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Research Report

A toggle switch of visual awareness?

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ABSTRACT

Major clues to the human brain mechanisms of spatial attention and visual awareness have come from the syndrome of neglect, where patients ignore one half of space. A longstanding puzzle, though, is that neglect almost always comes from right-hemisphere damage, which suggests that the two sides of the brain play distinct roles. But tests of attention in healthy people have revealed only slight differences between the hemispheres. Here we show that major differences emerge if we look at the timing of brain activity in a task optimized to identify attentional functions. Using EEG to map cortical activity on a millisecond timescale, we found transient (20–30 ms) periods of interhemispheric competition, followed by short phases of marked right-sided activity in the ventral attentional network. Our data are the first to show interhemispheric interactions that, much like a toggle switch, quickly allocate neural resources to one or the other hemisphere.

1. Introduction

Imagine browsing a busy store. You gaze at a shelf, then a face, and then your mind focuses on a coat's price tag, yet you never stop noticing the surrounding buzz as you continue to explore. Underlying your explorations are mechanisms of spatial attention and visual awareness, fundamental to human cognition. Key aspects of these mechanisms must be implemented in the right hemisphere because they fail in right-brain damaged patients with spatial neglect who cease to perceive and respond to the world on their left (Karnath, Fruhmann Berger, Kuker, & Rorden, 2004; Mort et al.,, 2003; Verdon, Schwartz, Lovblad, Hauert, & Vuilleumier, 2010).

But research to date has not been able to consistently isolate equivalent right-dominant mechanisms in healthy participants. Probing intact visuospatial functions in several tasks has revealed two attentional networks (Corbetta & Shulman, 2002; Corbetta, Patel, & Shulman, 2008; Vossel, Geng, & Fink, 2013): One dorsal attentional network (DAN) responds during goal-directed behavior, involving superior frontal and intra-parietal areas mainly in both hemispheres as early as 150 ms post-stimulus onset (Simpson et al., 2011). A ventral attentional network (VAN) responds to unexpected events, implicating the temporo-parietal junction and middle and inferior frontal cortex, starting from around 200 ms or later, coinciding in time with the N2pc, an ERP component that is sensitive to spatial attention (Hickey, Di Lollo, &

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McDonald, 2009). Furthermore, the VAN tends to be more lateralized to the right hemisphere than the left, but not always (Asplund, Todd, Snyder, & Marois, 2010).

To chart right-dominant mechanisms related to neglect, research has turned neglect tests into experimental paradigms for healthy participants. As such, perceptual judgment tasks, known to capture strong rightward attentional biases in patients (Mattingley et al., 2004; Schenkenberg, Bradford, & Ajax, 1980), have revealed small leftward biases in healthy people (Mattingley, Bradshaw, Nettleton, & Bradshaw, 1994; McCourt & Jewell, 1999). This "pseudoneglect" complements biases in neglect; it activates areas (Çiçek et al., 2009; Fink et al., 2000; Loftus et al., 2012) similar to lesion sites in patients (Rorden, Fruhmann Berger, & Karnath, 2006), and responds to similar modulations of stimuli (McCourt & Jewell, 1999), attention (Bultitude & Aimola, 2006; McCourt, Garlinghouse, & Reuter-Lorenz, 2005), and cognitive load (Emrich, Burianova, & Ferber, 2011; O'Connell, Schneider, Hester, Mattingley, & Bellgrove, 2011). Still, the right-brain dominance is relative because activation tends to vary with task (Cavézian et al., 2012), control condition (Revill, Karnath, & Rorden, 2011), and instruction (Fink, Marshall, Weiss, Toni, & Zilles, 2002); moreover, perceptual measures tend to show inconsistent results, such as limited correlations of biases across similar tasks (Mattingley et al., 2004) and limited test-retest reliability with longer presentation times (McCourt, 2001).

Three factors could obscure right-brain dominance. (1) Mechanisms could be short-lived and missed by temporally sluggish imaging. (2) Pseudoneglect paradigms could activate unrelated functions, thus requiring better control. (3) Intact right dominance could be subtle. Asymmetries could surge when lesions push interhemispheric competition out of balance (Koch et al., 2008). However, interactions between competition and right dominance have yet to be demonstrated.

Here we show that all three factors are crucial to identify right-dominant visuospatial functions. We capture pseudoneglect with a sensitive grating-scales task (Niemeier, Stojanoski, & Greco, 2007; initially derived from tasks such as the "greyscales task", e.g., Nicholls, Bradshaw, & Mattingley, 1999) that asks people to compare compound gratings (Fig. 1a). Importantly, only comparing the higher spatial frequencies of the stimuli (HI condition) produces more attention-sensitive biases than lower frequencies (LO condition), due to lower stimulus salience in the latter (Singh, Stojanoski, Le, & Niemeier, 2011). Using continuous electroencephalography (EEG) to map correlates of the HI/LO contrast, we expected modulations with the right hemisphere starting at around the N2, and as expected, we observe transient interhemispheric competition followed by pronounced right dominance in the posterior and frontal VAN from 242 to 394 ms.

2. Materials and methods

2.1. Participants

Nineteen right-handed undergraduate students (8 females, median age 19, no history of neurological or vision problems) at the University of Toronto Scarborough gave their informed and written consent to participate. All procedures were approved by the Human Participants Review Subcommittee of the University of Toronto.

2.2. Procedure

Participants fixated the centre of a 19″ CRT monitor (768 by 1024 pixels, 100 Hz) at a distance of 90 cm and performed a grating-scales task (Fig. 1a; Niemeier et al., 2007), a sensitive and specific measure of pseudoneglect (Niemeier et al., 2007; Singh et al., 2011). The task presented pairs of horizontal bars (14.5° wide) filled with luminance-defined sine wave gratings (.6–2 cycles/°). Spatial frequency increased as a function of a half-cycle of a cosine within an approximately central area (dashed rectangle, not shown during experiment), and was constant outside the area. The central area was placed at 11 different positions from ± 12.5% left or right of bar center (positions −12.5%, 0%, and +12.5% are shown). Participants chose the upper or lower bar depending on which appeared to have "more of the thinner" or "thicker stripes" (HI and LO condition, respectively).

