Event-related EEG lateralizations mark individual differences in spatial and non-spatial visual selection

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Abstract

Selective attention controls the distribution of our visual system's limited processing resources to stimuli in the visual field. Two independent parameters of visual selection can be quantified by modeling an individual's performance in a partial-report task based on the computational Theory of Visual Attention (TVA): i) *top-down control* α, the relative attentional weighting of relevant over irrelevant stimuli and ii) *spatial bias* w_λ, the relative attentional weighting of stimuli in the left versus right hemifield. In this study, we found that visual event-related EEG lateralizations marked inter-individual differences in these two functions. First, individuals with better top-down control showed higher amplitudes of the *posterior contralateral negativity* (PCN) than individuals with poorer top-down control. Second, differences in spatial bias were reflected in asymmetries in earlier visual ERLs depending on the hemifield position of targets; specifically, individuals showed a positivity contralateral to targets presented in their prioritized hemifield and a negativity contralateral to targets presented in their non-prioritized hemifield. Thus, our findings demonstrate that two functionally different aspects of attentional weighting quantified in the respective TVA parameters are reflected in two different neurophysiological measures: the observer-dependent spatial bias influences selection by a bottom-up processing advantage of stimuli appearing in the prioritized hemifield. By contrast, task-related target selection governed by top-down control involves active enhancement of target, and/or suppression of distracter, processing. These results confirm basic assumptions of the TVA theoretical framework, complement the functional interpretation of ERL components in selective attention studies, and are of relevance for the development of neuro-cognitive attentional assessment procedures.

Keywords: visual attention, spatial bias, top-down control, individual differences, event-related potentials

1. Introduction

At any given point, we can consciously process only a small proportion of the massive visual input we are exposed to. The cognitive function that deals with distributing our highly limited processing resources is visual selective attention (Desimone & Duncan, 1995). Top-down control over selection enables the observer to focus attention on objects that are relevant to immediate goals, while ignoring irrelevant distracters. Efficient top-down attentional control is thus critical for acting intelligently in our visual environment and has been proposed to account for individual differences in general fluid cognitive abilities (Kane, Poole, Tuholski, & Engle, 2006). Accordingly, impaired top-down control, for example under normal aging or clinical psychiatric and neurological conditions, causes difficulties in a variety of tasks (e.g., Bishop, 2008; Gold, Fuller, Robinson, Braun, & Luck, 2007; Madden, 2007; Parasuraman & Haxby, 1993). How attentional resources are shared among objects in the visual field is not only determined by the relevance of the object, but also their spatial locations (e.g., the visual hemifield). Marked spatial processing asymmetries are associated with attentional dysfunction following brain damage, such as hemispatial neglect (Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005). In healthy subjects, the amount of attentional capacity allocated to the left and right hemifields is largely balanced. When sufficiently sensitive measures are applied in larger samples, a slight left-ward bias ("pseudo-neglect") is reliably observed on the group level (Bowers & Heilman 1980; Nicholls, Bradshaw, & Mattingly, 1999), and, in line with this, a left visual field advantage often manifests in lateralized attention tasks (Carlei & Kerzel, 2017; Śmigasiewicz, Asanowicz, Westphal, & Verleger, 2014; Verleger et al., 2009). At the single-subject level, however, side and degree of the spatial bias vary considerably among individuals, while being relatively stable within a given person. Accordingly, the spatial bias has been suggested to be a trait-like attribute (Benwell, Thut, Learmonth, & Harvey, 2013; Tomer et al., 2013) that potentially impacts the person's attentional performance (Bellgrove, Dockree, Aimola, & Robertson, 2004; Benwell, Harvey, Gardner, & Thut, 2013; Finke, et al., 2005; Matthias, Bublak, Costa, Müller, Schneider, & Finke, 2009). Together, spatial and non-spatial selection can be regarded as two fundamental features of the visual and fronto-parietal attention systems (Corbetta & Shulman, 2002; 2011), which constitute critical determinants of individual differences in visual cognitive abilities both under normal and clinical conditions.

Individual estimates of spatial and non-spatial attentional selection can be derived from parametric assessment based on the computational Theory of Visual Attention (TVA, Bundesen, 1990). TVA is closely related to the 'biased competition' account (Desimone & Duncan, 1995) and assumes that multiple objects in the visual field compete for access to a limited visual-short term memory (vSTM) store. An object's competitive strength depends on its attentional weight, which determines the fraction of the total processing capacity allocated to the object. An object will be selected and stored in vSTM when its encoding process is completed before the stimulus presentation terminates, given that vSTM has not yet been filled up. In a further development of the model, the processes have been interpreted on a neuronal level (NTVA, Bundesen, Habekost, & Kyllingsbæk, 2005; 2011). Specifically, the number of neurons representing an object categorization is assumed to be proportional to the attentional weight allocated to it and, thus, its probability of being selected.

TVA partitions attentional functions into distinct parameters that can be modeled based on an individual's accuracy in simple letter report tasks (Duncan, Bundesen, Olson, Humphreys, Chavda, & Shibuya, 1999). Specifically, selective attentional weighting is quantified in two parameters, i) *top-down control* α, the efficiency of selecting task-relevant target letters over task-irrelevant distracter letters, and ii) *spatial bias* w_λ, the distribution of attention to letters in the left versus right hemifield.

That the two parameters can indeed be taken to reflect stable processing characteristics for a given individual is substantiated by high internal (> 0.9) and test-retest reliability (> 0.8) of the α and w_{λ} parameters (Habekost, Petersen, & Vangkilde, 2014). The high reliability of the w_{λ} estimates mirrors the high (test-retest) reliability of spatial bias measures derived from the landmark (or the line bisection) task (Benwell, Thut, et al., 2013), which is frequently used to quantify hemispatial processing asymmetries in healthy individuals and neglect patients (Harvey, Milner, & Roberts, 1995). Furthermore, TVA parameters have been demonstrated to selectively correlate with other neuropsychological tests measuring related functions. In particular, *top-down control* α was found to be related to interference in a Stroop task (Bäumler, 1985); and a stronger degree of *spatial bias* $w_{\lambda,}$, that is, absolute deviation from balanced processing regardless of direction (Dev(w_{λ})), was shown to be associated with poorer performance in a visuo-spatial scanning task (Zimmermann & Fimm, 1993), in which participants had to decide whether a 'target' square having a gap in the upper edge was present in a 5 x 5 matrix of squares having a gap either in the left, the right, or the lower edge (Finke, Bublak, Krummenacher, Kyllingsbæk, Müller, & Schneider, 2005) – indicative of a more general, stable tendency to prefer on side of space.

