

BIROn - Birkbeck Institutional Research Online

Wiegand, I. and Napiórkowski, N. and Töllner, T. and Petersen, A. and Habekost, T. and Muller, Hermann J. and Finke, K. (2018) Event-related electroencephalographic lateralizations mark individual differences in spatial and nonspatial visual selection. *Journal of Cognitive Neuroscience* 26 (3), pp. 194-198. ISSN 0898-929X.

Downloaded from: <https://eprints.bbk.ac.uk/id/eprint/21583/>

Usage Guidelines:

Please refer to usage guidelines at <https://eprints.bbk.ac.uk/policies.html>

or alternatively

contact lib-eprints@bbk.ac.uk.

Event-related Electroencephalographic Lateralizations Mark Individual Differences in Spatial and Nonspatial Visual Selection

Iris Wiegand^{1,2,3*}, Natan Napiórkowski^{4*}, Thomas Töllner⁴, Anders Petersen⁵,
Thomas Habekost⁵, Hermann J. Müller⁴, and Kathrin Finke^{4,6}

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 electroencephalographic lateralizations marked interindividual differences in these two functions. First, individuals with better top-down control showed higher amplitudes of the posterior contralateral negativity than individuals with poorer top-down control. Second, differences in spatial bias were reflected in asymmetries in earlier visual event-related lateralizations depending on the hemifield position of targets; specifically, indi-

viduals showed a positivity contralateral to targets presented in their prioritized hemifield and a negativity contralateral to targets presented in their nonprioritized 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 distractor, processing. These results confirm basic assumptions of the TVA framework, complement the functional interpretation of event-related lateralization components in selective attention studies, and are of relevance for the development of neurocognitive attentional assessment procedures. ■

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 distractors. 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 determined by not only the relevance of the object but also their spatial locations (e.g., the visual hemifield). Marked spatial processing asymmetries are associated with attentional dysfunction after brain damage, such as hemispatial neglect (Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005). In healthy participants, 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 leftward bias ("pseudo-neglect") is reliably observed on the group level (Nicholls, Bradshaw, & Mattingley, 1999; Bowers & Heilman, 1980), and in line with this, a left visual field advantage often manifests in lateralized attention tasks (Carlei & Kerzel, 2018; Śmigajewicz, Asanowicz, Westphal, & Verleger, 2015; Verleger et al., 2009). At the single-participant level,

¹Max Planck UCL Centre for Computational Psychiatry and Ageing Research, ²Max Planck Institute for Human Development, ³Brigham and Women's Hospital and Harvard Medical School, ⁴LMU Munich, ⁵University of Copenhagen, ⁶Jena University Hospital

*I. W. and N. N. contributed equally to the work.

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 (Benwell, Harvey, Gardner, & Thut, 2013; Matthias et al., 2009; Finke et al., 2005; Bellgrove, Dockree, Aimola, & Robertson, 2004). Together, spatial and nonspatial selection can be regarded as two fundamental features of the visual and frontoparietal attention systems (Corbetta & Shulman, 2002, 2011), which constitute critical determinants of individual differences in visual cognitive abilities under both normal and clinical conditions.

Individual estimates of spatial and nonspatial 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 STM (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 et al., 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 distractor letters, and (ii) spatial bias w_λ , the distribution of attention to letters in the left versus right hemifield.

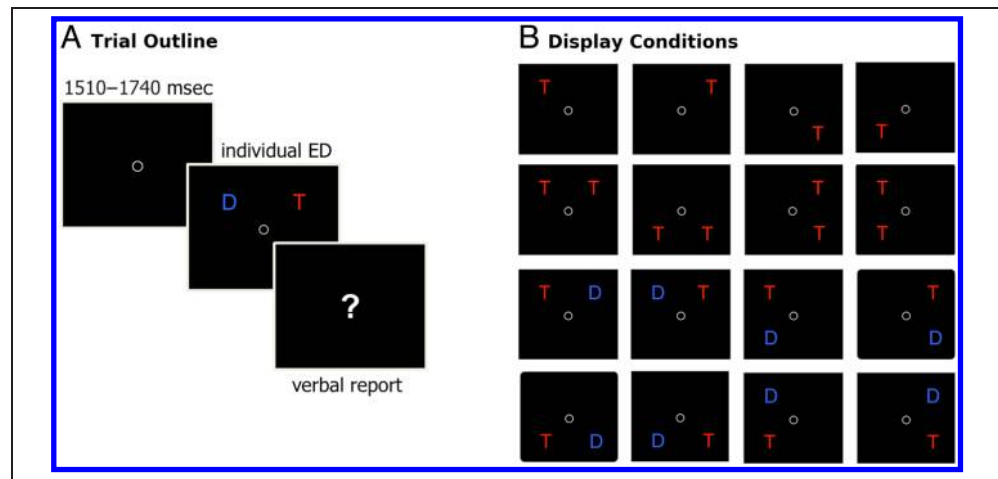
That the two parameters can indeed be taken to reflect stable processing characteristics for a given individual is substantiated by high internal (>0.9) and test-retest (>0.8) reliabilities of the α and w_λ parameters (Habekost, Petersen, & Vangkilde, 2014). The high reliability of the w_λ estimates 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 patients with neglect (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_λ , that is, absolute deviation from balanced processing regardless of direction [$\text{Dev}(w_\lambda)$], was shown to be associated with poorer performance in a visuospatial 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 5×5 matrix of squares having a gap in either the left, the right, or the lower edge (Finke et al., 2005)—indicative of a more general, stable tendency to prefer one side of space.