Both tasks produce biases, and these biases are positively correlated. Nevertheless, these biases exhibit some important properties, suggesting that the tasks trigger different neural mechanisms. First, only HI biases interact with attentional cues (Singh et al., 2011), as mentioned earlier. Second, HI and LO biases respond differently when distracting pixel noise is added to the stimuli such that HI biases shift exponentially to the left, whereas LO biases shift rightward (Chen & Niemeier, 2014; Niemeier, Singh, Keough, & Akbar, 2008a).

The two grating-scales bars were surrounded by one white and one black frame, respectively. During the FRAME control condition participants indicated which frame was black. Stimuli were presented for 75 ms to discourage attempts to count the stripes of the stimuli or to make exploratory eye movements. Systematic differences in fixation across conditions could be ruled out given the nil effects of the early ERP components, as will be seen in the Results (Section 3.2).

The HI, LO, and FRAME conditions were administered in 18 separate blocks (96 trials each) and the order of blocks was randomly chosen from 1 of 6 possible ones: AABBCCCCB-BAAAABBCC, where letters A, B, and C could indicate any of the three conditions. Participants were asked to delay their response by about 1 s to separate readiness potential over premotor and motor cortex from stimulus-related ERPs (Foxe, McCourt, & Javitt, 2003), and subsequent trials started 500 ms after their responses.

2.3. Data analysis

2.3.1. Behavioral measures

Based on 11 levels of (a)symmetry of the grating-scales stimuli and participant responses (Fig. 1a) we used sigmoid Weibull functions to model probabilities of choosing the grating-scales bar with the target feature (high or low spatial frequencies) on the left and to estimate the asymmetry that would produce a probability of .5. This point of subjective equality tends to be biased to the left in the HI condition (Niemeier et al., 2007). For instance, the second grating-scales stimulus in Fig. 1a consists of two mirror-symmetric bars, but most people would perceive the lower rectangle as carrying "more of the thinner stripes". In contrast, in the LO condition people tend to show