In this study, we aimed at identifying neurophysiological indices of individual differences in these two parameters by combining TVA-based assessment with recordings of event-related potentials (ERPs). ERPs can be used as online markers of several independent but overlapping subcomponents of visual attention in one task (Luck, 2005) and were suggested to reflect neurophysiological correlates of individual differences in latent cognitive traits (Cassidy, Robertson, & O'Connell, 2012; McLoughlin, Makeig, & Tsuang, 2014). In this respect, we previously demonstrated that ERPs marked inter-individual differences in the two distinct TVA parameters of visual capacity, *processing speed C* and *storage capacity K* (Wiegand, Töllner, Habekost, Dyrholm, Müller, & Finke, 2014; Wiegand, Töllner, Dyrholm, Müller, Bundesen, & Finke, 2014).

Specifically visual selection processes can be examined by means of event-related lateralizations (ERLs) over posterior-occipital sites (Luck, Woodman, & Vogel, 2000). Visual ERLs are computed as the difference in activity over the hemispheres contra- and ipsilateral to laterally presented stimuli. They are considered to reflect stimulus processing in visuo-topically organized extrastriate areas recurrently linked to higher-level fronto-parietal areas in the attention network (Eimer, 2015; Hopf et al., 2006). When a lateral target stimulus is presented together with a physically similar distracter stimulus in the opposite hemifield, a negativity contralateral to the attended target stimulus is elicited around 175-300 ms following its onset, referred to as *Posterior Contralateral Negativity* (PCN, or N2-posterior-contralateral; Eimer, 1996; Luck & Hillyard, 1994; Töllner, Rangelov, & Müller, 2012). The PCN amplitude is interpreted as reflecting the amount of attentional resources recruited to select a target in the presence of distracting stimuli (Töllner, Zehetleitner, Gramann, & Müller, 2012; Woodman & Luck, 1999). The component was suggested to subsume activations related to multiple mechanisms acting simultaneously to resolve this attentional competition, specifically: activity to enhance processing of the target plus activity to suppress processing of the distracters (Hickey, Di Lollo, & McDonald, 2009). In some studies, a positivity that precedes the PCN can be observed contralateral to the target (Corriveau, Fortier-Gauthier, Pomerleau, McDonald, Dell'Acqua, & Jolicoeur, 2012; Jannati, Gaspar, & McDonald, 2013). This Posterior Positivity Contralateral (Ppc) was suggested to reflect bottom-up processing differences between the target and distracter stimuli that may also contribute to selection (Gokce, Geyer, Finke, Müller, & Töllner, 2014; Wiegand, Finke, Töllner, Starman, Müller, & Conci, 2015).

To investigate electrophysiological correlates of TVA parameters of spatial and non-spatial selective attention, we recorded EEG while participants performed a partial-report letter task

(Wiegand, Petersen, Finke, Bundesen, Lansner, & Habekost, 2017) in which subjects had to identify target letters and ignore distracter letters pre-specified with respect to color. For each participant, we derived quantitative and independent TVA-based estimates of *top-down control* α and *spatial bias* w_λ from their report accuracy under different display conditions (Fig. 1): a target letter was presented either alone, accompanied by another target letter, or accompanied by a distracter letter, in the same or the opposite hemifield. We analyzed visual ERLs in response to target displays with a distracter in the opposite hemifield. ERLs were i) averaged across trials with targets in the left and right hemifields (PCN), to derive ERL correlates of parameter *top-down control* α; and ii) averaged separately for trials with a target in the left (and a distracter in the right) hemifield and a target in the right (and a distracter in the left) hemifield to derive ERL correlates of parameter *spatial bias* w_λ. First, we hypothesized that the PCN, as a marker of resource allocation for visual selection, would mark individual differences in the parameter *top-down control* α. Specifically, we expected larger PCN amplitudes to indicate better top-down control over target selection. Second, we hypothesized that hemifield-specific ERLs might reveal asymmetries in the resource allocation to targets in the left versus right hemifield, which would be related to individual differences in the parameter *spatial bias* w_λ.

2. Methods

Participants. Thirty-three healthy volunteers participated in the experiment. Two participants were excluded whose PCN amplitude deviated more than 3 standard deviations from the average amplitude of -1.88 μV. In the remaining sample of 31 participants, mean age was 26.74 years (SD: 4.60, range: 20-35 years; 16 male, 15 female). All participants had normal or corrected-to-normal vision and none of them reported color blindness, any chronic eye disease, or any psychiatric or neurological impairments; also, none exhibited symptoms of depression (scores < 18 in Beck's depression inventory, Beck, Steer, & Brown, 1996) or anxiety (scores < 59 in the State-Trait Anxiety Inventory, Spielberger, Gorsuch, & Lushene, 1970). Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). Twenty-eight participants had a right-hand dominance and three participants had a left-hand dominance. Written informed consent according to the Declaration of Helsinki II was obtained from all participants, and they received payment of 10€/h for their service. The study was approved by the ethics committee of the Department of Psychology, Ludwig-Maximilians-Universität München.

Design and Procedure. The PC-controlled experiment was conducted in a dimly lit, sound-attenuated and electrically shielded cabin. Stimuli were presented on a 24-inch monitor (800×600 pixel screen resolution; 100-Hz refresh rate). Participants were seated in a comfortable chair at a viewing distance of approximately 65 cm to the screen. The entire test session lasted approximately 2 hours, including completion of a demographic questionnaire as well as neuropsychological screening assessing visuo-motor speed, depression, anxiety, and verbal IQ. Tests were completed in random order before the experiment, followed by preparation of the EEG recording and, finally, the partial-report task, which took some 45 minutes to perform. Participants were given standardized written and verbal instructions, and they were presented with example displays on the screen to illustrate the task before the experiment started.

Figure 1 about here

In the partial-report task, on each trial (Fig. 1A), either a single target, two targets, or a target and a distracter were presented. Two letters were either presented vertically (unilateral display) or horizontally (bilateral display), but never diagonally, resulting in 16 different display configurations (Fig. 1B). A trial started with the presentation, for a variable duration (see below), of a white circle (diameter of 0.9º) with a white dot in the middle in the center of the screen, which participants were instructed to fixate throughout the whole trial. Then, the letter array was presented on a black background for an exposure duration that was determined individually for each participant in a pre-test (see below). Participants' task was to verbally report only the red target letters, and to ignore the blue distracter letters. The report could be performed in any (arbitrary) order and without emphasis on response speed. Participants were instructed to report only those letters they were 'fairly certain' of recognizing. The experimenter entered the responses on the keyboard and pressed a button to initiate the next trial. To avoid response preparation varying with build-up of temporal expectancy as time elapses (Vangkilde, Coull, & Bundesen, 2012), the inter-trial intervals (ITIs) were drawn from a geometrical distribution with a constant hazard rate of 1/5 and a range of 1510-1740 ms using time steps of 10 ms.

