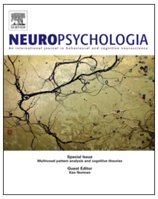
Neuropsychologia 70 (2015) 350–357

Contents lists available at ScienceDirect

Neuropsychologia

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



Right hemisphere control of visuospatial attention in near space

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ARTICLE INFO

Available online 6 November 2014

Keywords:
Near Space
Landmark Task
Pseudoneglect
Peripersonal Space
Hemispheric Asymmetries

ABSTRACT

Traditionally, the right cerebral hemisphere has been considered to be specialized for spatial attention and orienting. A large body of research has demonstrated dissociable representations of the near space immediately surrounding the body and the more distance far space. In this study, we investigated whether right hemisphere activations commonly reported for tasks involving spatial attention (such as the line bisection and landmark tasks) are specific to stimuli presented in near space. In separate blocks of trials, participants judged either whether a vertical transector was to the left or right of the centre of a line (landmark task) or whether the line was red or blue (colour task). Stimuli were seen from four distances (30, 60, 90, 120 cm). We used EEG to measure an ERP component (the 'line-bisection effect') specific to the direction of spatial attention (i.e., landmark minus colour). Consistent with previous results, spatial attention produced a right-lateralized negativity over occipito-parietal channels. The magnitude of this negativity was inversely related to viewing distance, being largest in near space and reduced in far space. These results suggest that the right occipito-temporal cortex may be specialized not just for the orientation of spatial attention generally, but specifically for orienting attention in the near space immediately surrounding the body.

1. Introduction

Perceiving the space around us is critical both for controlling skilled action and for defending the body against potentially threatening stimuli in the environment. Accordingly, researchers in several disciplines have differentiated the space close to the body from that farther away (e.g., Brain, 1941; Hall, 1966; Sommer, 1969). Within cognitive neuroscience, a large literature has demonstrated that the near (or *peripersonal*) space immediately surrounding the body is represented differently from the far (or *extrapersonal*) space, farther away. For example, neurophysiological studies in monkeys have identified neurons in frontal and parietal cortices maximally responsive to the visual perception of objects near to or approaching the body surface (e.g., Graziano et al., 1994; Rizzolatti et al., 1981). Analogously, double dissociations have been reported in neurological patients between attentional deficits in near and far space (e.g., Berti and Frassinetti, 2000; Cowey et al., 1994; Halligan and Marshall, 1991). These results suggest that the brain maintains specialized mechanisms for the perception of near space.

Studies of healthy human adults have also provided evidence for distinct representations of near and far space. For example, lateral attentional biases have been found to differ as a function of viewing distance. Studies using both the *line bisection* task (i.e., marking the perceived centre of a horizontal line) and the *landmark* task (i.e., judging whether a vertical transector is to the left or right of the centre of a horizontal line) have found that people tend to show small leftward biases, known as *pseudoneglect* (Bowers and Heilman, 1980; for review, see Jewell and McCourt, 2000). With the bisection task, however, this effect appears to be limited to lines presented very close to the body, with bias shifting to the right of centre as viewing distance increases (Ferrè et al., 2013; Gamberini et al., 2008; Longo and Lourenco, 2006, 2007, 2010; Lourenco and Longo, 2009; Lourenco et al., 2011; Varnava et al., 2002). This shift in bias is generally continuous, and the rate at which it occurs has been taken as an index of the extent, or "size," of near space. Indeed, this method has been used to show expansion of near space following tool use (Gamberini et al., 2008; Longo and Lourenco, 2006), contraction of near space when participants wear heavy wrist weights (Lourenco and Longo, 2009), and systematic inter-individual relations between the extent of near space and arm length (Longo and Lourenco, 2007) as well as claustrophobic fear (Lourenco et al., 2011). Studies using the landmark task have reported a similar rightward shift in bias with increased viewing distance, though not an absolute right bias

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http://dx.doi.org/10.1016/j.neuropsychologia.2014.10.035
0028-3932/

at the farthest viewing distances (Bjoertomt et al., 2002; McCourt and Garlinghouse, 2000).

The exact causes of pseudoneglect and its reversal with increased viewing distance remain poorly understood. One possibility is suggested by the activation-orientation theory of spatial attention (Reuter-Lorenz et al., 1990), which proposes that attention will be biased in the direction contralateral to whichever cerebral hemisphere is more strongly activated. This is based on the well-established finding that each hemisphere directs attention contralaterally (Corbetta et al., 1995; Kinsbourne, 1987). Manipulations that produce increased activation in the left hemisphere should lead to a rightward attentional bias, and vice versa. Longo and Lourenco (2006) proposed that the transition in bisection bias from a left bias (i.e., pseudoneglect) in near space to a right bias in far space could result from the combination of an overall rightward attentional bias combined with a right hemisphere specialisation for near space. Kinsbourne (1987) reviews a number of pieces of evidence for a baseline rightward bias (see also Làdavas et al., 1989). When lines are presented in far space, the baseline rightward attentional bias predominates, producing a right bisection bias. As lines are presented closer to the participant, representations of near space in the right hemisphere become progressively more strongly activated, producing an increasing leftward bias counter to the baseline rightward bias. Finally, for lines presented very close to the participant, the leftward bias resulting from right hemisphere activation may exceed the baseline rightward bias, producing an overall leftward bias (i.e., pseudoneglect).