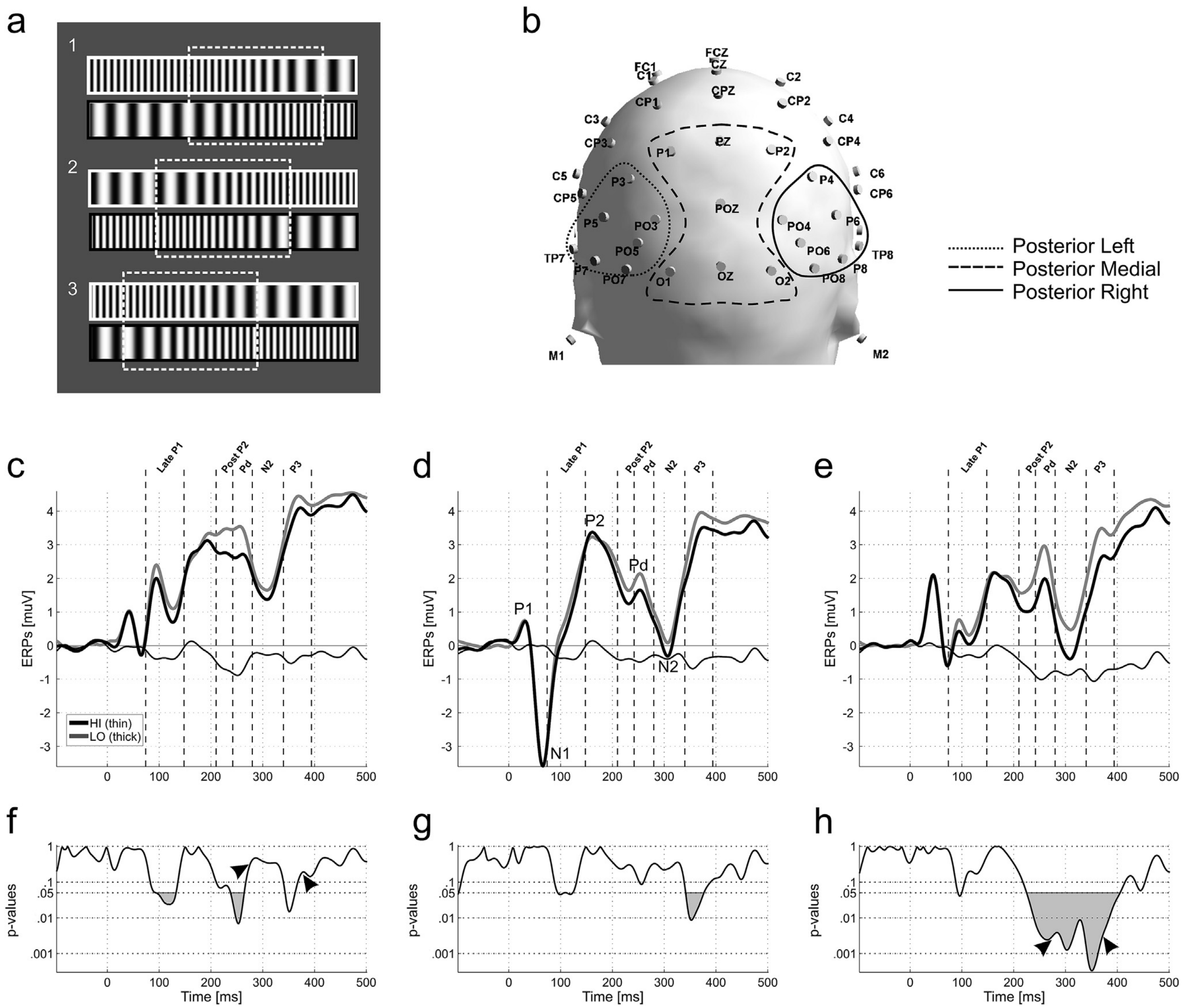

Fig. 1 – **The grating-scales task and event-related potentials (ERPs). (a) The task presented pairs of horizontal bars filled with sine wave gratings. Participants chose the upper or lower bar depending on which appeared to have "more of the thinner" or "thicker stripes" (HI and LO condition, respectively). During the FRAME control condition participants indicated which frame was black. (b) Posterior scalp regions. (c) ERPs for HI and LO conditions aligned relative to stimulus onset averaged over left, (d) medial, (e) right posterior scalp-sites demonstrated typical visual ERP components with the P1 outlasting the N1 at lateral electrodes (peak electrodes yielded very similar results). Vertical dashed lines indicate phases derived from a k-means cluster analysis (see Methods; clusters with significant HI/LO effects: *late P1*: 74–148 ms, *post-P2*: 210–242 ms, P_D: 242–280 ms, *N2*: 280–340 ms, *P3*: 340–394 ms). (f) *p*-Value curves of point-by-point *t*-test comparisons of HI and LO ERPs over left, (g) medial, (h) right posterior scalp sites. Shaded areas mark significant differences based on a significance criterion of 11 consecutive time-points with *p*-values <5%. (Guthrie & Buchwald, 1991)**

smaller leftward biases or even rightward biases. However, such HI/LO differences are mainly apparent with pixel noise added to the stimuli (Chen & Niemeier, 2013, abstract), or when using attention-distracting cues (Singh et al., 2011). This was beyond the scope of the current study.

2.3.2. *Electrophysiological measures*

With an ASA system (ANT Neuro, Enschede) we recorded from 64 sintered Ag/AgCl scalp electrodes mounted in a 10–5 array on an elastic cap. Electrode impedances were kept below 10 kΩ and sampled at 512 Hz with the left mastoid as a reference. We re-referenced data off-line to the average of all electrodes, bandpass filtered between .5 and 30 Hz.

We epoched data from −100 ms before to 500 ms after stimulus onset, and baselined relative to the prestimulus period. Epochs with eye-movement artefacts (blinks or saccades; >30 μV at Fp1 and Fp2) or other artefacts (±30 μV at all other electrodes) were rejected. Average rejection rate was 13.8% ± 14.8%. For 5 participants, up to 5 noisy electrodes were interpolated. The data were then grand-averaged to obtain

ERPs for the HI, LO and FRAME conditions separately. However, for 5 other participants 30 or more electrodes were noisy or entirely dysfunctional due to cap failure. These data sets were removed from EEG analysis.

To examine the resulting ERPs we focused on HI/LO differences because we were mainly interested in mechanisms specific to the HI but not the LO condition. Given the lack of a priori knowledge about ERP specific to the HI/LO difference we used a hierarchical data-driven approach to curb type I errors. To this end we first submitted the data to a topographic k-means cluster analysis using Cartool (Murray, Foxe, Javitt, & Foxe, 2004). Specifically, we submitted the HI/LO difference waves rather than the ERPs for separate experimental conditions to enhance the method's sensitivity to HI/LO effects and to obtain time segments of whole-scalp maps of the HI/LO effect (Murray et al., 2004). The analysis is suitable because brain electric field configurations remain stable for longer stretches of time reflecting stable functional brain states (Pascual-Marqui, Michel, & Lehmann, 1995) with relatively quick transitions. Briefly, the analysis uses linear correlations between electric field distributions at individual time points to sort the data into a subset of temporal clusters. We optimized the number of clusters according to standard criteria ensuring the best trade-off between a small amount of clusters (Pascual-Marqui et al., 1995) and a maximum of explained variance (Krzanowski & Lai, 1985). Next, temporally discontinuous clusters were broken up and clusters shorter than 10 ms were merged with neighboring clusters based on correlations so that we arrived at 14 clusters of which we further examined 5 because only these phases showed significant HI/LO differences (based on more than 11 significant consecutive time points at individual electrodes and scalp regions, to correct for multiple comparisons; see Guthrie & Buchwald, 1991; Figs. 1c–h and 2a; and Suppl. Fig. 1).

Within the preselected phases (as defined above), we next averaged voltages across time but relaxed the spatial scope of analysis to explore the factorial structure of the data with repeated measures analysis of variances (ANOVAs) with one task factor (HI/LO) and two scalp factors: Sagittal (frontal/central/posterior) and Coronal (left/medial/right; Table 1). That is, we segmented the scalp into 9 regions with posterior regions following the topography of the P1 (posterior left: TP7, CP5, P3, P5, P7, PO3, PO5, PO7; posterior medial: P1, Pz, P2, POz, O1, Oz, O2; posterior right: TP8, CP6, P4, P6, P8, PO4, PO6, PO8) and equivalent regions at central and frontal scalp sites (central left: T7, FT7, FC3, FC5, C3, C5, CP3; central medial: FC1, FCz, FC2, C1, Cz, C2, CP1, CPz, CP2, central right: T8, FT8, FC4 FC6, C4, C6, CP4; frontal left: F3, F5, F7, AF3, AF7, Fp1; frontal medial: F1, Fz, F2; frontal right: F4, F6, F8, AF4, AF8, Fp2). Subsequently, we relaxed the temporal criterion to inspect consecutive paired *t*-tests for scalp regions and electrodes for more detailed aspects of timing. We examined equivalent HI/FRAME contrasts for an approximation of contrasts reported in publications on line bisection.

3. Results

3.1. *Behavioral results*

We expected leftward biases for the HI condition, and relatively smaller leftward biases or even rightward biases for the LO condition. As expected, we found an overall trend for a difference between HI and LO biases [$t(18) = 1.47$, $p = .159$; individual biases did not differ from zero: p's > .50]. HI and LO biases differed significantly during earlier blocks of trials [blocks 1–6: $t(18) = 2.80$, $p = .012$; blocks 1–9: $t(18) = 2.17$, $p = .044$] consistent with a time-on-task effect (Manly, Dobler, Dodds, & George, 2005). We found no equivalent time-on-task effect for the ERP data and therefore focused our ERP analysis on data from all experimental blocks.