The experiment consisted of a total of 504 trials: 112 in the single-target condition, 112 in the dual-target condition, and 280 in the target-distracter conditions (112 unilateral, 168 bilateral displays). For the ERL analyses, only conditions in which the target and distracter appeared in opposite hemifields were relevant, while all of the 16 display conditions were important for the parameter fitting based on the behavioral data (Duncan et al., 1999). The experiment was divided into 14 blocks of 36 trials each. Conditions were balanced across blocks and each participant was presented with the same displays, though in a different random sequence. Letter stimuli were presented in Arial font size 16, with equal frequency at each of four possible display locations forming an imaginary square, with a distance of approximately 10 cm from the fixation circle, corresponding to a visual angle of 8.75°. Red target letters (CIE xyY: .534, .325, 3.25) and blue distracter letters (CIE xyY: .179, .118, 3.15) were of comparable luminosity and size (0.9° of visual angle). The letters presented on a given trial were randomly chosen from a pre-defined sub-set (ABDEFGHJKLMNOPRSTVXZ) without replacement.

Determination of individual exposure durations. Before the experimental session, a pre-test was conducted to familiarize participants with the partial-report task and determine the exposure duration (ED) for the test individually for each participant, thus controlling for potential individual differences in task difficulty. First, 16 trials were run with an ED of 80 ms to acquaint the participant with the trial procedure. Then, an adaptive test procedure containing 24 trials followed, in which the ED was adapted stepwise based on performance in 12 dual-target trials: when the participant reported both targets correctly, ED was decreased by 10 ms; when the participant reported one letter correctly, the ED was kept at the current value; and when the participant reported no letter correctly, the ED was increased by 10 ms. Another 24 trials were then run using the ED identified by this procedure, with participants receiving feedback on their performance after the block. The ED thus determined was accepted for the test when performance ranged between 70% and 90% correct with single-target displays and exceeded 50% correct with dual-target displays (i.e. reached a level indicating that the participant was, in principle, able to identify more than one letter at the given exposure duration). Otherwise, the determination procedure was continued until the criterion was reached, which was the case for the majority of our participants.

Participants' final ED was 20.97 ms on average (range: 10-90 ms). Note that the individual TVA parameter estimates of *top-down control* α and *spatial bias* w_λ are independent from the individual EDs. In any case, the EDs were sufficiently short to mostly prevent saccades during display exposure, which could have contaminated the ERLs (Luck, 2005). ERLs were previously shown to be unaffected by variations in short EDs up to 200 ms (Brisson & Jolicœr, 2007), and in fact, in the present study, EDs did not correlate with TVA parameter estimates or ERLs [all rs < .24, all ps > .17].

Parameter estimation. TVA parameters were derived by modeling individual performance accuracy across the different partial-report conditions (see Fig 1B) using a TVA-based algorithm with a maximum likelihood estimation procedure (see Dyrholm, Kyllingsbæk, Espeseth, & Bundesen, 2011, and Kyllingsbæk, 2006, for details). The parameters of main interest in the present study were the two TVA parameters related to *selective* attention. The top-down control parameter, α, reflects the task-related differences in weights for targets (w_T) and distracters (w_D), and is defined as the ratio w_D/w_T. Theoretically, perfect selection would imply that all attentional weight was on targets and none on distracters, resulting in $\alpha = 0$. By contrast, completely unselective processing would imply equally weighted target and distracter processing, resulting in $\alpha = 1$. Accordingly, lower α values indicate more efficient top-down control. The spatial bias parameter, w_λ, reflects the spatial distribution of attentional weights across the left (w_{left}) and the right (w_{right}) visual hemifield and is defined as the ratio $w_{left}/(w_{left} + w_{right})$. A value of $w_\lambda = 0.5$ indicates balanced weighting, a value of $w_\lambda > 0.5$ a leftward bias, and a value of $w_\lambda < 0.5$ a rightward spatial bias. In addition to the parameters related to selection, we estimated the *sensory effectiveness*, *a*, which is a measure of the total processing capacity (in number of letters) at a given exposure duration, independent of how attentional resources are divided across different objects in the visual field.

TVA parameters are considered latent parameters, that is, entities of the processing system operating at any instance. They are inferred from modeling the observed raw data (report accuracy) in those partial-report conditions assumed to be most influenced by the respective parameter. We verified the correspondence between parameters and raw performance by calculating selection indices, which we then correlated with the estimates derived from the model. Specifically, parameter α is estimated mainly from performance decrements in the target-distracter condition, relative to performance conditions without distracters; thus, we computed a '*target selection index*' as the mean performance accuracy in the single-target and dual-target conditions divided by performance accuracy in the target-distracter condition ($[0.5*ACC_{1T}+0.5*ACC_{2T}]/ACC_{TD}$). Parameter w_λ is estimated mainly from performance in display conditions with targets presented bilaterally in both the left and the right visual hemifield; thus, we computed a ‘*spatial selection index*’ as the relative difference in correctly reporting targets in the right vs. left hemifield in the bilateral dual-target condition ($ACC_{left}/[ACC_{right\,+}\,ACC_{left}]$).