In this study, we aimed to identify neurophysiological indices of individual differences in these two parameters by combining TVA-based assessment with recordings of 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 (McLoughlin, Makeig, & Tsuang, 2014; Cassidy, Robertson, & O'Connell, 2012). In this respect, we previously demonstrated that ERPs marked interindividual differences in the two distinct TVA parameters of visual capacity, processing speed C and storage capacity K (Wiegand, Töllner, Dyrholm, et al., 2014; Wiegand, Töllner, Habekost, et al., 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 contralateral and ipsilateral to laterally presented stimuli. They are considered to reflect stimulus processing in visuotopically organized extrastriate areas recurrently linked to higher-level frontoparietal areas in the attention network (Eimer, 2014; Hopf et al., 2006). When a lateral target stimulus is presented together with a physically similar distractor stimulus in the opposite hemifield, a negativity contralateral to the attended target stimulus is elicited around 175–300 msec after its onset, referred to as posterior contralateral negativity (PCN, or N2-posterior-contralateral; Töllner, Rangelov, & Müller, 2012; Eimer, 1996; Luck & Hillyard, 1994). 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, 2011; 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 distractors (Hickey, Di Lollo, & McDonald, 2009). In some studies, a positivity that precedes the PCN can be observed contralateral to the target (Jannati, Gaspar, & McDonald, 2013; Corveau et al., 2012). This posterior positivity contralateral (Ppc) was suggested to reflect bottom-up processing differences between the target and distractor stimuli that may also contribute to selection (Wiegand et al., 2015; Gokce, Geyer, Finke, Müller, & Töllner, 2014).

Figure 1. Task procedure and stimuli. (A) Trial outline of the partial-report task. (B) Sixteen different display configurations presented in the partial report. Targets (“T”) were presented in red, and distractors (“D”) were presented in blue. Targets and distractors were chosen randomly from a predefined subset of 20 letters.



To investigate electrophysiological correlates of TVA parameters of spatial and nonspatial selective attention, we recorded the electroencephalogram (EEG) while participants performed a partial-report letter task (Wiegand, Petersen, Finke, et al., 2017) in which participants had to identify target letters and ignore distractor 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 (Figure 1): A target letter was presented either alone, accompanied by another target letter, or accompanied by a distractor letter, in the same or opposite hemifield. We analyzed visual ERLs in response to target displays with a distractor 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 distractor in the right) hemifield and a target in the right (and a distractor 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 .

METHODS

Participants

Thirty-three healthy volunteers participated in the experiment. Two participants were excluded whose PCN amplitude deviated more than 3 *SDs* from the average

amplitude of $-1.88 \mu\text{V}$. In the remaining sample of 31 participants, mean age was 26.74 years ($SD = 4.60$ years, range = 20–35 years; 16 men, 15 women). 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; in addition, 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€/hr 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-in. 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 hr, including completion of a demographic questionnaire as well as neuropsychological screening assessing visuomotor 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 min 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.

In the partial-report task, on each trial (Figure 1A), either a single target, two targets, or a target and a distractor were presented. Two letters were either presented vertically (unilateral display) or horizontally (bilateral display), but never diagonally, resulting in 16 different display configurations (Figure 1B). A trial started with the presentation, for a variable duration (see below), of a white circle (diameter of 0.9°) 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 (ED) that was determined individually for each participant in a pretest (see below). Participants' task was to verbally report only the red target letters and to ignore the blue distractor 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 buildup of temporal expectancy as time elapses (Vangkilde, Coull, & Bundesen, 2012), the intertrial intervals were drawn from a geometrical distribution with a constant hazard rate of $1/5$ and a range of 1510–1740 msec using time steps of 10 msec.

The experiment consisted of 504 trials: 112 in the single-target condition, 112 in the dual-target condition, and 280 in the target–distractor conditions (112 unilateral and 168 bilateral displays). For the ERL analyses, only conditions in which the target and distractor appeared in opposite hemifields were relevant, whereas 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, although 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: 0.534, 0.325, 3.25) and blue distractor letters (CIE xyY: 0.179, 0.118, 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 predefined subset (ABDEFGHJKLMNPRSTVXZ) without replacement.

Determination of Individual Exposure Durations

Before the experimental session, a pretest was conducted to familiarize participants with the partial-report task and determine the 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 msec 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 msec; 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 msec. 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 ED). Otherwise, the determination procedure was continued until the criterion was reached, which was the case for most of our participants.