3.2. *Electrophysiological results*

3.2.1. *HI/LO contrasts*

As expected, event-related potentials (ERPs), time-locked to task onset, revealed brief right-dominant HI/LO modulations with greater negativity for the HI than the LO condition between the P2 and P3 components (Figs 1c–e and 2a). To inspect the effect, we submitted the HI/LO contrasts to a hypothesis-free k-means cluster analysis (see Methods). The data pooled, based on similar topography, into four clusters or phases with significant, right-biased differences. For ease of communication, we will refer to these phases using the names of the ERP component that coincide with the respective phase. The first phase, called "post-P2 phase" after the ERPs at posterior electrodes, showed a HI/LO difference at central and latero-posterior electrodes, although posterior left electrodes reached significance only during the following, "distractor positivity (P_D; Hickey et al., 2009) phase". The "N2 phase" then marked a 60-ms period of absolute dominance of the HI/LO effect at posterior right electrodes. Finally, the effect spread, during the "P3 phase", to central right and posterior medial scalp (Figs. 1d and 2a) with greater HI than LO positivity at frontal sites (Fig. 3), although posterior right dominance reemerged briefly near the end of the cluster. ANOVAs (task factor HI/LO and topography factors Sagittal: frontal/central/posterior, and Coronal: left/medial/right; Table 1 for details) confirmed the topography of the effect (3-way interactions during post-P2, PD, and N2 phases: $p < .002$; HI/LO × Sagittal interaction during P3 phase: $p = .034$). An additional "late P1 phase" captured an earlier trend for a HI/LO difference, especially at left posterior electrodes, although too small for the ANOVA (HI/LO related p's > .18).

We used multiple signal classification (Mosher & Leahy, 1998) to estimate which neural structures generated the HI/LO effect (Fig. 3). For the post-P2 phase, the algorithm extracted a range of possible posterior dorsal and ventral sources, with a relative focus around the lingual gyrus. After that, sources settled more narrowly in structures consistent with the VAN: first in posterior middle and inferior temporal areas, including Brodmann area 37 (P_D phase), then in a similar middle temporal region and also an emerging focus in inferior and middle frontal gyrus (N2 phase), and finally in inferior frontal cortex (P3 phase). In addition, sources during the late P1 phase involved occipito-parietal regions, roughly the precuneus.

3.2.2. *Contrasting the HI condition with a less specific control condition*

Other contrasts, unlike the HI/LO difference, may produce effects that are less specific. We demonstrated this with a