EEG recordings and ERLs. The EEG was recorded continuously from 64 active Ag/AgCl electrodes (ActiCAP system, Brain Products) using BrainAmp DC amplifiers (Brain Products). Sixty-three electrodes were mounted on an elastic cap (Falk Minow Service), with positions placed according to the international 10/10 system (American Electroencephalographic Society, 1994). One additional electrode was placed at the inferior orbit below the left eye in order to further control for blinks and saccadic eye activity. The impedances of all electrodes were kept below 5 kΩ, and regularly controlled every 4 blocks. All signals were recorded at a sampling rate of 1 kHz and filtered online with a 0.1- 250 Hz bandpass filter. Electrode FCz was used as online reference. During offline pre-processing, the raw data of each participant was first visually inspected to detect and manually remove artifacts of nonstereotypic noise (e.g., electromyographic bursts). We ran an infomax independent component analysis (Bell & Sejnowski, 1995) to identify and backtransform components representing ocular artifacts (Jung et al., 2000). After ICA inspection, the continuous EEG was low-pass filtered at 40 Hz (Butterworth zero phase filter, 24 dB/oct) and re-referenced to averaged mastoids (channels TP9/10). The EEG was segmented into 1000-ms epochs, ranging from 200 ms before to 800 ms after stimulus onset. The pre-stimulus interval was used for baseline corrections. Trials containing signals exceeding ±30 μV in channels at the outer left and right canthi of the eye (F9/F10) were marked as artifacts associated with residual eye-related activity and not included in the analyses (7% of all trials). Trials including voltage steps larger than ± 50 μV/ms and activity lower than ± 0.5 μV within intervals of 500 ms or signals exceeding ± 60 μV in any channel were marked as artifacts and removed from the analysis on an individual-channel basis.

We computed ERLs based on trials in which a target and a distracter letter were presented bilaterally (i.e., in opposite hemifields) on lateral parieto-occipital electrodes (PO7/PO8). Only trials on which the target letter was reported correctly were included in the analyses. Note that, although w_λ is estimated mainly from bilateral target displays in the TVA fitting, the latent spatial bias parameter is assumed to be also realized in the magnitude of the relative attentional weights to targets presented in the left compared to the right hemifield when a distracter is in the opposite hemifield, or no stimulus is in the opposite field. We chose bilateral target-distracter displays for the analyses because it is only in this condition that the sensory input is balanced across hemifields, with contra-vs.-ipsilateral hemispheric differences reflecting attention-related differences in target and distracter processing; by contrast, no reliable lateralization in ERPs can be measured in displays with targets in both hemifields.

ERLs were calculated by subtracting ERPs at electrodes ipsilateral from those at electrodes contralateral to the target, averaged over presentations in the upper and lower visual field. Time windows used for analyses were based on visual inspection of individual differences in grand-averaged ERLs. For the PCN analyses, we computed grand-average (contralateral-minus-ipsilateral) difference waves averaged across left and right targets ($[(\mathrm{PO8}\text{-}\mathrm{PO7}_{\text{left target}}) + (\mathrm{PO7}\text{-}\mathrm{PO8}_{\text{right target}})]/2$), and extracted peak amplitudes (mean +/- 10 ms around the maximum deflection) in the 130-350 ms post-stimulus time window. For analyzing hemifield asymmetries in the ERLs, we extracted mean amplitudes 140-200 ms post-stimulus from grand-averaged event-related (contralateral-minus-ipsilateral) difference waves on parieto-occipital electrodes separately for displays in which the target was presented in the left hemifield and the distracter in the right hemifield ($\mathrm{PO8}\text{-}\mathrm{PO7}_{\text{left target}}$), and vice versa for trials in which the target was presented in the right hemifield and the distracter in left hemifield ($\mathrm{PO7}\text{-}\mathrm{PO8}_{\text{right target}}$). We measured mean amplitudes, rather than peak amplitudes, because individual peaks could not be reliably determined, owing to the lower signal-to-noise ratio in the hemifield-specific ERLs as compared to the PCN (the latter being based on averaging across double the amount of trials).

Statistical analyses. First, we examined whether target selection was effective in our sample by a one-sample *t*-test testing whether α–values would be significantly lower than 1 (indicating unselective processing). Second, we tested whether there was a spatial bias to the left or right hemifield in our sample by a one-sample *t*-test against 0.5 (indicating balanced spatial weighting). We further confirmed that the correspondence between the performance pattern in the raw data and the parameter estimates by correlating individual α- and w_λ-values with the *target selection* and, respectively, *spatial selection indices* computed from the observed performance data. To test the independence of the two parameters of selection, we computed Pearson correlations between the α and w_λ estimates, and also between α and the general degree of spatial bias irrespective of direction (i.e., the deviation from balanced weighting, $w_\lambda = 0.5$).

For the following examinations for individual differences, we split the sample twice into two groups: first, into groups with better vs. poorer top-down control according to the median value of α; second, into groups with left vs. right spatial bias according to the median value of w_λ. The resulting differences between the respective groups in the parameter estimates and report accuracy in the relevant display conditions of the (partial-report) task were examined by *t*-tests.

We assumed that individual differences in the PCN would reflect the relative distribution of attentional weights among target and distracter letters, quantified as parameter α. We further hypothesized that individual differences in the left-right asymmetry of ERLs would be related to the observer-specific relative spatial distribution of weights between hemifields, quantified as parameter w_λ. Finally, we assumed that these associations would be independent of each other, that is, individual differences in α would not be reflected in hemispheric asymmetries of the ERL, and individual differences in w_λ would not be reflected in overall amplitudes of the PCN.

To test these hypotheses, we analyzed the PCN in two one-way ANOVAs, one with the between-subject factor Top-down Control (better/poorer), and another with the between-subject factor Spatial Bias (leftward bias/rightward bias). We analyzed hemifield-specific ERLs in two mixed ANOVAs, one with the within-subject factor Target Hemifield (left/right) and the between-subject factor Spatial Bias (leftward bias/rightward bias), and another with the within-subject factor Target Hemifield (left/right) and the between-subject factor Top-down Control (better/poorer). Significant interactions were followed-up by *t*-tests (Bonferroni corrected). Finally, we repeated the analyses with handedness as a covariate, as handedness has been suggested to co-vary with asymmetries in other cognitive and perceptual processes (Jewell & McCourt, 2000).