Thus, on Longo and Lourenco's (2006) interpretation, pseudoneglect reflects the sum of two distinct spatial attentional biases: (1) a baseline rightward bias (Kinsbourne, 1987; Làdavas et al., 1989), and (2) a leftward bias caused by activation of near space representations in the right hemisphere. There is less evidence, however, for a right hemisphere specialisation of near space. A large number of studies have found right-lateralized activations for line bisection and landmark judgments (e.g., Billingsley et al., 2004; Çiçek et al., 2009; Fink et al., 2000, 2001, 2002; Flöel et al., 2002; Marshall et al., 1997). All of these studies, however, used only a single viewing-distance, making the specificity of these right-lateralized activations to near space unclear.

Indeed, the use of functional neuroimaging methods such as MRI and PET to investigate the neural bases of the representation of near and far space is complicated by the difficulty of manipulating viewing distance while participants are laying down in a narrow tube. First, vision is typically indirect, through a mirror, making viewing distance somewhat ambiguous in the first place, since the direction of gaze does not match the direction of sight. For example, in the study of Fink et al. (2001), participants saw lines reflected in a mirror which was 14 cm from the screen and an additional 12 cm from the their eyes. Second, participants are instructed to remain completely still with their heads immobilised with padding. This is potentially problematic given that the ability to act is known to alter spatial perception (e.g., Proffitt et al., 2003; Witt et al., 2004; Lourenco and Longo, 2009). Finally, the supine posture required of MRI/PET is highly unusual, with unknown effects on spatial perception. Nevertheless, despite these difficulties, two studies by Weiss et al. (2000, 2003) used PET (which is somewhat less spatially restrictive than MRI) to investigate bisection in near and far space, reporting largely left-lateralised activations for near, compared to far, space, opposite to the pattern predicted by Longo and Lourenco (2006).

A potentially more suitable method for investigating near and far space is EEG, since participants can be tested while standing in a normal laboratory room. Foxe et al. (2003) used EEG to investigate the neural bases of line bisection, finding evidence for a distinct ERP component (the 'line-bisection effect') generated by the right occipito-parietal cortex when participants performed the landmark task compared to a control task in which participants judged whether or not a transector was present at all. This component was comprised of three sequential phases of activations specific to the landmark task, from 170 to 400 ms after stimulus presentation, shifting progressively from a right occipito-parietal to a right central parietal distribution. Similar results were subsequently reported by Waberski et al. (2008). Foxe et al. (2003) found that the onset of the line-bisection effect systematically tracked the latency of the N1 visual-evoked potential, known to reflect object processing in the ventral visual pathway (e.g., Allison et al., 1999; Murray et al., 2002). Critically, however, the onset of the line-bisection effect followed N1 peak latency. Foxe et al. (2003) suggested that the line-bisection effect reflects the relay between ventral stream object processing and dorsal stream space processing. It is also worth noting that the line-bisection effect emerges well after the P1 component of the visual-evoked potential, which is known to be modulated by direction of attention to specific locations in the visual field (e.g., Martinez et al., 1999; Van Voorhis and Hillyard, 1977). Thus, the line-bisection effect appears to be a distinct ERP component in its own right, rather than reflecting modulation of the amplitude or latency of standard components of the visual evoked-potential. In both the studies of Foxe and colleagues and of Waberski and colleagues, as with the MRI studies described above, only a single viewing distance was used (108 cm in Foxe et al. (2003); 50 cm in Waberski et al. (2008)), making it unclear to what extent these right lateralized activations reflect direction of spatial attention in near or far space.

In the current study, we adapted the paradigm of Foxe et al. (2003) to investigate the neural bases of control over spatial attention in near and far space. Participants performed either the landmark task, or a control, colour task in which they judged whether the presented line was red or blue. Across blocks of trials, they stood at four distances from the screen (30, 60, 90, 120 cm). We could therefore investigate how the effects of spatial attention reported by Foxe and colleagues change as a function of viewing distance. If representations of near space are right-lateralized (Longo and Lourenco, 2006), then the differences between the landmark and control task should decrease as viewing distance increases.

2. Methods

2.1. Participants

Eighteen individuals (seven female), between the ages of 19 and 36 years (*M*: 24.2, *SD*: 5.2), participated for payment or course credit. Participants were on average right-handed as assessed by the Edinburgh Inventory (Oldfield, 1971; *M*: 54.33; range: −100 to 100). Procedures were approved by the local ethics committee.

2.2. Procedures

Stimuli were lines of 23 cm in length and.25 cm in height (480 × 5 pixels) presented on a 22 in. flat-screen computer monitor. Lines were transected by a vertical line at one of 11 equally-spaced locations, ranging from 2.3% of line length to the left of centre to 2.3% to the right. Stimuli were presented using a custom MATLAB (Mathworks, Natick, MA) script and the Cogent Graphics Toolbox (developed by John Romaya, Wellcome Department of Imaging Neuroscience, University College London).