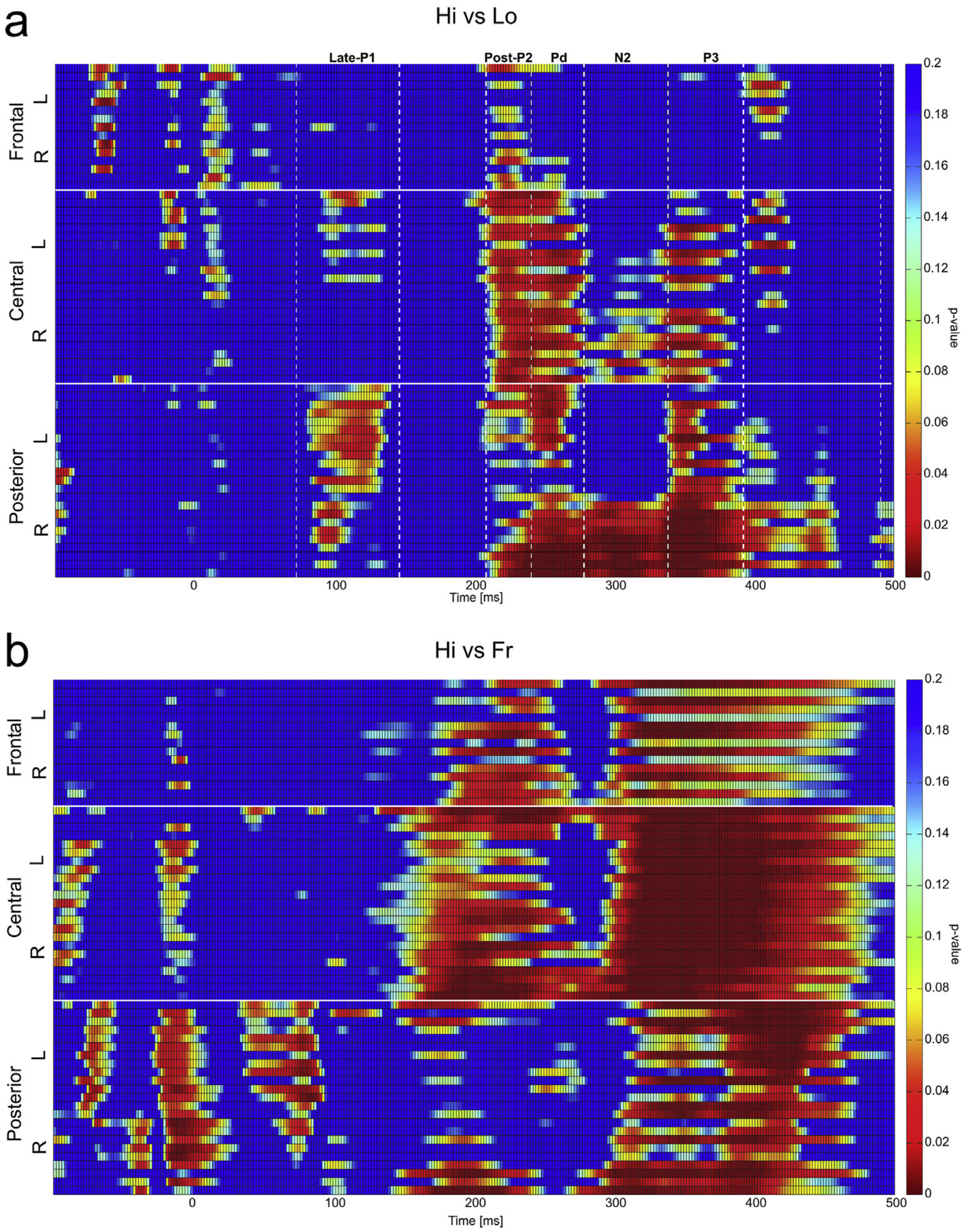

Fig. 2 – *p*-Value heat maps of *t*-tests at all electrodes and time points. (a) HI/LO contrast. Vertical dashed lines and numbers indicate phases with significant HI/LO effects. (b) HI/FRAME contrast.

FRAME control condition, where participants viewed the same grating-scales stimuli but performed an unrelated task (Fig. 1a), similar to control tasks in other pseudoneglect studies (Cavézian et al., 2012; Çiçek et al., 2009; Fink et al., 2000; Foxe et al., 2003; Waberski et al., 2008). We found, the HI/FRAME contrast largely obscured the right-posterior effects between P2 and P3 (Fig. 2b and Suppl. Fig. S1), although it did generate strong effects at other times, especially over central scalp that agree well with previous reports (Cavézian et al., 2012; Çiçek et al., 2009). However, the effects were only somewhat right-lateralized, indicating that the HI/FRAME contrast was less effective at controlling for functions unrelated to the core of right-dominant visuospatial mechanisms compared to the HI/LO contrast.

3.2.3. *Comparing left and right scalp*

Inspecting the HI/LO contrasts once more, we noted signs of left-brain suppression during the period of right dominance. That is, left-brain dipole sources disappeared after the post-P2 phase (Fig. 3). What is more, the left posterior difference wave (Fig. 1c) and corresponding *p*-value curve (Fig. 1f) declined rapidly, first towards the end of the P_D phase and again during the P3 phase whereas right posterior effects remained or declined later (e.g., arrow heads in Fig. 1f *vs* h). We plotted the left and right posterior difference waves in Fig. 4a together with the difference between them. To calculate the latter, we subtracted the HI/LO difference over left posterior scalp (dashed curve) from the HI/LO difference over the right posterior scalp (thin solid curve). The resulting lateralization

Table 1 – F and p-values for 3-way ANOVAs (F1: HI/LO, F2: Frontal/Central/Posterior, F3: Left/Medial/Right) for Each Cluster Time Period.

Cluster	Effect	F's	p's
Late P1 (74–148 msec)	F1	1.96	.185
	F2	6.53	.005**
	F3	5.54	.010**
	F1 × F2	.43	.654
	F1 × F3	.04	.963
	F2 × F3	1.04	.394
	F1 × F2 × F3	.21	.932
Post P2 (210–242 msec)	F1	5.77	.032*
	F2	14.96	.000**
	F3	5.95	.008**
	F1 × F2	.25	.782
	F1 × F3	.08	.920
	F2 × F3	2.30	.071
	F1 × F2 × F3	4.90	.002**
P_D (242–280 msec)	F1	6.32	.026*
	F2	32.39	.000**
	F3	4.99	.015*
	F1 × F2	1.17	.326
	F1 × F3	.91	.413
	F2 × F3	1.19	.328
	F1 × F2 × F3	6.42	.0003**
N2 (280–340 msec)	F1	2.14	.167
	F2	19.26	.000**
	F3	2.77	.081
	F1 × F2	2.53	.099
	F1 × F3	2.17	.135
	F2 × F3	2.85	.033*
	F1 × F2 × F3	5.70	.001**
P3 (340–394 msec)	F1	.73	.410
	F2	15.13	.000**
	F3	1.84	.179
	F1 × F2	3.88	.034*
	F1 × F3	2.39	.111
	F2 × F3	4.03	.006**
	F1 × F2 × F3	2.24	.077

$^{*}p < .05$, $^{**}p < .01$. *Note*: An analysis of variance (ANOVA) of the post-P2 cluster or phase revealed a main effect of HI/LO ($p = .03$) and a 3-way interaction ($p = .002$). Next, the P_D phase showed bilateral differences across central and lateral posterior electrodes, which disappeared after 17–31 ms, except for differences at posterior right electrodes (Figs. 1c–h and 2a; main HI/LO effect: $p = .026$; 3-way interaction: $p = .0003$). During the N2 phase, only posterior right electrodes showed the HI/LO effect (Figs. 1e and 2a; 3-way interaction: $p = .0007$) with mere trends elsewhere (Fig. S1). During the P3 phase, the HI/LO effect spread to central right and posterior medial regions (Figs. 1d and 2a), and at frontal sites it produced a greater positivity for HI than LO (Fig. S1; Fig. 3) that resulted in an interaction with the frontal/central/posterior factor ($p = .034$). In addition, the late P1 phase captured an earlier HI/LO difference, especially at left posterior electrodes (95–132 ms; Fig. 2a), although the effect was brief and too small for the ANOVA (HI/LO related p's > .18).

curve showed two negative-going maxima of right-dominance at 300 ms and at 355 ms, shortly after the left posterior HI/LO effect declined.