3. Results

Behavioral data and model fit summary. The model explained on average 80% (mean R^2) of the variability in the observed mean scores, and the estimated parameters were comparable to previous TVA-based studies with young, healthy participants (Bundesen, 1998; Finke et al., 2005; Matthias et al., 2009). The overall performance accuracy was 79.84%, and the performance pattern between conditions was in line with TVA predictions and the group differences in *top-down control* α and *spatial bias* w_λ (Fig. 2): Participants reported most letters correctly in the single-target condition, in which all attentional resources were expended on only one item, and performance was comparable across groups. For dual-letter displays, report performance (for one target in the display) was reduced more in the dual-target conditions compared with the target-distracter conditions, indicating that participants shared resources among the targets in the dual-target conditions, whereas they allocated more attentional weights to the targets than to the distracters in the target-distracter conditions. Paired-samples *t*-tests confirmed that, across all participants, mean accuracy was significantly lower in the dual-target conditions [Mean = 76.28, SD = 7.93] compared to both the single-target [Mean = 81.97, SD = 6.75] and target-distractor [Mean = 81.28, SD = 6.95] conditions [both $t(30) > 6.1$, both $p < .001$]. Individuals with poorer compared to better top-down control showed smaller performance differences between the conditions with and without distracters [Mean = 1.76, SD = 2.21 vs. Mean = 8.45, SD = 2.67 $t(29) = 7.626$, $p < .001$], indicating that they allocated relatively less attentional weight to distracters (Figures 2A and 2B). Furthermore, individuals showed higher report accuracy for targets that occurred in their prioritized hemifield in bilateral display conditions (in which another stimulus appeared in the opposite hemifield), indicating that more attentional weight was allocated to the stimulus on the preferred side (Figures 2 C and D). In trials with two targets in opposite hemifields, for individuals with a leftward bias, report accuracy was significantly higher for targets in the left than in the right hemifield [$t(15) = 2.995$, $p = .009$]. Conversely, for individuals with a rightward bias, there was a trend towards higher report accuracy for targets in the right versus the left hemifield [$t(14) = -1.729$, $p = .106$] (note that the degree of spatial bias was also higher in the leftward-bias group, see below).

Figure 2 about here

The estimates of *top-down control* α indicated that target selection was effective (i.e., $\alpha < 1$) across the entire sample [Range = 0.17–0.67, Mean = 0.42, SD = 0.14, $t(30) = -22.34$, $p < .001$] (Fig. 3A). The estimates of *spatial bias* w_λ indicated a slight, but non-significant leftward bias (i.e., $w_\lambda > 0.5$) across the entire sample [Range = 0.39–0.68, Mean = 0.52, SD = 0.06, $t(30) = 1.66$, $p = .107$] (Fig. 3B). The groups split according to the median value of α, naturally, differed in their estimates of α [better top-down control Mean = 0.30, SD = 0.11 vs. poorer top-down control Mean = 0.53, SD = 0.07, $t(29) = -7.443$, $p < .001$], but not in their estimates of w_λ [better top-down control Mean = 0.52, SD = 0.07 vs. poorer top-down control Mean = 0.52, SD = 0.05, $t(29) = 0.021$, $p =$

.98]. Conversely, the groups split according to the median value of w_λ (0.51) differed in their estimates of w_λ, [leftward bias: Mean = 0.56, SD = 0.04 vs. rightward bias: Mean = 0.47, SD = 0.03, $t(29) = -5.942$, $p < .001$], but did not differ in their estimates of α [leftward bias Mean = 0.43, SD = 0.15 vs. rightward bias Mean = 0.42, SD = 0.15, $t(29) = 0.153$, $p = .88$].

Figure 3 about here

Significant correlations between the parameter estimates and selection indices based on raw scores confirmed that the values derived from the modeling procedure corresponded to the pattern in the observed performance: *top-down control* α correlated with the target selection index [$r(29) = .956$, $p < .001$], and *spatial bias* w_λ correlated with the spatial selection index [$r(29) = .736$, $p < .001$]. By contrast, α and w_λ did not correlate significantly with each other [$r(29) = -.076$, $p = .684$]. And neither did α correlate with the spatial selection index [$r(29) = .032$, $p = .866$], nor did w_λ correlate with the target selection index [$r(29) = -.020$, $p = .914$]. Top-down control α did also not significantly correlate with the degree of spatial bias Dev(w_λ), regardless of direction [$r(29) = -0.292$, $p = 0.111$].

TVA parameters and ERLs. Characteristic visual potentials over parieto-occipital electrode sites were elicited in the bilateral target-distracter condition of the partial-report task, which were larger over the hemisphere contralateral to the hemifield in which a target letter was presented. The amplitudes of ERLs further varied with individuals' level of *top-down control* α and *spatial bias* w_λ (Fig. 4 and 5).

The ANOVA on PCN amplitudes averaged across the hemifields with the between-subject factor Top-down Control revealed a significant effect of Top-down Control [$F(1,29) = 5.72$, $p = .02$]. Amplitudes were higher in individuals with better as compared to individuals with poorer top-down control (-2.21 μV vs. -1.57 μV) (Fig. 4B). The same analyses with the between-subject factor

Spatial Bias revealed no significant effect of Spatial Bias [$F(1,29) = 2.74$, $p = .11$], indicating that the PCN was modulated by individual differences in parameter α, but not in parameter w_λ (Fig. 4C). The ANCOVAs including handedness as a covariate revealed essentially the same results, with a significant effect of Top-down Control [$F(1,28) = 5.437$ $p = .027$], but not of Spatial Bias [$F(1,28) = 2.610$ $p = .117$], on PCN amplitudes.

Figure 4 about here

The ANOVA on hemifield-specific ERLs with the between-subject factor Spatial Bias revealed a significant interaction between Spatial Bias and Target Hemifield [$F(1,29) = 8.29$, $p = .007$], showing that ERL lateralization to left vs. right targets varied with participants' prioritized hemifield (Figure 5C and D). Post-hoc tests revealed that ERL amplitudes in response to right-target displays were negative in individuals with a left-ward spatial bias and positive in individuals with a right-ward spatial bias [-1.32 µV vs. 0.99 µV, $t(29) = 2.897$, $p < .01$], while ERL amplitudes in response to left-target displays were negative in individuals with a right-ward spatial bias and positive in individuals with a left-ward spatial bias [-0.72 µV vs. 1.69 µV, $t(29) = -2.689$, $p = .012$]. Two paired-samples *t*-tests revealed that amplitudes in response to right- and left-target displays differed significantly for the group of participants with a left-ward bias [$t(15) = 2.799$, $p = .013$], but not the group with a right-ward bias [$t(14) = -1.377$, $p = .190$].

Figure 5 about here

The ANOVA on hemifield-specific ERLs with the between-subject factor Top-down Control did not reveal an interaction of Top-down Control and Target Hemifield [$F(1,29)<0.01$, p

=0.96] (Fig. 5C). Thus, the results indicate that hemispheric asymmetries in the ERL varied with individual differences in the parameter w_λ, but not in the parameter α.

The ANCOVAs including handedness as a covariate revealed the same results: a significant interaction of Target Hemifield and Spatial Bias [$F(1,28) = 15.634$, $p < .001$], but not of Target Hemifield and Top-down Control [$F(1,28) = 0.273$, $p = .606$], on amplitudes of the hemifield-specific ERLs.