The experiment was divided into 48 blocks of 22 trials each. In each block, participants were instructed to complete one of two tasks, modelled after those of Foxe et al. (2003). As a control task, Foxe et al. (2003) asked participants to judge whether or not the presented lines were transected. This control task has the effect that the actual stimuli delivered in the two conditions differ, since the landmark task can only be performed when lines are transected. We therefore used a different control task in which participants judged whether the presented line was red or blue. Thus, in the *landmark* task, participants judged whether the transector was to the left or to the right of the centre of the horizontal line. In the *colour* task, participants judged whether the line was displayed in red or in blue. Thus, in the landmark task, participants make visuo-spatial judgments, whereas in the colour task, they do not, though the stimuli are exactly the same in both conditions. In both tasks, participants responded by pressing one of the two buttons on a mouse held in their right hand. The 22 trials in each block consisted of one of each combination of the 11 transector locations and two colours, in random order. Lines were displayed for 150 ms. Following responses, there was a random inter-trial-interval of between 500 and 800 ms.

In each block, participants stood at one of four locations marked on the floor with tape, either 30, 60, 90, or 120 cm from the monitor. The monitor rested on a podium, which was adjusted so that the centre of the monitor was approximately at eye level for each participant. The 48 blocks were divided into 6 sequential groups, with each group consisting in one repetition of each block type in random order.

2.3. EEG recording

A SynAmp amplifier system and Scan 4.3 software (Neuroscan, El Paso, TX) were used to record EEG data. Recordings were obtained from 26 scalp electrodes, the 21 electrodes of the standard 10–20 system (Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, O1, Oz, O2) plus an additional 5 electrodes over the occipital–parietal scalp (PO7, PO3, POz, PO4, PO8), placed according to the 10–10 system. Horizontal electroculogram was recorded bipolarly from electrodes placed on the outer canthi of each eye, and vertical electrocologram was recorded from an electrode below the right eye. The reference electrode was placed on the nose, and the ground electrode on the chin. Electrode impedances were kept below 5 KΩ. EEG signals were amplified and digitised at 1000 Hz.

2.4. Analyses

For behavioural data, the percentage of trials in the landmark blocks on which the transector was judged as being right of centre was calculated for each transector location and distance. These psychometric functions were modelled using Cumulative Gaussian functions which were fit to data from each participant at each distance separately using R 2.11.1 software using least-squares regression. Transector locations to the left of centre were coded as negative and those to the right of centre as positive. Three participants were excluded from analyses (behavioural and EEG) as the R^2 value was below 5 for at least one of the distances. Data from the remaining participants showed good fit (mean $R^2=0.844$, $SD=0.051$).

EEG data were analysed using the EEGLAB toolbox (Delorme and Makeig, 2004). Data were downsampled to 250 Hz, digitally low-pass filtered at 30 Hz, and divided into epochs time-locked to the appearance of each line (−100 to 500 ms). Epochs were baseline corrected using the 100 ms before the appearance of each line. Data were cleaned using blind source separation using independent components analysis (Jung et al., 2000) to remove ocular artifacts before automated rejection. Epochs with remaining ocular artifacts (voltage at FPz exceeding $\pm 70\,\mu V$) or other artifacts (voltage at any scalp channel exceeding $\pm 100\,\mu V$) were eliminated (0.16% of trials).

We conducted two types of analyses on the event-related potential (ERP) data. First, we conducted a traditional ERP analysis, calculating mean voltage at each combination of time-point, channel, distance, and task. Second, we used linear regression to quantify change with viewing distance, regressing mean voltage on viewing distance at each combination of time-point, channel, and task, and treating the regression coefficient as the dependent measure (rather than voltage). Foxe et al. (2003) identified three phases of activations specific to spatial attention over the posterior scalp. As our procedure was closely modelled on that study, we adopted these time windows: *Early Phase* (170−190 ms), *Middle Phase* (190–240 ms), and *Late Phase* (240–400 ms). Thus, for both the ERP and regression analyses, mean values within each phase were calculated at right and left posterior channels (PO7/8, PO3/4, P7/8, P3/4), which were averaged within each hemisphere. These electrodes were selected based on the distribution of the line-bisection effect as reported by Foxe et al. (2003).

3. Results

3.1. Behavioural data

For each curve, bias was measured as the point-of-subjective-equality (PSE), calculated as the point at which the curve crossed a *y*-value of.5 (i.e., the point at which participants were equally likely to judge the transector as being to the right or to the left of centre). Fig. 1 shows these values as a function of viewing distance. Change in bias with viewing distance for each participant was quantified by regressing these PSEs on distance using least-squares regression. These regression coefficients were significantly greater than 0 (mean $\beta=0.459\%$ Line Length/Metre), $t(14)=2.73$, $p<0.02$, $d=0.713$. This indicates that bias shifted rightwards with increased viewing distance, consistent with previous results using the landmark task (Bjoertomt et al., 2002; McCourt and Garlinghouse, 2000) and line bisection task (Gamberini et al., 2008; Longo and Lourenco, 2006, 2007, 2010; Lourenco and Longo, 2009; Lourenco et al., 2011; Varnava et al., 2002).