To see whether the left decline and right dominance were caused by interhemispheric competition (Kinsbourne, 1977; Koch et al., 2008; Niemeier et al., 2007), we reasoned that competing brain regions should be negatively correlated in their activity. Although, their ERPs should show no more than reduced positive correlations given the spread of voltages at the scalp and topographical symmetry. Indeed we obtained highly significant positive correlations between left/right posterior electrodes throughout the entire epoch. However, there were three spike-like declines in correlation (Fig. 4b; similar trends also observed in left/right central electrodes). Spikes 2 and 3 occurred at 296 ms and 345 ms, respectively, and so just before the two HI/LO lateralization maxima during the P_D and the P3 phases (Fig. 4a *vs* b). Spike 1, during the late-P1 phase, was succeeded by a small maximum emerging at the end of cluster (Fig. 4a). The three decorrelation spikes were associated with the precuneus, middle temporal cortex, and inferior frontal cortex, respectively (Fig. 4b). These spikes in interhemispheric decorrelation were specific to the lateral posterior electrodes: We did not observe decorrelation spikes for any other interhemispheric comparisons (left *vs* right/left *vs* medial/right *vs* medial; see Suppl. Fig. S2). Correlations at lateral central electrodes confirmed the second spike, due to spatial overlap of ERP signals.

The spikes at posterior electrodes did not reflect artifacts. First, the spikes occurred during times of significant HI/LO differences with better signal-to-noise ratios than elsewhere. Second, we could rule out numerical causes related to ERP maxima. That is, the spikes preceded but never coincided with lateralization maxima and they never coincided with peaks in the HI/LO difference waves. Moreover, no spikes were paired with the bilateral HI/LO peaks during the P_D phase. Third, decorrelation spikes were not due to some form of commotion when participants switched to right-brain dominance at slightly different times. To look at this we calculated individual changes in HI/LO lateralization (i.e., the derivative of individual lateralization curves) but neither averages nor standard deviations of the derivative curves revealed maxima that aligned with decorrelation spikes (Fig. 4c, d). Fourth, the spikes were not caused by outliers as confirmed with scatter plots of individual data and rank correlations that, although more robust to outliers, produced similar spikes (Suppl. Fig. S3).

4. Discussion

Identifying the neural signature of the right-dominant functions of spatial attention and visual awareness in the human brain has met with limited success. Intact functions do not consistently reveal the marked right-dominant lateralization (Asplund et al., 2010; Benwell, Harvey, & Thut, 2014; Cavézian et al., 2012; Çiçek et al., 2009; Fink et al., 2000, 2002; Foxe et al., 2003; Waberski et al., 2008) that lesion studies suggest, where right- but rarely left-brain damage causes severe deficits of attention and awareness in patients with neglect (He et al., 2007; Karnath, Himmelbach, & Rorden, 2002, 2004; Mort et al., 2003; Verdon et al., 2010). Here we show that 3 factors explain the discrepancy. First, capturing brain activity accurately in time with EEG we found that pronounced right-dominant mechanisms of spatial attention and visual awareness did arise but within a short stretch of time that could be easily overlooked with the coarser temporal resolution of functional imaging. Second, right dominance only became