Participants' final ED was 20.97 msec on average (range = 10–90 msec). 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 msec (Brisson & Jolicoeur, 2007), and in fact, in this study, EDs did not correlate with TVA parameter estimates or ERLs (all $r_s < .24$, all $p_s > .17$).

Parameter Estimation

TVA parameters were derived by modeling individual performance accuracy across the different partial-report conditions (see Figure 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 this 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 distractors (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 was on distractors, resulting in $\alpha = 0$. By contrast, completely unselective processing would imply equally weighted target and distractor 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 right (w_{right}) visual hemifields and is defined as the ratio $w_{\text{left}}/(w_{\text{left}} + w_{\text{right}})$. 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 ED, 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–distractor condition, relative to performance conditions without distractors; thus, we computed a “target selection index” as the mean performance accuracy in the single- and dual-target conditions divided by performance accuracy in the target–distractor 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 right visual hemifields; thus, we computed a “spatial selection index” as the relative difference in correctly reporting targets in the right versus 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, München, Germany) using BrainAmp DC amplifiers (Brain Products). Sixty-three electrodes were mounted on an elastic cap (Falk Minow Service, Herrsching-Breitbrunn, Germany), 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 to further control for blinks and saccadic eye activity. The impedances of all electrodes were kept below 5 k Ω and regularly controlled every four blocks. All signals were recorded at a sampling rate of 1 kHz and filtered online with a 0.1- to 250-Hz bandpass filter. Electrode FCz was used as online reference. During offline preprocessing, the raw data of each participant were first visually inspected to detect and manually remove artifacts of nonstereotypic noise (e.g., EMG bursts). We ran an Infomax independent component analysis (Bell & Sejnowski, 1995) to identify and back-transform components representing ocular artifacts (Jung et al., 2000). After independent component analysis inspection, the continuous EEG was low-pass filtered at 40 Hz (Butterworth zero phase filter = 24 dB/oct) and rereferenced to averaged mastoids (channels TP9/10). The EEG was segmented into 1000-msec epochs, ranging from 200 msec before to 800 msec after stimulus onset. The prestimulus interval was used for baseline corrections. Trials containing signals exceeding $\pm 30 \mu V$ 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 $\pm 50 \mu V/msec$ and activity lower than $\pm 0.5 \mu V$ within intervals of 500 msec or signals exceeding $\pm 60 \mu V$ 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 distractor 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 with the right hemifield when a distractor is in the opposite hemifield or no stimulus is in the opposite field. We chose bilateral target–distractor displays for the analyses because it is only in this condition that the sensory input is balanced across hemifields, with contralateral-versus-ipsilateral hemispheric differences reflecting attention-related differences in target and distractor 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 fields. Time windows used for analyses were based on visual inspection of individual differences in grand-averaged ERLs. For the PCN analyses, we computed grand-averaged (contralateral-minus-ipsilateral) difference waves averaged across left and right targets $([(PO8-PO7_{lefttarget}) + (PO7-PO8_{righttarget})]/2)$ and extracted peak amplitudes (mean ± 10 msec around the maximum deflection) in the 130- to 350-msec poststimulus time window. For analyzing hemifield asymmetries in the ERLs, we extracted mean amplitudes 140–200 msec poststimulus 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 distractor was presented in the right hemifield (PO8-PO7_{lefttarget}), and vice versa for trials in which the target was presented in the right hemifield and the distractor was presented in the left hemifield (PO7-PO8_{righttarget}). 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 with 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 the correspondence between the performance pattern in the raw data and the parameter estimates by Pearson correlations between individual α and w_λ values with the target selection and 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 versus poorer top-down control according to the median value of α and, second, into groups with left versus 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 distractor 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-participant factor Top-Down control (better/poorer) and another with the between-participant factor Spatial bias (leftward/rightward bias). We analyzed hemifield-specific ERLs in two mixed ANOVAs, one with the within-participant factor Target hemifield (left/right) and the between-participant factor Spatial bias (leftward/rightward bias) and another with the within-participant factor Target hemifield (left/right) and the between-participant 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 covary with asymmetries in other cognitive and perceptual processes (Jewell & McCourt, 2000).

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 esti-

mated parameters were comparable with previous TVA-based studies with young healthy participants (Matthias et al., 2009; Finke et al., 2005; Bundesen, 1998). 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 (Figure 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-distractor 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 distractors in the target-distractor conditions. Paired-samples t tests confirmed that, across all participants, mean accuracy was significantly lower in the dual-target conditions ($M = 76.28$, $SD = 7.93$) compared with both the single-target ($M = 81.97$, $SD = 6.75$) and target-distractor ($M = 81.28$, $SD = 6.95$) conditions (both $t(30) > 6.1$, both $p < .001$). Individuals with poorer compared with better top-down control showed smaller performance differences between the conditions with and without distractors ($M = 1.76$, $SD = 2.21$ vs. $M = 8.45$, $SD = 2.67$; $t(29) = 7.626$, $p < .001$), indicating that they allocated relatively less attentional weight to distractors (Figure 2A and B). 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 (Figure 2C 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 toward 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).