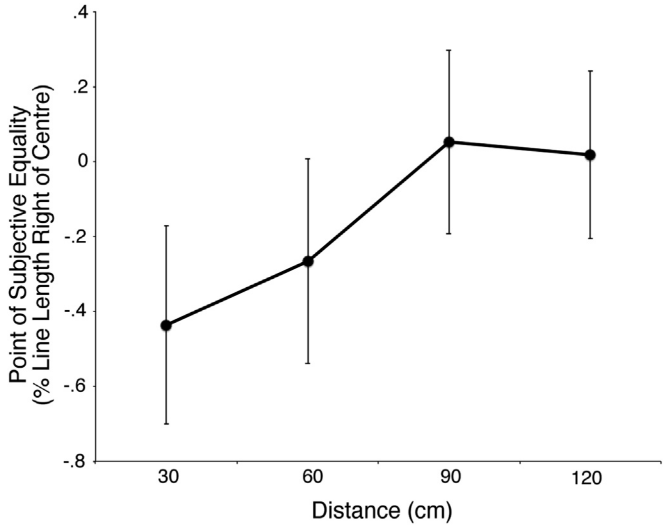

Fig. 1. Behavioural data from landmark judgments. At each distance, the point of subjective equality (PSE) was calculated as the transector location at which participants were equally likely to judge it as being to the left or right of centre. Consistent with previous findings, the small leftward bias seen in near space shifted rightwards with increased viewing distance. Error bars are one standard error.

3.2. Event-related potentials (ERPs)

Fig. 2 shows ERPs in the left and right hemisphere channels for the landmark and colour tasks (left and centre panels) and the difference between the landmark and colour tasks (right panel), all averaged across the four viewing distances. Fig. 3 shows the distribution of voltage across the scalp in the landmark and colour conditions, averaged across time points within each phase and across the four viewing distances. Foxe et al. (2003) reported a right-lateralized negativity associated with the landmark task from approximately 170–400 ms after stimulus presentation, starting out over the occipito-parietal scalp and changing to a central parietal distribution. This effect is clearly apparent in the present data as well. To investigate this effect in more detail, and to determine whether it is affected by distance, we conducted a $4\times2\times2$ repeated-measures analysis of variance (ANOVA) for each phase, with factors *distance* (30, 60, 90, 120 cm), *task* (landmark, colour), and *hemisphere* (left, right).

3.2.1. Early phase (170–190 ms)

There was a marginally-significant main effect of task, $F(1,14)=4.27$, $p=0.058$, $\eta_p^2=0.234$, with amplitude being reduced in the landmark compared to the colour task. There was also a significant main effect of distance, $F(1,68, 23.52)=3.74$, $p<0.05$, $\eta_p^2=0.211$.

3.2.2. Middle phase (190–240 ms)

There was a significant interaction between hemisphere and task, $F(1, 14)=5.60$, $p<0.05$, $\eta_p^2=0.286$. There was a significant reduction in voltage in the landmark task in the right hemisphere,