4. Discussion

We identified distinct ERL correlates of individual differences in TVA-based parameters of task-specific and hemifield-specific visual selection. First, the PCN varied with parameter *top-down control* α, but not with parameter *spatial bias* w_λ. Second, hemifield-specific asymmetries in the ERLs varied with parameter *spatial bias* w_λ, but not with parameter *top-down control* α.

The PCN amplitude as a neural marker of individual differences in top-down control. Parameter estimates of *top-down control* α showed that selection of task-relevant over -irrelevant objects was overall effective (i.e., targets received higher attentional weights than distracters), while this selection efficiency varied considerably among the individual participants (Figure 3A). These inter-individual differences in top-down control were reflected in the PCN; specifically, individuals with more efficient top-down control exhibited larger PCN amplitudes in response to bilateral target-distracter displays compared to individuals whose task-related selection was less efficient.

The large majority of PCN studies investigated the component using variants of visual search tasks (Eimer, 2015; Töllner et al., 2012), and the mechanisms assumed to be reflected in the PCN have been interpreted in influential visual search models developed to explain search performance under varying target-distracter configurations (Found & Müller, 1996; Müller &

Krummenacher, 2006; Wolfe, Cave, & Franzel, 1989; Wolfe, 1994, 2007). Within subjects, the PCN amplitude varies with the demands of top-down control in the task: it decreases when selection is made easier, for example, by eliminating or lowering the number of distracters (Luck & Hillyard, 1994); and it increases when selection becomes harder, such as in visual search for targets defined by feature conjunctions as compared to single features (Luck & Hillyard, 1995; Luck, Girelli, McDermott, & Ford, 1997). The PCN is sensitive to voluntary preparation, for example, when setting oneself to a target expected to be defined within a particular feature dimension – corroborating the component's association with task-dependent, top-down modulation of processing the selection-relevant target feature (Töllner, Zehetleitner, Gramann, & Müller, 2010; Töllner, Müller, & Zehetleitner, 2012). Given these (and numerous other) reports of within-subject PCN variations resulting from experimental visual-search manipulations, the consensus view is that the component reflects a filtering mechanism subserving the selection of task-relevant stimuli, whereby the processing of targets is enhanced at the expense of distracters (Eimer, 2015; Luck, 2012). The PCN amplitude specifically is assumed to reflect the amount of attentional resources allocated to the task-relevant stimulus (Eimer et al., 1996; Luck & Hillyard, 1994; Töllner et al., 2008). Following this, we interpret the between-subject differences we found under constant selection demands in the partial-report task to indicate that individuals with better top-down control allocate relatively more of their available attentional resources to the task-relevant object, compared to individuals with poorer top-down control. In terms of TVA, this translates into a stronger competitive advantage of the target over the distracter in the selection process (Bundesen & Habekost, 2008).

(N)TVA (Bundesen 1990, Bundesen et al., 2005), as a more general theory of visual selection, has direct implications for visual search performance (Bundesen & Habekost, 2008) and provides a complementary theoretical background for interpreting the ERP modulations.[1] Specifically, the mechanisms assumed to be reflected in the PCN are reconcilable with the mechanism of attentional weighting which, on TVA, underlies top-down selection (Bundesen et al., 2005). TVA assumes that objects are selected by a “filtering” mechanism, in which attentional weights are computed for all objects in the visual field based on their current importance. The available processing resources are then distributed among objects according to their weights. As a result, objects with higher weights are processed faster and more likely to be selected, which, in terms of TVA, corresponds to being encoded into vSTM. In a partial-report situation (or, similarly, in visual search), in which stimuli fall into categories of targets and distracters, effective top-down control devotes relatively more visual processing resources to the behaviorally important target objects by assigning higher weights to them compared to less important distracter objects. The individual efficiency of this filtering process is reflected in the parameter estimate of *top-down control* α. In line with this, given its association with α, the PCN amplitude could be interpreted as a marker of the relative difference in the weighting of targets in one and distracters in the opposite hemifield, on an individual-subject level. NTVA further proposes that the distribution of neural resources according to the attentional weights is governed by higher-order cortical areas that project to visual areas via the pulvinar nucleus of the thalamus (Bundesen et al., 2005). In line with this proposed implementation of top-down processing, generator sources of the PCN have been identified within the ventral occipito-temporal cortex, where processing is influenced by top-down signals from frontal and parietal areas (Buschman & Miller, 2007; Hopf et al., 2002).

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[1] Guided Search and related models distinguish between an early stage of preattentive, capacity-unlimited parallel processing of simple sensory information, which is followed by a capacity-limited, serial selection process required for recognition of the selected items. TVA also envisages a first stage of preattentive parallel processing of the objects in the visual field (though not necessarily limited to simple sensory features), on which the computation of attentional weights is based. However, in contrast to the serial selection process in Guided Search, in TVA, the second stage of processing is assumed to be a parallel capacity-limited process that is biased by the outcome of the first processing stage (for details, see Bundesen & Habekost, 2008).

In order to integrate the results with other theoretical accounts of visual attention (Guided Search: Wolfe, 1994, 2007; Dimension-Weighting Account: Müller et al., 1995) and to test the generalizability of the association between PCN amplitudes and individuals' ability to effectively filter target and distracter information, testing the relationship between individual differences in performance in other selective attention tasks, specifically visual search, would be informative. In fact, there is accumulating evidence that PCN amplitudes are larger in individuals with faster as compared to slower response times in visual search tasks (Töllner, Conci, & Müller, 2015; Williams & Drew, 2017).

Hemifield-specific ERL asymmetries are related to individual differences in spatial bias. On the group level, parameter estimates of spatial bias, w_λ, indicated largely balanced spatial weighting. However, a slight, non-significant, leftward "pseudoneglect" was found, which mirrors the rightward spatial bias found in patients with visual hemi-neglect in such TVA-based letter report paradigms (Duncan et al., 1999; Finke, Matthias, Keller, Müller, Schneider, & Bublak, 2012), albeit to a much lower degree. This finding in healthy individuals is common (Finke et al., 2005) and in accordance with the right-hemisphere dominance-hypothesis for visuo-spatial attention (Heilman & Van den Abell, 1980; Posner & Petersen, 1990). For single participants, however, sizable spatial biases to either left or the right hemifield were apparent (Figure 3B). This implies that, on the individual level, attentional resources deployed to locations in the left and right hemifields are asymmetrical, and that the direction and degree of this asymmetry varies among individuals.