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, $M = 0.42$, $SD = 0.14$; $t(30) = -22.34$, $p < .001$; Figure 3A). The estimates of spatial bias w_λ indicated a slight but nonsignificant leftward bias (i.e., $w_\lambda > 0.5$) across the entire sample (range = 0.39–0.68, $M = 0.52$, $SD = 0.06$; $t(30) = 1.66$, $p = .107$; Figure 3B). The groups split according to the median value of α naturally differed in their estimates of α (better top-down control: $M = 0.30$, $SD = 0.11$ vs. poorer top-down control: $M = 0.53$, $SD = 0.07$; $t(29) = -7.443$, $p < .001$), but not in their estimates of w_λ (better top-down control: $M = 0.52$, $SD = 0.07$ vs. poorer

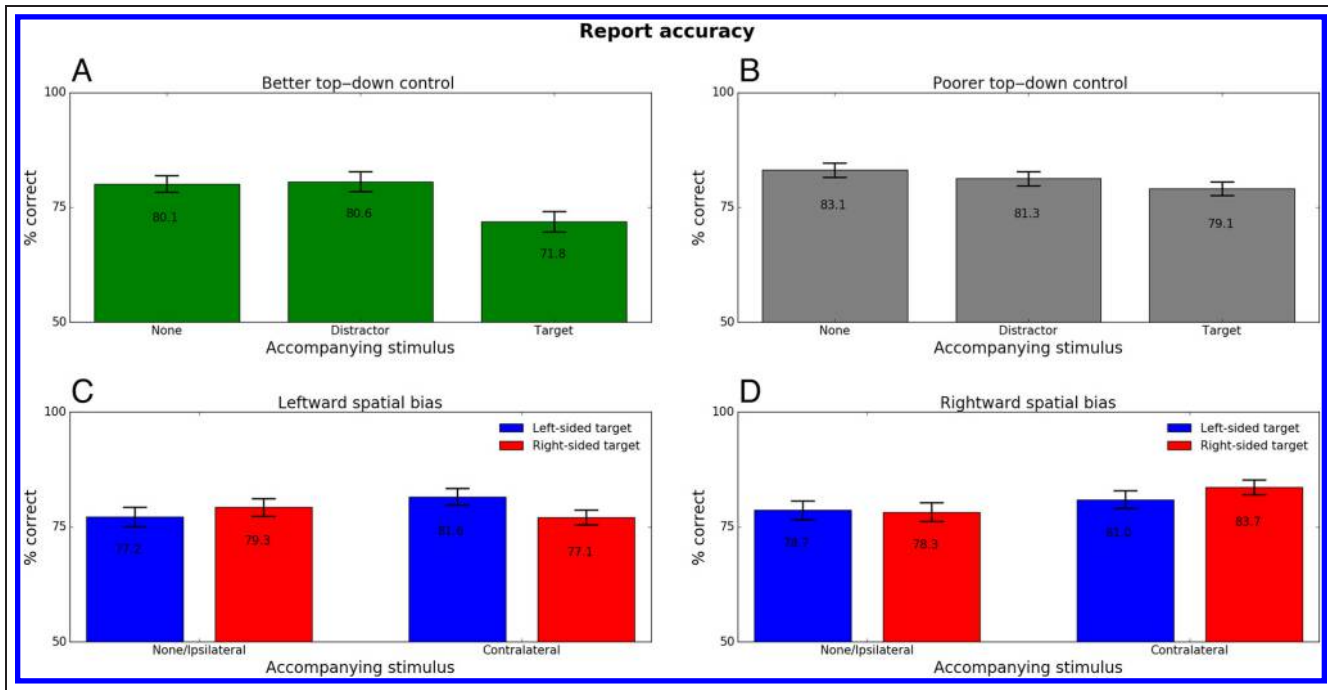


Figure 2. Report accuracy in the partial-report task. Bars depict percentage of correctly reported target letters and standard errors of the means in different conditions of the partial-report task. For groups of individuals with better top-down control (A, green bars) and poorer top-down control (B, gray bars), performance is shown for conditions in which a target was presented without accompanying stimulus, in which a target was accompanied by a distractor, and in which a target was accompanied by a second target. For groups of individuals with leftward spatial bias (C, blue bars) and rightward spatial bias (D, red bars), performance is shown for conditions in which a target was presented either alone or with an accompanying stimulus in the 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 hemifield (red).

top-down control: $M = 0.52$, $SD = 0.05$; $t(29) = 0.021$, $p = .98$). Conversely, the groups split according to the median value of w_λ (0.51) differed in their estimates of w_λ , (leftward bias: $M = 0.56$, $SD = 0.04$ vs. rightward bias:

$M = 0.47$, $SD = 0.03$; $t(29) = -5.942$, $p < .001$) but did not differ in their estimates of α (leftward bias: $M = 0.43$, $SD = 0.15$ vs. rightward bias: $M = 0.42$, $SD = 0.15$; $t(29) = 0.153$, $p = .88$).