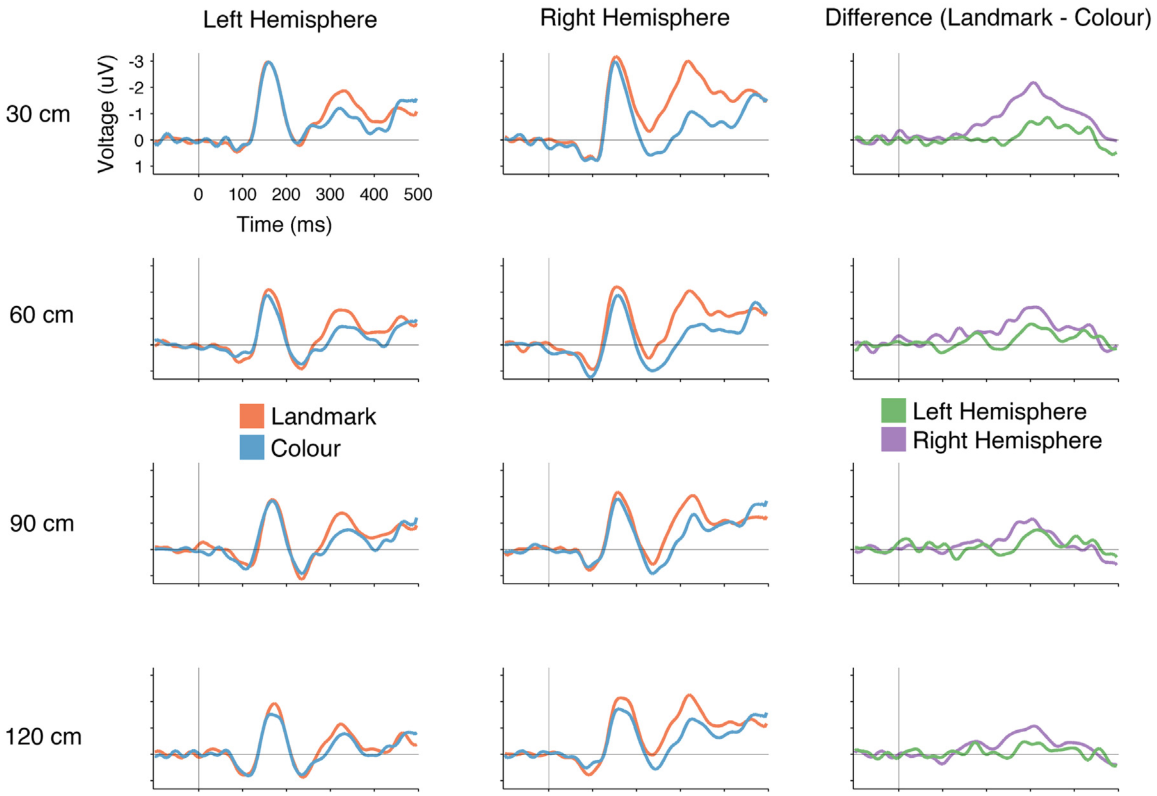

Fig. 2. ERPs in the landmark and colour tasks for each viewing distance in the left hemisphere (left panel, channels PO3, PO7, P3, P7), right hemisphere (centre panel, channels PO4, PO8, P4, P8), and difference waveforms (landmark – colour) in both hemispheres (right panel). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

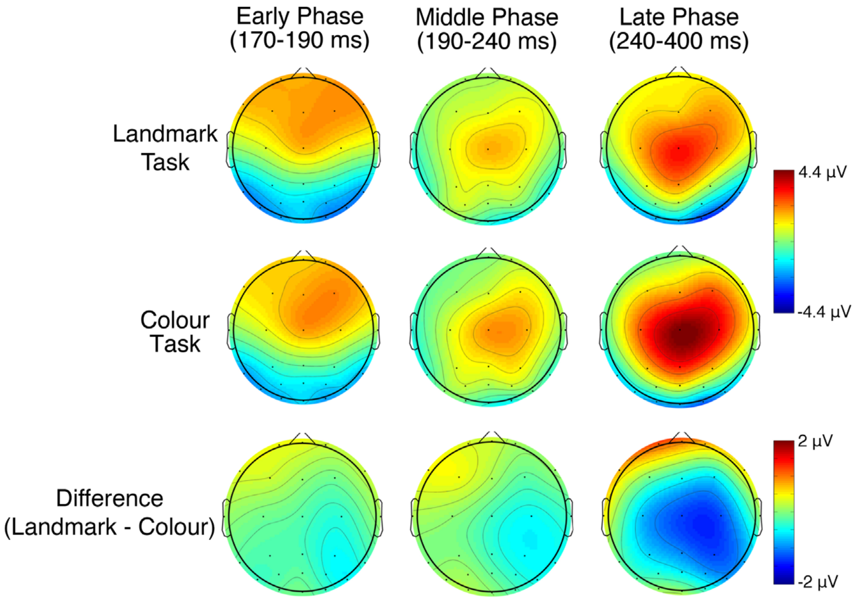

Fig. 3. Scalp maps showing mean voltage across the scalp in the two tasks (and their difference) in each of the three phases.

$t(14) = -2.47$, $p < 0.05$, $d = 0.637$, but not in the left hemisphere, $t(14) = 0.20$, *n.s.* There was a marginally-significant main effect of distance, $F(1.38, 19.36) = 3.69$, $p = 0.058$, $\eta_p^2 = 0.209$, but no interactions between distance and the other factors.

3.2.3. *Late phase (240–400 ms)*

There was a significant main effect of task, $F(1, 14) = 26.62$, $p < 0.001$, $\eta_p^2 = 0.655$, with greater negativity in the landmark than the colour task. Further, there was also a significant interaction between task and hemisphere, $F(1, 14) = 5.41$, $p < 0.05$, $\eta_p^2 = 0.279$. Clear negativities associated with the landmark task were found both in the left, $t(14) = -2.22$, $p < 0.05$, $d = 0.57$, and right, $t(14) = -4.60$, $p < 0.001$, $d = 1.19$, hemisphere, with the effect of task being larger in the right. These results are consistent with the results of Foxe et al. (2003).

There was also a significant main effect of distance, $F(1.90, 26.59) = 4.84$, $p < 0.05$, $\eta_p^2 = 0.257$, which was modulated by a significant interaction of task and distance, $F(3,\ 42)=5.08$, $p<0.005$, $\eta_p^2=0.266$, and a three-way interaction, $F(3,\ 42)=3.13$, $p<0.05$, $\eta_p^2=0.183$.

In order to explore this significant three-way interaction, separate two-way ANOVAs were conducted on the right and left hemispheres. Fig. 4 shows mean voltage as a function of task and viewing distance for the left and right hemisphere channels. In the right hemisphere, there was a clear main effect of task, $F(1,\ 14)=21.16$, $p<0.0001$, $\eta_p^2=0.602$, with increased negativity for the landmark task. The main effect of distance did not quite reach significance, $F(4.42,\ 20.72)=2.99$, $p=0.071$, but there was a clear interaction of task and distance, $F(3,\ 42)=6.56$, $p<0.002$, $\eta_p^2=0.319$. As can be seen in Fig. 4, the difference between the landmark and colour tasks is larger at the closer distance (near space), and smaller at farther distances.

In the left hemisphere, there was a main effect of task, $F(1, 14)=4.94$, $p<0.05$, $\eta_p^2=0.261$, with increased negativity for the landmark task. There was also a significant main effect of distance, $F(7.55,\ 19.61)=5.39$, $p<0.02$, $\eta_p^2=0.278$, with negativity decreasing with increased viewing distance. Critically, however, this change with distance showed up for both the colour and landmark tasks, resulting in no significant interaction of task and distance, $F(3, 42)=0.572$, $p=0.637$. Thus, while there is an effect of viewing distance in the left hemisphere, this effect – in contrast to the right hemisphere – was not modulated by task, suggesting it that not specific to spatial attention.