While inter-individual differences in spatial biases have previously been linked to other aspects of neural hemispheric asymmetries, such as white matter volume (Thiebaut de Schotten et al., 2011) and activity in the fronto-parietal attention network (Szczepanski & Kastner, 2013), our study is the first to link intrinsic hemifield asymmetries in spatial prioritization (or weighting) to asymmetries in ERLs marking visual selection processes. Typically, on the assumption that the visual system is organized contralaterally in a symmetrical fashion, left-right asymmetries in ERLs such as the PCN are rarely reported (Mazza & Pagano, 2017). However, by taking individual differences in *spatial bias* w_{λ} into account, we revealed potentially meaningful asymmetries in early EEG lateralizations elicited by correctly identified targets in the left versus right hemifield: individuals with a leftward bias exhibited a negative ERL in response to right-target displays, but, within the same time range, a positive ERL in response to left-target displays; conversely, individuals with a rightward bias showed a negative ERL in response to left-target displays, but a positive ERL in response to right-target displays.

A subdivision into negative and positive ERLs that co-occur in the broader PCN time range has previously been noted by Hickey et al. (2009). In particular, they proposed the PCN to reflect the summation of a positivity contralateral to the distracter (P_D) that is related to a spatially-specific active suppression mechanism and a negativity contralateral to the target (N_T) that is related to target selection. In the present study, we observed a negativity contralateral to the target (or positivity contralateral to the distracter) only when the target appeared in the individual's non-prioritized hemifield. This may be taken to indicate that more activity related to enhance target- (or suppress distracter-) processing was engaged by our participants if the relevant information was presented at a non-favored location.[2]

Of note, the spatial bias-related asymmetry in ERLs occurred in a time window before the maximum deflection of the overall PCN (Fig. 3 and 4). Several recent studies have pointed out that the Ppc can precede the PCN with some display configurations (Corriveau et al., 2012; Jannati et al., 2013). The functional interpretation of the Ppc is still under debate. The component has been suggested to mark an early, attention-driven location-specific signal to a salient, task-relevant or

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[2] Recall that we analyzed only bilateral target-distracter displays. Accordingly, ERLs always reflected the summation of both components. Future studies may compare hemifield differences in ERLs as a function of individuals' spatial bias using displays with both laterally and vertically presented target and distracter stimuli, which permit the P_D and N_T to be distinguished (see Hickey et al., 2009).

irrelevant stimulus (Corriveau et al., 2012; Fortier-Gauthier, Dell'Acqua, & Jolicœur, 2013). This can be distinguished from the later Pd component that has been related to the active suppression of a salient distracter (Sawaki & Luck, 2013). While our study is the first to suggest the Ppc's relation to spatial attentional bias, the component has recently also been reported to be sensitive to individuals' attentional biases towards certain stimulus features; specifically, a processing advantage for targets colored red over other target colors (Pomerleau, Fortier-Gauthier, Corriveau, Dell'Acqua, & Jolicœur, 2014), as well as to "global preference", that is, preferential processing of object configurations that form a global shape over non-shape configurations with otherwise equal physical features (Wiegand et al., 2015). In the present study, participants showed a Ppc for targets that appeared in their prioritized hemifield (recall that the target-distracter color assignments and shapes were the same for all participants) associated with a processing advantage for stimuli in this over stimuli in the opposite hemifield. Accordingly, the Ppc might be regarded as a marker of bottom-up signals for selection strongly driven by intrinsic observer preferences, creating "subjective saliency" of the target in the prioritized compared to the stimulus in the contralateral hemifield. This early, rather automatic processing advantage may then bias the subsequent stage of target selection reflected by the PCN, which, in contrast, is strongly influenced by top-down processes of attentional control and marks task-related selection by actively enhancing target-related, or suppressing distracter-related, information (Gokce et al., 2014; Wiegand et al., 2015).

In terms of NTVA, the early spatial bias-specific asymmetry seen in the Ppc might reflect a bottom-up mechanism of spatial weighting generating a topographic priority map during some early, spatially specific processing wave – consistent with the view that the Ppc reflects laterally imbalanced activity to the most salient item on a salience map (Jannati et al., 2013). An individual's spatial bias would translate into higher weights for stimuli at locations in the preferred hemifield, compared to weights for stimuli in the opposite hemifield. As a consequence, stimuli at prioritized locations have a competitive advantage in the second processing wave of selection, in which resources are re-distributed according to weighting of both spatial and non-spatial features of stimuli in the visual field (Bundesen et al., 2005; Habekost & Bundesen, 2008).

Our results lend support to the notion that the spatial bias is a generalizable, trait-like characteristic of an individual's attentional system (Benwell, Thut et al., 2013). This, however, does not imply that spatial processing asymmetries are non-malleable. Rather, individual differences in (baseline) spatial biases can co-occur, or even interact, with task-dependent changes in spatial bias (Benwell, Harvey et al., 2013; Matthias et al., 2010). Of note, in TVA-based tests, letter stimuli are used, which may induce an asymmetry due to left-hemisphere dominance for processing verbal stimuli (Gross, 1972). In fact, TVA parameters *processing speed C* and *vSTM storage capacity K* measured in a letter whole-report paradigm are typically found to be slightly higher in the right than in the left hemifield (Brosnan et al., 2017; Kraft et al., 2015; Wiegand et al., in press). This indicates that stimulus material-dependent lateralizations become prominent in parameters of visual attention capacity. In fact, in a vSTM task with non-verbal stimuli, a left-hemifield advantage was found, at least for simple-feature stimuli (Sheremata, Bettencourt, & Somers, 2010; Sheremata & Shomstein, 2014). Importantly, in TVA, visual capacity is measured independently of the relative spatial distribution of available processing resources reflected in parameter w_λ, with the latter typically revealing the slight leftward pseudo-neglect also in tasks that use letter stimuli (Finke et al., 2005). Similarly, a left-hemifield advantage is observed in rapid visual presentation tasks with letter stimuli, together with a stronger PCN over the right compared to left hemisphere, which was attributed to the right-hemispheric dominance for attention (Śmigasiewicz, et al., 2014; Verleger et al., 2009). In future experiments, task demands and stimulus material should be manipulated to systematically investigate whether and how those factors affect spatial bias, asymmetries in attention capacity, and hemifield-specific ERLs within individuals.