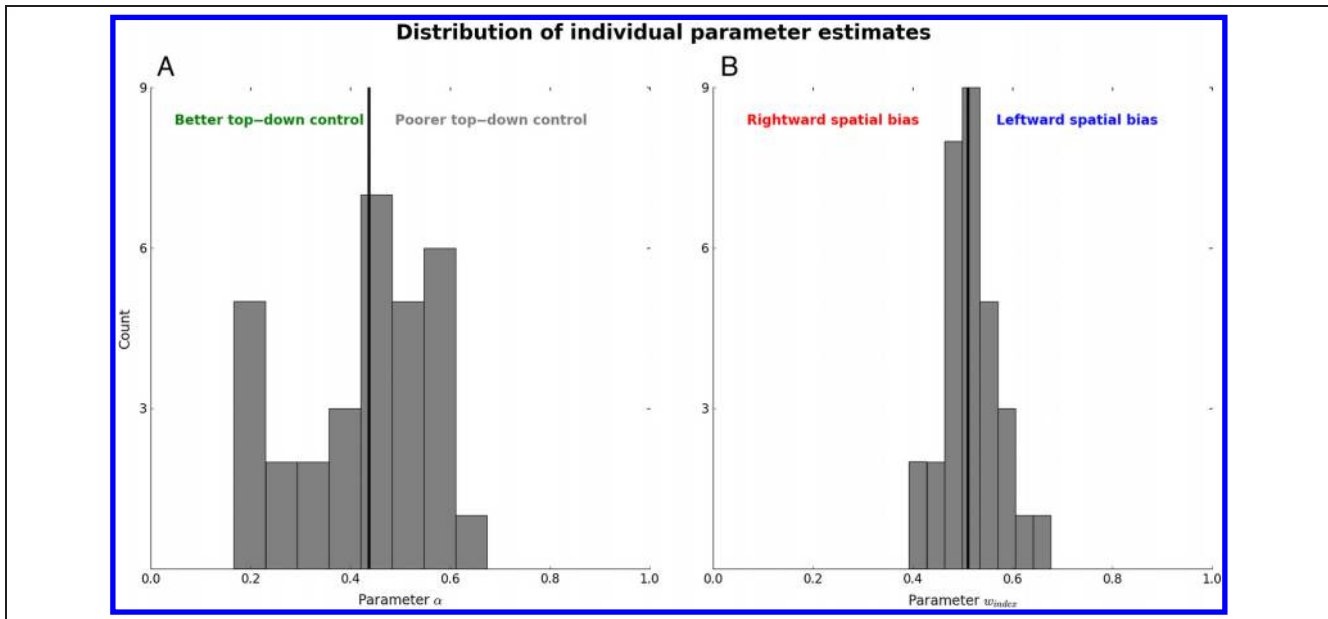


Figure 3. Distribution of individual parameter estimates. Histograms showing the distribution of individual values of top-down control α (A) and spatial bias w_λ (B). The black lines indicate the median of the sample based on which participants were assigned to groups of better and poorer top-down control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

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 also did not significantly correlate with the degree of spatial bias $Dev(w_\lambda)$, regardless of direction ($r(29) = -.292, p = .111$).