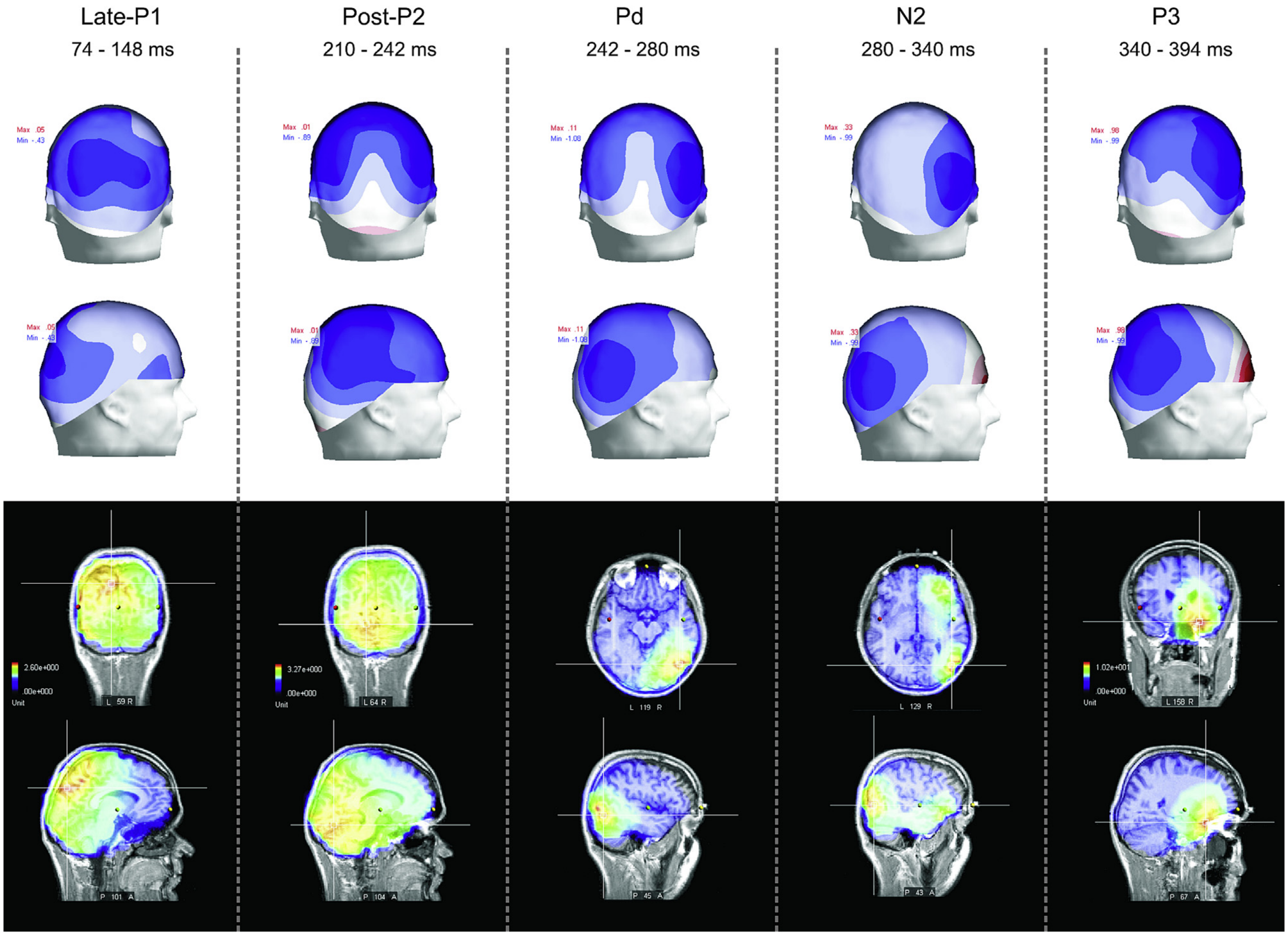

Fig. 3 – **Scalp plots and source localization estimates for each cluster with significant HI/LO effects. Scalp plots were based on HI minus LO ERPs (upper panel). We found that the HI/LO related activity during the post-P2 phase was present at lateral and dorsal scalp sites. More demarcated activity occurred during the P_D phase involving right posterior scalp. Activity in a similar right-posterior region was identified for the N2 phase with a second focus emerging in a frontal region, also associated with the P3 phase. In addition, the brief HI/LO effect during the late P1 phase was associated with occipito-parietal regions. To investigate these activities further, we used the HI minus LO difference waves in a source localization algorithm (Mosher & Leahy, 1998; lower panel). See text for a description of the results.**

visible with special HI/LO contrasts of a sensitive pseudoneglect task (Niemeier et al., 2007, 2008a, 2008b; Singh et al., 2011; Fig. 1a) but not with other contrasts. Third, transient phases of decorrelated activity between the two hemispheres preceded peaks of right dominance, apparently reflecting interhemispheric competition that, when out of balance after damage, would magnify behavioral deficits in patients (Kinsbourne, 1977; Koch et al., 2008). This, to our knowledge, is the first report of such a form of fast interhemispheric competition; it suggests a mechanism that rapidly shifts neural resources to one or the other hemisphere like a toggle switch.

4.1. *Involvement of the VAN and DAN*

Our results further suggest that the functions of spatial attention and visual awareness originate from structures of the VAN (Corbetta & Shulman, 2002), that is, the posterior temporal cortex, in the vicinity of the temporo-parietal junction, and ventral frontal cortex. The finding agrees with previous proposals that neglect is caused by damage to the circuitries of the VAN, perhaps deteriorating into extensive breakdown of right-brain functions (He et al., 2007). More support comes from intracranial stimulation (Thiebaut de Schotten et al., 2005; Vallar et al., 2013) and anatomical studies (Thiebaut de Schotten et al., 2011) that show that postero-frontal fiber tracts are involved in visuospatial asymmetries. For example, the second branch of the superior longitudinal fasciculus (SLF II) projecting to the medio-frontal cortex (Makris et al., 2005) is larger on the right than the left side by an amount that predicts the degree of pseudoneglect (Thiebaut de Schotten et al., 2011). No such correlation occurred for the third branch (SLF III) which projects to the inferior frontal gyrus (Thiebaut de Schotten et al., 2011). But it still is possible that the SLF III does subserve spatial attention and that its additional functions blur any simple relationship between attentional and structural asymmetries. Our current data, despite the limited precision of EEG source localization, do point at a possible role of SLF II as well as III. More reliably though, our data chart in time how VAN activity flows from posterior to anterior regions.

This flow of activity might reflect task-relevant perceptual processes in the TPJ and then decisional mechanisms in ventral frontal regions (Geng & Mangun, 2011) that the brain uses to resolve the perceptual conflict between gratings in the left and right visual fields. Similar forms of competition might trigger VAN activity in other tasks. For example, Posner's invalid cuing condition, known to activate the TPJ, creates competition between a falsely cued location and a target appearing on the opposite side (Corbetta & Shulman, 2002). Other paradigms present tasks in one visual field but relevant information on the opposite side (Geng & Mangun, 2011), or they surprise participants with objects appearing in the fovea so that events in the periphery go unnoticed (Asplund et al., 2010). A related, although pathological form of unawareness, called extinction, occurs after TPJ lesions (Karnath, Himmelbach, & Kuker, 2003) when objects appear briefly left and right of each other. Finally, competition might grow stronger and activate the TPJ more with larger angular distances, for example when pseudoneglect tasks use bisected lines that are long as opposed to short (Benwell et al., 2014). Although in that case, further research should clarify the role of physical differences of the lines, regardless of task, compared to differences in instructions in the present study with later, strongly right-lateralized effects.

Following perceptual conflict resolution, the VAN could interface with frontal parts of the DAN to initiate associated goal-directed behavior (Geng & Mangun, 2011) later on. But within the time window of our experiment we found no evidence that core aspects of underlying right-dominant functions involve the DAN. This said, two pieces of evidence seem to contradict this notion. The first is that the HI/FRAME contrast showed extensive activity at central electrodes, apparently in alignment with imaging studies where tests for pseudoneglect activated posterior portions of the DAN, such as around the intraparietal sulcus (Cavézian et al., 2012; Çiçek et al., 2009; Fink et al., 2000; Foxe et al., 2003; Waberski et al., 2008). However, we argue that these findings result from less specific contrasts with less clear right-brain dominance that isolated processes that were merely co-activated by the tasks. In particular, the activity patterns suggest a major influence of exploratory processes. This seems to make sense because tests of pseudoneglect prompt participants to explore, overtly or covertly, the left and right side of stimuli (McCourt, 2001), whereas the control tasks require much less exploration. But exploration is not necessary to produce pseudoneglect;