3.3. Regression analyses

The ERP analyses have Proffitt et al. (2003) and shown further that these effects are modulated by distance. In order to investigate in more detail how the ERPs are modulated by distance, we used regression to quantify changes in voltage with viewing distance. At each combination of participant, time point, channel, and task, we calculated the linear regression coefficient, regressing mean voltage on viewing distance. The logic of this analysis is analogous to the use of regression to investigate changes in lateral attentional biases with viewing distance as in the current study with the landmark task and previous studies using overt line bisection (e.g., Longo and Lourenco, 2006, 2007; Lourenco and Longo, 2009; Lourenco et al., 2011; Varnava et al., 2002). By thus regressing voltage on viewing distance, the time-course and scalp-distribution of neural responses modulated by viewing-distance can be assessed and compared between the landmark and colour tasks. Fig. 5 shows time-series of the regression coefficient regressing voltage on viewing distance, whereas Fig. 6 shows corresponding scalp maps averaged within each of the three periods. Although the resulting waves are not ERPs (reflecting change in voltage with distance, rather than voltage per se), they can be treated statistically in exactly the same way as the ERPs. Thus, within each phase, a 2×2 ANOVA was conducted with factors *hemisphere* (left, right) and *task* (landmark, colour).

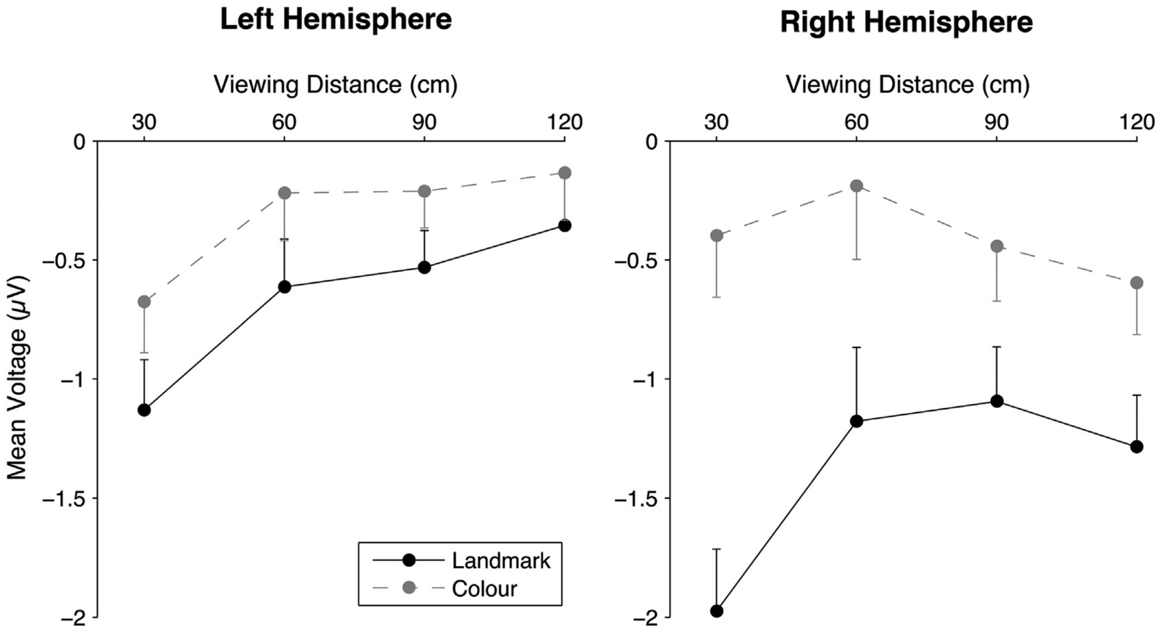

Fig. 4. Mean voltage in the *Late Phase* (240–400 ms) as a function of hemisphere, viewing distance, and task. Error bars are one standard error of the difference between the landmark and colour tasks at each combination of distance and hemisphere. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

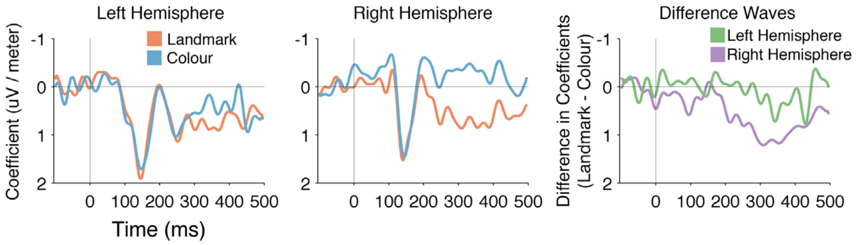

Fig. 5. Time-series of the regression coefficient regressing voltage on viewing distance. At each channel and time-point, least-squares regression was used to quantify the change in voltage with viewing distance.