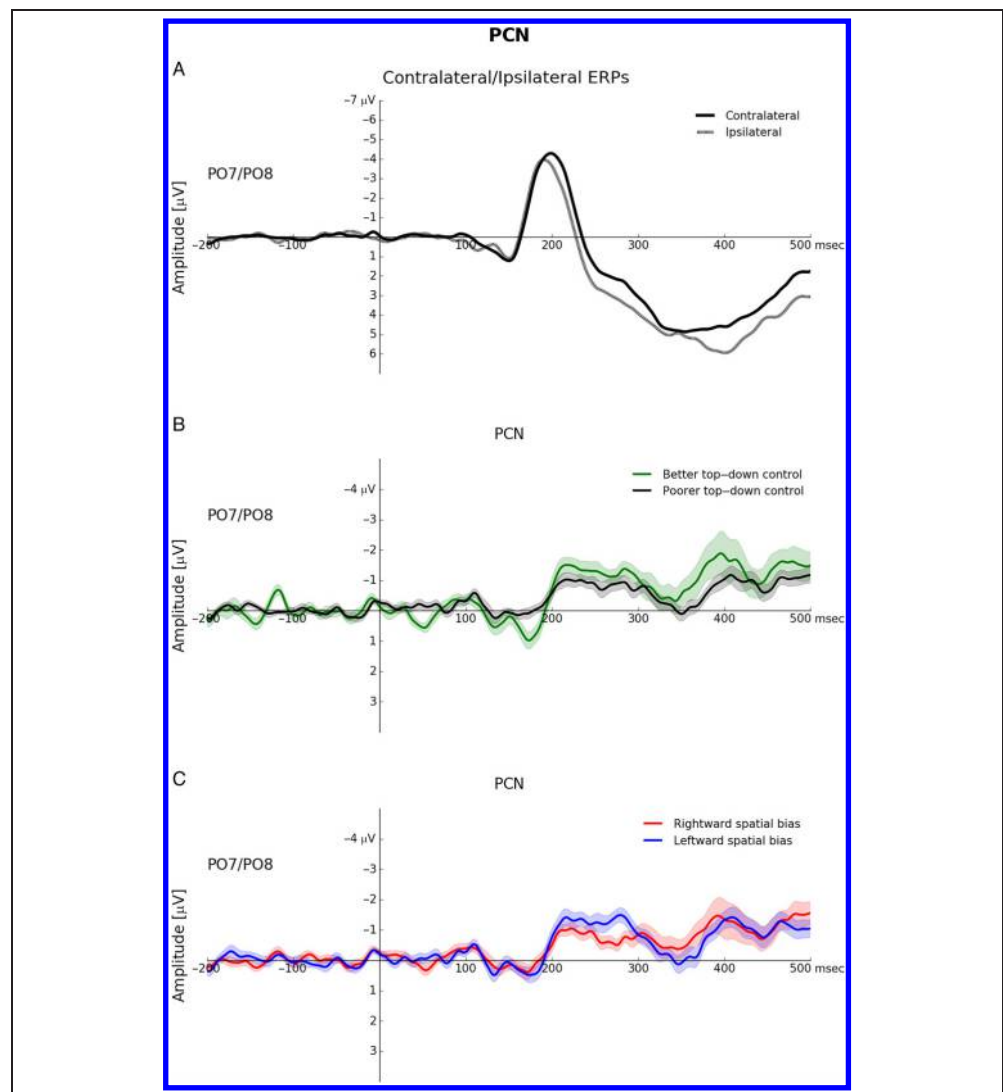
TVA Parameters and ERLs

Characteristic visual potentials over parieto-occipital electrode sites were elicited in the bilateral target-distractor

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 (Figures 4 and 5).

The ANOVA on PCN amplitudes averaged across the hemifields with the between-participant 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 with individuals with poorer top-down control (-2.21 vs. $-1.57 \mu\text{V}$; Figure 4B). The same analyses with the between-participant 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 (Figure 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. PCN ERPs contralateral and ipsilateral to the target across all participants (A) and PCN (contralateral-minus-ipsilateral difference) in response to displays with bilateral target-distractor 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 (gray 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.