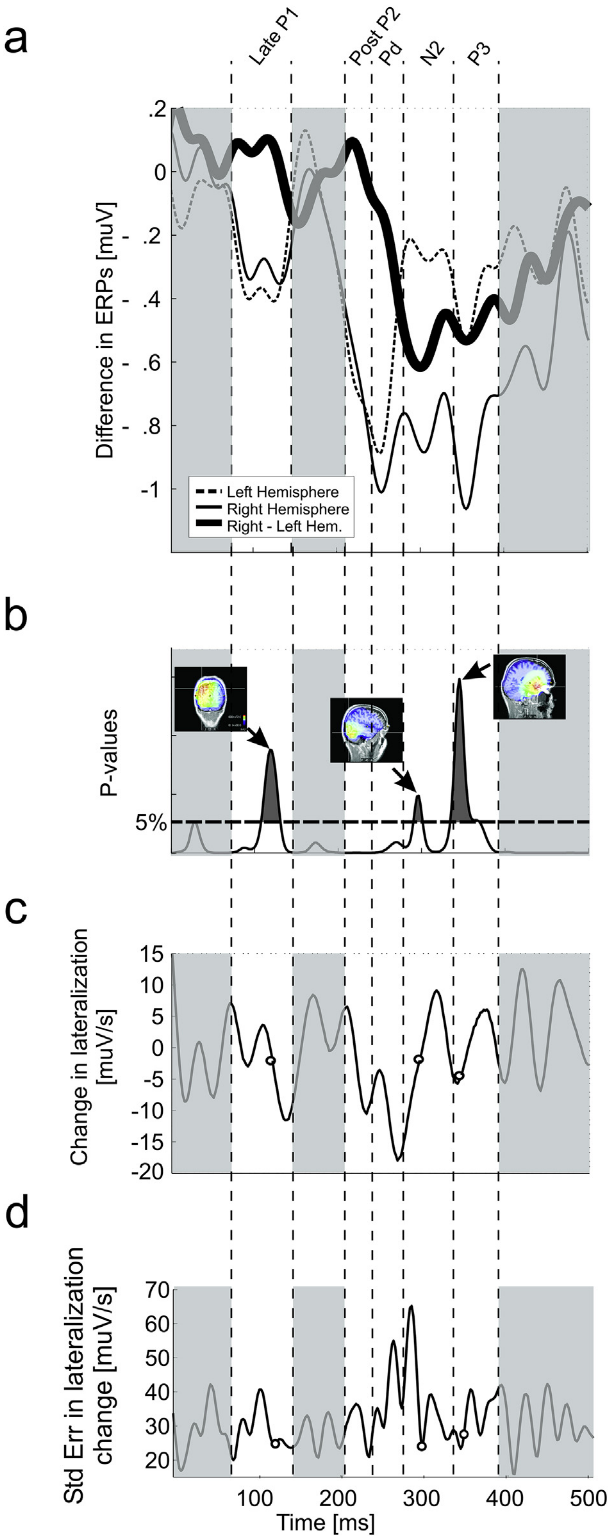

Fig. 4 – The HI/LO effect at postero-lateral scalp sites. (a) Lateralization of the HI/LO effect (thick solid curve) calculated as the HI/LO difference over right posterior scalp (thin solid curve, also see Fig. 1e) minus the HI/LO difference over left posterior scalp (dashed curve, also see Fig. 1c). The lateralization curve revealed two negative-going maxima of right-dominance during the N2 and P3 phases. A third maximum after the P3 phase was based on insignificant HI/LO differences. Vertical dashed lines and labels indicate the clusters of the k-means cluster analysis. Shaded regions demarcate non-significant clusters. (b) *p*-Value curve of the correlations between the HI/LO effect over left and right posterior scalp. Dark grey shaded regions indicate peaks of decorrelations ($p > .05$). Insets present source localization estimates for the HI/LO difference wave of all electrodes at the time of maximum decorrelation. For all time points, *r* values were positive ($.4 < r's < .95$). (c) Average derivative of HI/LO lateralization. (d) Standard deviation of individual derivative curves.

measures of pseudoneglect even improve when visual masking and brief stimulus presentation block exploration (McCourt, 2001). Thus, sorting out exploration-based brain activity helps identify core functions of pseudoneglect, such as with the two conditions of the HI/LO contrast that are based on the same task, except that participants pay attention to different features (high and low spatial frequencies) of the grating-scales.

The difference in feature-based attention is arguably seen in the small HI/LO effect during the late P1 phase, likely because the lower spatial frequencies were less salient (Singh et al., 2011) and required more attentional effort. An influence of feature-based attention is consistent with the timing of the effect (Stojanoski & Niemeier, 2011; Zhang & Luck, 2009) and with source localization, estimating that the effect originated from the dorsal parietal cortex (Liu, Hospadaruk, Zhu, & Gardner, 2011). It showed a trend of left-sided activation, perhaps due to a task-specific larger P1 amplitude and better signal-to-noise ratio on the left. Thus, the late P1 contrast seems to reveal DAN activity in response to surface properties of the grating-scales task.

4.2. *Interhemispheric competition*

Remarkably, we found that right-brain lateralization followed brief periods of decorrelation that seems to mark competition between hemispheres. Interhemispheric competition (Duque et al., 2007) and its disruptions (Kinsbourne, 1977; Koch et al., 2008) are well documented, but to our knowledge this is the first study to show that competition can be fast, only taking a few intercallosal iterations. Such a fast mechanism would help to quickly direct resources to the desired hemisphere, similar to a toggle switch. Equivalent switch mechanisms might be implemented in different, but not all neural systems: our data revealed decorrelations during TPJ and frontal activation of the VAN as well as during the late P1 phase, arguably within the DAN. However, we found no evidence for competition during the post-P2 and the P_D (Hickey et al., 2009) phases, indicating that certain processes, such as distractor removal, may occur for the two visual fields separately.

In conclusion, we found electrophysiological evidence that the mechanisms of spatial attention and visual awareness are governed by short periods of strongly right-dominant activity in the VAN. Within these structures, our data reveal a delicate system of fast interhemispheric competition in normal healthy participants and, thus, offer novel insights into the effects of brain lesions resulting in spatial neglect.

Conflict of interest

There are no conflicts of interest.

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Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2014.09.015.

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