it merely represent a harmless by-product of the healthy aging brain? To answer this, it would be valuable to assess whether these laboratory-based measures of spatial attention asymmetry correlate with performance on more ecologically valid tasks, such as driving, and navigating within a complex environment. Finally, despite the fact that our older age group showed normal perimetry, task precision and no neurological history, we did not explicilty test their global cognitive status with, for example, the Mini-Mental State Examination. Although we observed a reduction of spatial bias in the older group, further studies are needed to establish whether this effect is related specifically to healthy physiological aging or due to early neurodegeneration.

Methodological considerations

The lack of strong group-level spatial biases on the behavioural level in the current study may be explained by methodological factors. Firstly, the leftward pseudoneglect bias in young adults for long lines was transient and limited only to the baseline experimental block. Spatial bias tends to drift rightward as time-on-task increases, probably as a consequence of depleted right ventral network resources driving a reduction in general arousal (Benwell et al., 2013a; 2013b; Bellgrove et al., 2004; Dodds et al., 2008; Dufour et al., 2007; Manly et al., 2005; Newman et al., 2013). We hypothesise that this time-on-task effect might have been hastened by a prolonged EEG setup period, and by participants undergoing the visual acuity screening. As a result, we may have observed both a less pronounced pseudoneglect bias, and thus a weaker lateralisation of EEG signals given that the analysis was performed on the pooled trials from all 5 experimental blocks.

The fixed viewing distance of 80 cm (due to laboratory restrictions) may also have contributed to this reduced bias. The magnitude of the leftward pseudoneglect bias tends to increase as stimuli are presented in close peri-personal, rather than extra-personal, space (Longo et al., 2015; Longo and Lourenco 2006, 2007, 2010; Lourenco and Longo, 2009) and indeed Longo et al. (2015) report a larger asymmetric engagement of the right (vs left) parietal cortex for peri- vs extra-personal landmark task judgements. However we have reported both pseudoneglect and a right parieto-occipital asymmetry at a viewing distance of 100 cm previously (Benwell et al., 2014a) and therefore this is unlikely to be the sole contributing factor to this reduced spatial bias.

In conclusion, we report an age-related reduction of right hemispheric control for spatial attention in older adults. This effect was stimulus-driven, with a strong differentiation of long and short lines in the right hemisphere observed in young adults, which was absent in the

older group. Our results most closely align with the HAROLD model of neurocognitive aging (although we cannot exclude the possibility that they represent an early indication of neurodegeneration), yet current models are underspecified in fully accounting for our findings. Based on our observations, we propose that aging models need to incorporate stimulus-driven asymmetry reductions and also a reduced lateralisation within the posterior, in addition to the frontal, cortex.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neuroimage.2017.03.050.

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