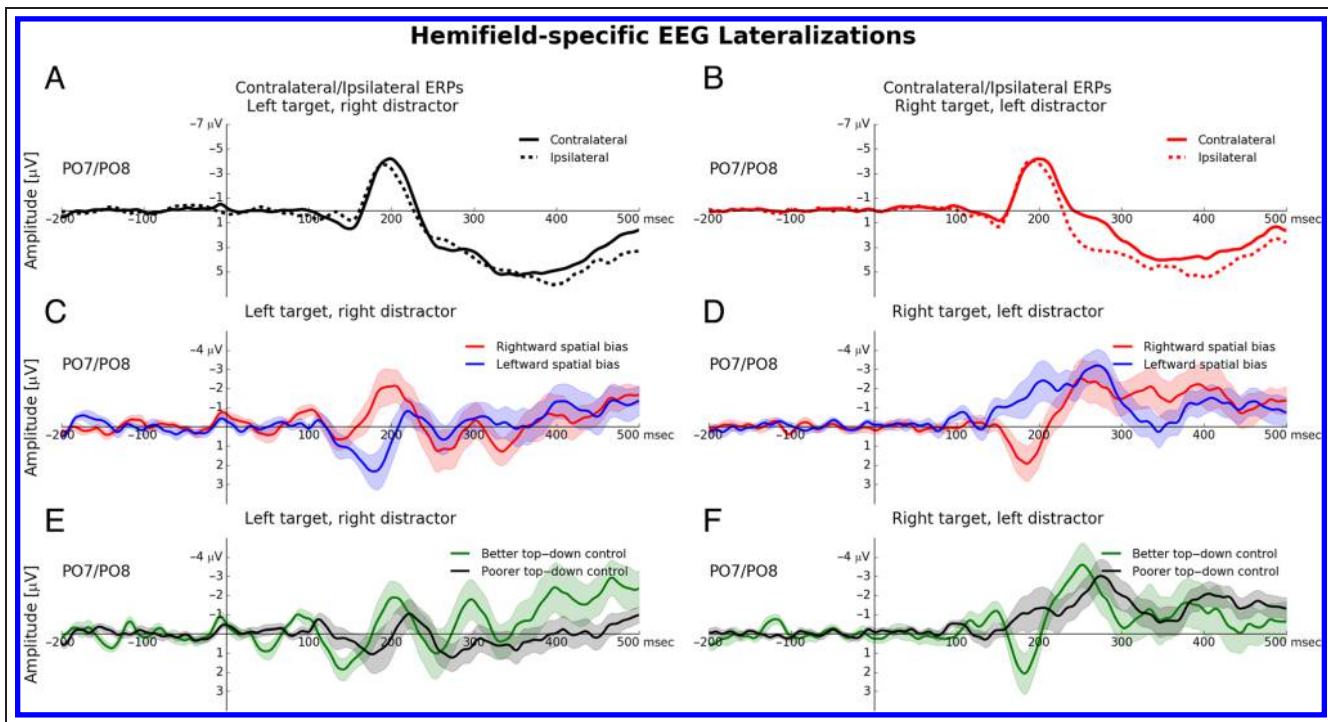


Figure 5. Hemifield-specific asymmetries in ERLs. Grand-averaged ERPs across all participants contralateral and ipsilateral to the target in response to displays with targets presented in the right hemifield and distractors in the left hemifield (A) and to displays with targets presented in the left hemifield and distractors in the right hemifield (B). ERLs (contralateral-minus-ipsilateral difference) are shown separately for groups of individuals with a rightward spatial bias (red lines) and a leftward spatial bias (blue lines) in response to displays with targets presented in the right hemifield and distractors in the left hemifield (C) and to displays with targets presented in the left hemifield and distractors in the right hemifield (D) and for individuals with a better top-down control (green lines) and poorer top-down control (gray lines) in response to displays with targets presented in the right hemifield and distractors in the left hemifield (E) and to displays with targets presented in the left hemifield and distractors in the right hemifield (F).

The ANOVA on hemifield-specific ERLs with the between-participant factor Spatial bias revealed a significant interaction between Spatial bias and Target hemifield ($F(1, 29) = 8.29, p = .007$), showing that ERLs to left versus 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 leftward spatial bias and positive in individuals with a rightward spatial bias (-1.32 vs. $0.99 \mu\text{V}$; $t(29) = 2.897, p < .01$), whereas ERL amplitudes in response to left-target displays were negative in individuals with a rightward spatial bias and positive in individuals with a leftward spatial bias (-0.72 vs. $1.69 \mu\text{V}$; $t(29) = -2.689, p = .012$). 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 leftward bias ($t(15) = 2.799, p = .013$), but not the group with a rightward bias ($t(14) = -1.377, p = .190$).

The ANOVA on hemifield-specific ERLs with the between-participant factor Top-Down control did not reveal an interaction of Top-Down control and Target hemifield ($F(1, 29) < 0.01, p = .96$; Figure 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.

DISCUSSION

We identified distinct ERL correlates of individual differences in TVA-based parameters of task- 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 task-irrelevant objects was overall effective (i.e., targets received higher attentional weights than distractors), although this selection efficiency varied considerably among the individual participants

(Figure 3A). These interindividual 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-distractor displays compared with 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-distractor configurations (Wolfe, 1994, 2007; Müller & Krummenacher, 2006; Found & Müller, 1996; Wolfe, Cave, & Franzel, 1989). Within participants, 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 distractors (Luck & Hillyard, 1994), and it increases when selection becomes harder, such as in visual search for targets defined by feature conjunctions as compared with single features (Luck, Girelli, McDermott, & Ford, 1997; Luck & Hillyard, 1995). 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, Müller, & Zehetleitner, 2012; Töllner, Zehetleitner, Gramann, & Müller, 2010). Given these (and numerous other) reports of within-participant 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 distractors (Eimer, 2014; Luck, 2012). The PCN amplitude specifically is assumed to reflect the amount of attentional resources allocated to the task-relevant stimulus (Töllner, Gramann, Müller, Kiss, & Eimer, 2008; Eimer 1996; Luck & Hillyard, 1994). After this, we interpret the between-participant 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 with individuals with poorer top-down control. In terms of TVA, this translates into a stronger competitive advantage of the target over the distractor in the selection process (Bundesen & Habekost, 2008).

(N)TVA (Bundesen et al., 2005; Bundesen, 1990), 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 ERL modulations.¹ Specifically, the mechanisms assumed to be reflected in the PCN are reconcilable with the mechanism of attentional weighting, which, in TVA, underlies top-down se-

lection (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 distractors, effective top-down control devotes relatively more visual processing resources to the behaviorally important target objects by assigning higher weights to them compared with less important distractor 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 distractors in the opposite hemifield, on an individual-participant 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, Boelmans, Schoenfeld, Heinze, & Luck, 2002).

To integrate the results with other theoretical accounts of visual attention (guided search: Wolfe, 1994, 2007; dimension-weighting account: Müller, Heller, & Ziegler 1995) and to test the generalizability of the association between PCN amplitudes and individuals' ability to effectively filter target and distractor 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 with slower RTs in visual search tasks (Williams & Drew, 2017; Töllner, Conci, & Müller, 2015).

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, nonsignificant, leftward “pseudo-neglect” was found, which mirrors the rightward spatial bias found in patients with visual hemineglect in such TVA-based letter report paradigms (Finke et al., 2012; Duncan et al., 1999), 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 visuospatial attention (Posner & Petersen, 1990; Heilman & Van Den Abell, 1980). For single participants, however, sizable spatial biases to either the left or right hemifield were apparent (Figure 3B). This implies that, on the individual level, attentional resources deployed to locations in the left and right hemifields were asymmetrical and that the direction and degree of this asymmetry varied among individuals.