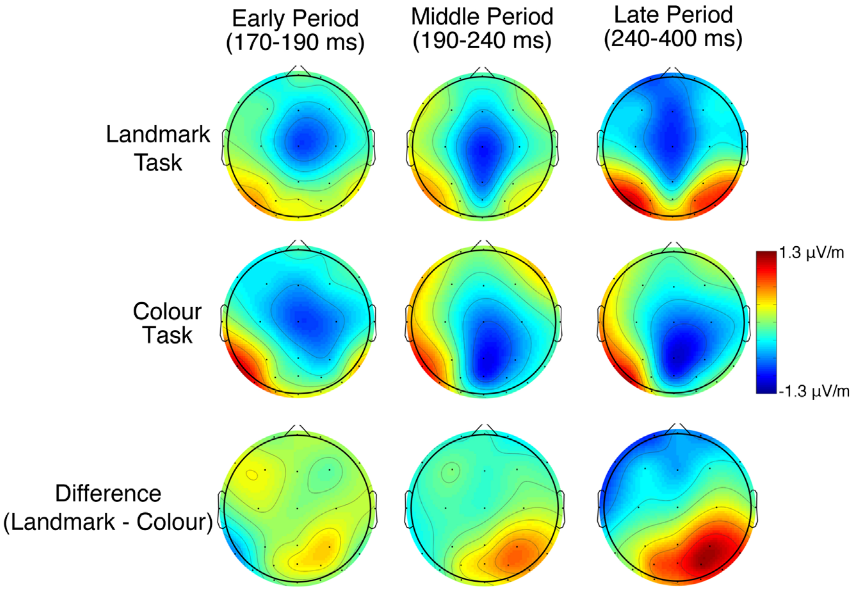

Fig. 6. Scalp maps showing mean regression coefficients for the two conditions and their difference in each of the three phases.

3.3.1. *Early phase (170–190 ms)*

There were no significant effects of hemisphere, task, or their interaction (all *p*'s > 0.20).

3.3.2. *Middle phase (190–240 ms)*

There was a significant main effect of task, $F(1, 14)=4.79$, $p<0.05$, $\eta_p^2=0.255$, with coefficients being larger in the landmark than the colour task. There was also a marginally-significant interaction of task and hemisphere, $F(1, 14)=3.65$, $p=0.077$, $\eta_p^2=0.207$. As is clear in Figs. 5 and 6, regression coefficients were greater for the landmark than for the colour task in the right hemisphere, $t(14)=3.31$, $p<0.01$, $d=0.85$, but the tasks did not differ in the left hemisphere, $t(14)=-0.256$, *n.s.*, $d=0.07$.

3.3.3. *Late phase (240–400 ms)*

There was a significant effect of task, $F(1, 14)=22.30$, $p<0.0005$, $\eta_p^2=0.614$, with coefficients being larger in the landmark task than the colour task. There was also a significant interaction of task and hemisphere, $F(1, 14)=5.31$, $p<0.05$, $\eta_p^2=0.275$. There was a clear effect of task in the right hemisphere, $t(14)=4.91$, $p<0.0005$, $d=1.27$, but not in the left hemisphere, $t(14)=1.19$, *n.s.*, $d=0.31$.

4. Discussion

A large literature has linked performance on line bisection and landmark tasks to activations of the right occipital and parietal cortices (e.g., Çiçek et al., 2009; Fink et al., 2000, 2001, 2002; Foxe et al., 2003; Waberski et al. 2008). The present results are consistent with this literature, Proffitt et al. (2003) that spatial attention in the landmark task produces clear negativities over the right occipito-parietal scalp. Further, we show that these responses are strongest for stimuli presented in near space, and become weaker for stimuli presented farther away. These results suggest that the right occipito-parietal cortex may be specialised not for the orientation of spatial attention generally, but more specifically for the orientation of spatial attention in the near space immediately surrounding the body.

4.1. *Spatial attention and the right hemisphere*

That the right hemisphere is specialized for visuospatial attention has long been argued on the basis of neuropsychological dissociations in split-brain (e.g., Sperry, 1974) and neglect (e.g., Kinsbourne, 1987; Mesulam, 1981) patients, as well as the neuroimaging results discussed above. Consistent findings have also come from studies using transcranial magnetic stimulation (TMS; Bjoertomt et al., 2002; Oliveri and Vallar, 2009) and voxel-based lesion-symptom mapping (Verdon et al., 2010). A recent study by Thiebaut de Schotten et al. (2011) used diffusion imaging to identify a potential structural basis for such lateralization. These authors found three longitudinal white-matter tracts connecting the parietal and frontal cortices in humans, analogous to those previously reported in monkeys (Schmahmann and Pandya, 2006). They found that one of these, the ventral superior longitudinal fasciculus (SLF III) was strongly right-lateralised with larger volume in the right than in the left hemisphere, while another, the middle superior longitudinal fasciculus (SLF II) showed more modest lateralisation. Further, they found that the degree of lateralization of the SLF II was correlated across participants with the magnitude of pseudoneglect measured with a line bisection test as well as lateralization of reaction times to stimuli on the left side of space using a Posner paradigm.

These results provide an intriguing anatomical correlate to behavioural lateralizations reported previously and to the results of the present study. One possibility in light of the present results is that these SLF II and SLF III pathways may be specialised specifically for visuospatial attention in near space. This would provide a potential anatomical correlate of the right-hemisphere specialisation for near space suggested by the present results. This interpretation is consistent with results of an fMRI study by Quinlan and Culham (2007), who found activations in the parieto-occipital cortex that were stronger for stimuli presented near the participant than farther away, though there was no obvious lateralization in responses.