Top-down control and spatial bias are independent aspects of visual selection. TVA assumes that the relative weighting of objects for selection with respect to task relevance and spatial position are two independent processes, and accordingly the parameters reflecting those functions are estimated mathematically independently from each other, as well as independently of the overall available processing capacity. In accordance with this theoretical assumption, our study as well as previous reports yielded only small, non-significant correlations between the parameters top-down control and spatial bias (Finke et al., 2005; Habekost et al., 2014; Wiegand, Petersen, Bundesen et al., 2017). Furthermore, a double dissociation of the two functions has been demonstrated in brain-damaged patients (Bublak et al., 2005): a patient with a lesion in the inferior parietal region exhibited a rightward spatial bias and intact top-down control, whereas the opposite pattern, impaired top-down control in presence of balanced spatial processing, was found in a patient with a superior frontal lesion. In line with previous work (Wiegand, Töllner, Habekost et al., 2014; Wiegand, Töllner, Dyrholm, et al., 2014), here we further support TVA's independence assumption by showing distinct relationships between inter-individual differences in the model parameters and ERPs.

Apart from separating spatial and non-spatial selection processes, the TVA-based approach further permits those functions to be quantified independently of motor processes. Handedness has been shown to co-vary with asymmetries in other cognitive and perceptual processes, including spatial bias measured in the landmark task (Jewell & McCourt, 2000). However, the association between our TVA-based behavioral measures of spatial attentional processing asymmetries (and top-down control) and ERLs did not change when we included handedness as a covariate in the analysis. A crucial difference between the landmark task and TVA-based assessment is that the former requires hand responses, which is why the resulting measure of visual spatial bias might be more prone to be influenced by asymmetries in the motor system (Luh, 1995). In line with this view of differential motor involvement in spatial bias measures, recent neuroscientific studies indicate that asymmetries in frontal and parietal areas for visual spatial processing are unrelated to the degree of handedness (Badzakova-Trajkov, Häberling, Roberts, & Corballis, 2010; Szczepanski & Kastner, 2011). Similarly, handedness did modulate neither behavioral nor ERL hemifield asymmetries in a lateralized rapid serial visual presentation task (Śmigasiewicza, Liebrand, Landmesser, & Verleger, 2017).

5. Summary and Outlook

In the present study, we combined parametric assessment based on the computational TVA framework and visual ERLs, and established neuro-cognitive markers of individual differences in two distinct functions of selective visual processing: First, *top-down control*, quantified as parameter α, was related to the PCN amplitude, indicating that individuals with better top-down control engage more resources during attentional selection of task-relevant over irrelevant stimuli. Second, *spatial bias*, quantified as parameter w_λ, was related to hemispheric asymmetries of visual ERLs depending on the target and distracter position in the display, indicating differences in early bottom-up visual processing of stimuli in an individual's more, relative to less, preferred hemifield. The presumed neuronal mechanisms underlying the activation pattern are in line with assumptions of NTVA and support the view that the two aspects of spatial and non-spatial attentional weighting reflect independent functions of the human visual processing system (Bundesen et al., 2005; 2011).

TVA provides a formal theoretical framework for the interpretation of linked cognitive and neurophysiological processes, grounded on basic research. Typically, ERPs are examined with regard to their variation with experimental conditions; thus, inferences are biased by the investigators' pre-assumptions about the hypothesized variation of cognitive processes and ERPs in a given task manipulation. The present inter-individual differences approach therefore augments our understanding of the linkage between cognitive processes and ERP deflections (Braver, Cole, & Yarkoni, 2010). Finally, TVA-based assessment provides a proven methodological apparatus for quantifying attentional functions in the normal populations, lifespan changes (McAvinue et al., 2012), and subtle and severe dysfunctions under various clinical conditions (Habekost, 2015). On this basis, the present approach offers a promising method for deriving individual neuro-cognitive trait-markers of attentional functions, as well as indices of age- and disease-related changes in these functions (Wiegand, Töllner, Dyrholm et al., 2014; Wiegand et al., 2016; Wiegand, Petersen, Bundesen, & Habekost, 2017).

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Figure Captions

Figure 1: **Task procedure and stimuli.** Trial outline of the partial-report task (A). 16 different display configurations presented in the partial report (B). Targets ("T") were presented in red and distractors ("D") were presented in blue.

***Figure 2*.** **Report accuracy in the partial-report task.** Bars depict % of correctly reported target letters and standard errors of the means in different conditions of the partial report task. For groups of individuals with better top-down control (A, green bars) and poorer top-down control (B, grey bars), performance is shown for conditions in which a target was presented without accompanying stimulus, in which a target was accompanied by a distracter, and in which are a target was accompanied by a second target. For groups of individuals with left-ward spatial bias (C, blue bars) and right-ward spatial bias (D, red bars), performance is shown for conditions in which a target was presented either alone or with an accompanying stimulus in same (ipsilateral) hemifield and in which a target was presented with an accompanying stimulus in the opposite (contralateral) hemifield, separately for targets presented in the right hemifield (blue) and the left (red) hemifield.

Figure 3: **Distribution of individual parameter estimates.** Histograms showing the distribution of individual values of *top-down control* α (A) and *spatial bias* w_{λ} (B) for. The black lines indicate the median of the sample based on which participants were assigned to groups of better and poorer top-down control and to groups of leftward and rightward spatial bias, respectively.

Figure 4: **PCN.** ERPs contra- and ipsilateral to the target across all participants (A) and PCN (contra-minus-ipsilateral difference) in response to displays with bilateral target-distracter configurations averaged over left- and right-target displays at posterior-occipital electrodes, for groups of individuals with better top-down control (green line) and poorer top-down control (grey line) (B), and for groups of individuals with a leftward spatial bias (blue line) and individuals with a rightward spatial bias (red line) (C). Shaded areas represent standard error of the averaged waveforms.

***Figure 5*: Hemifield-specific asymmetries in ERLs.** Grand-averaged ERPs across all participants contra- and ipsilateral to the target in response to displays with targets presented in the right

hemifield and distracters in the left hemifield (A) and to displays with targets presented in the left hemifield and distracters in the right hemifield (B). ERLs (contra-minus-ipsilateral difference) are shown separately for groups of individuals with a rightward spatial bias (red lines) and leftward spatial bias (blue lines) in response to displays with targets presented in the right hemifield and distracters in the left hemifield (C) and to displays with targets presented in the left hemifield and distracters in the right hemifield (D) and for individuals with a better top-down control (green lines) and poorer top-down control (grey lines) in response to displays with targets presented in the right hemifield and distracters in the left hemifield (E) and to displays with targets presented in the left hemifield and distracters in the right hemifield (F).