It is unclear given the present results why previous neuroimaging studies have either no lateralisation (Quinlan and Culham, 2007) or even left-lateralised frontal responses (Weiss et al., 2000, 2003). One possibility is that space perception may be altered by the supine posture used in those previous studies. It is possible that near space reflects not just distance from the body per se, but some interaction between the body and the gravitational field. The possibility of such a connection is supported by the recent finding that lateralised galvanic vestibular stimulation alters spatial attention in the line bisection task (Ferrè et al., 2013). It will be important for future research to examine the factors which determine or modulate the lateralisation of neural mechanisms underlying spatial attention in near and far space.

One potential concern about the present results is that while stimuli were matched for actual physical size across viewing distances, they differed in terms of visual angle. It is important to note, however, that our main results cannot be interpreted as resulting from differences in visual angle, rather than viewing distance, since at any given distance stimuli were exactly matched in the landmark and colour conditions. Our finding that the line-bisection effect, indexed as the difference between the landmark and colour tasks itself scaled with viewing distance therefore cannot be interpreted as a simple effect of angular size. In our first study using the line bisection task (Longo and Lourenco, 2006), we held actual size constant, but used a range of stimulus sizes, which allowed us to analyse a subset of trials that held visual angle constant. Critically, both the left-to-right shift in bisection bias with increasing viewing distance and the reduction of this effect when a tool was used for responding showed up clearly whether stimuli were matched for actual or angular size. This result suggests that differences in visual angle do not play a critical role in determining the modulation of spatial attentional biases with viewing distance.

4.2. *Implications for the nature of pseudoneglect*

The activation-orientation theory of spatial attention (Bultitude and Aimola Davies, 2006; Reuter-Lorenz et al., 1990) proposes that attention will be biased in the direction contralateral to the most strongly activated cerebral hemisphere. Given that leftward biases on bisection and landmark tasks (i.e., pseudoneglect) are reduced or eliminated when stimuli are presented far from participants (e.g., Longo and Lourenco, 2006; McCourt and Garlinghouse, 2000; Varnava et al., 2002), Longo and Lourenco (2006) proposed that pseudoneglect may reflect representations of near space in the right parietal cortex. On this interpretation, the closer stimuli are presented to participants, the more strongly activated these representations would be, and the stronger pseudoneglect. As stimuli are presented at farther distances, in contrast, these right hemisphere representations would become progressively less strongly activated, resulting in a reduction or reversal of the leftward bias found in near space.

The present results are consistent with this interpretation. The occipito-parietal negativity specific to spatial attention (the ‘line-bisection effect’) originally reported by Foxe et al. (2003) was increased for stimuli presented close to the participant, in near space. On this interpretation, the pseudoneglect observed on paper-and-pencil tasks reflects the sum of two spatial biases, a baseline rightward attentional bias (cf. Kinsbourne, 1987) and a countervailing leftward bias induced by activation of representations in near space in the right hemisphere. On average, the latter bias may be slightly stronger, resulting in the pseudoneglect seen at the group level. However, the magnitude of these two biases may vary independently across individuals, which the baseline rightward bias being stronger in some individuals, perhaps related to known factors such as arm length (Longo and Lourenco, 2007) or characteristic activation asymmetries between the hemispheres (Levy et al., 1983). This may contribute to the notorious person-to-person (and study-to-study) variability seen in bisection and landmark tasks (Jewell and McCourt, 2000).

4.3. *Differences between landmark and bisection tasks*

Studies investigating line bisection in near and far space have typically found a small leftward bias in near space and a (somewhat larger) rightward bias in far space (e.g., Ferrè et al., 2013; Gamberini et al., 2008; Longo and Lourenco, 2006, 2007, 2010; Lourenco and Longo, 2009; Lourenco et al., 2011; Varnava et al., 2002). In contrast, studies using the landmark task have found a leftward bias in near space and a smaller leftward bias (or no bias at all) in far space (e.g., Bjoertomt et al., 2002; Bjoertomt et al., 2009; McCourt and Garlinghouse, 2000; this study). In both tasks, there is a rightward *shift* in bias as stimuli are presented farther away, consistent with the proposal that the right occipito-parietal cortex is specialized for representation of near space. However, this rightward shift only appears to develop into an absolute rightward bias for overt bisection.

This pattern suggests important functional differences between bisection and landmark tasks, consistent with dissociations between these tasks reported both in neuropsychological patients (e.g., Harvey et al., 2002; Ishiai et al., 1998) and healthy adults (e.g., Varnava et al., 2013). The meta-analysis of Jewell and McCourt (2000) found much larger effect sizes for pseudoneglect measured using landmark than manual (overt) bisection. One possible interpretation of this pattern is that the motoric component required on manual bisection tasks produces activations in the left hemisphere (particularly in right handed individuals) which has the effect of shifting attention rightward compared to the more perceptual landmark task.

Acknowledgements

This research was supported by an European Research Council Award (ERC-2013-StG-336050) under the FP7 to MRL.

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