Although interindividual differences in spatial biases have been linked to other aspects of neural hemispheric asymmetries, such as white matter volume (Thiebaut de Schotten et al., 2011) and activity in the frontoparietal 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 been noted by Hickey et al. (2009). In particular, they proposed the PCN to reflect the summation of a positivity contralateral to the distractor (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 this study, we observed a negativity contralateral to the target (or positivity contralateral to the distractor) only when the target appeared in the individual's nonprioritized hemifield. This may be taken to indicate that more activity related to enhance target (or suppress distractor) processing was engaged by our participants if the relevant information was presented at a nonfavored location.²

Of note, the spatial-bias-related asymmetry in ERLs occurred in a time window before the maximum deflection of the overall PCN (Figures 3 and 4). Several recent studies have pointed out that the Ppc can precede the PCN with some display configurations (Jannati et al., 2013; Corriveau et al., 2012). 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 task-irrelevant stimulus (Fortier-Gauthier, Dell'Acqua, & Jolicoeur, 2013; Corriveau et al., 2012). This can be distinguished from the later P_D component that has been related to the active suppression of a salient distractor (Sawaki & Luck,

2013). Although 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 toward certain stimulus features, specifically, a processing advantage for targets colored red over other target colors (Pomerleau, Fortier-Gauthier, Corriveau, Dell'Acqua, & Jolicoeur, 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 this study, participants showed a Ppc for targets that appeared in their prioritized hemifield (recall that the target–distractor color assignments and shapes were the same for all participants) associated with a processing advantage for stimuli in this hemifield 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 hemifield compared with 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 distractor-related, information (Wiegand et al., 2015; Gokce et al., 2014).

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 with 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 redistributed according to weighting of both spatial and nonspatial features of stimuli in the visual field (Bundesen & Habekost, 2008; Bundesen et al., 2005).

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 nonmalleable. 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., 2009). 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 (Wiegand et al., 2018; Brosnan et al., 2017; Kraft et al., 2015). This indicates that stimulus material-dependent lateralizations become prominent in parameters of visual attention capacity. In fact, in a vSTM task with nonverbal stimuli, a left hemifield advantage was found, at least for simple feature stimuli (Sheremata & Shomstein, 2014; Sheremata, Bettencourt, & Somers, 2010). 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 with left hemisphere, which was attributed to the right-hemispheric dominance for attention (Śmigasiewicz et al., 2015; Verleger et al., 2009). In future experiments, task demands and stimulus materials 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, nonsignificant correlations between the parameters top-down control and spatial bias (Wiegand, Petersen, Bundesen, & Habekost, 2017; Habekost et al., 2014; Finke et al., 2005). 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 the presence of balanced spatial processing, was found in a patient with a superior frontal lesion. In line with previous work (Wiegand, Töllner, Dyrholm, et al., 2014; Wiegand, Töllner, Habekost, et al., 2014), here, we further support TVA's independence assumption by showing distinct relationships between interindividual differences in the model parameters and ERPs.

Apart from separating spatial and nonspatial selection processes, the TVA-based approach further permits those functions to be quantified independently of motor processes. Handedness has been shown to covary 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 (Szczepanski & Kastner, 2013; Badzakova-Trajkov, Häberling, Roberts, & Corballis, 2010). Similarly, handedness did modulate neither behavioral nor ERL hemifield asymmetries in a lateralized rapid serial visual presentation task (Śmigasiewicz, Liebrand, Landmesser, & Verleger, 2017).

Summary and Outlook

In this study, we combined parametric assessment based on the computational TVA framework and visual ERLs and established neurocognitive 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 distractor positions 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 nonspatial 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' preassumptions about the hypothesized variation of cognitive processes and ERPs in a given task manipulation. The present interindividual difference 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 healthy populations, life span 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 neurocognitive trait markers of attentional functions as well as indices of age- and disease-related changes in these functions (Wiegand, Petersen, Bundesen, et al., 2017; Wiegand et al., 2016; Wiegand, Töllner, Dyrholm, et al., 2014).

Acknowledgments

This work was supported by a MOBILEX mobility grant (1321-00039B) from the Danish Council for Independent Research and European Union Marie Skłodowska-Curie COFUND actions (I. W.); the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement no. 702483 (I. W.); the European Union's Seventh Framework programme for research, technological development, and demonstration under the Marie Skłodowska-Curie Initial Training Network grant agreement no. 606901 (K. F., T. T., H. J. M., T. H., and A. P.); a grant (FI 1424/2-1) of the German Research Foundation (K. F.); a Sapere Aude grant (11-104180) from the Danish Council for Independent Research (T. H.); and the Graduate School of Systemic Neurosciences of the LMU Munich (N. N.). We thank Erika Kunstler for help with the data assessment.

Reprint requests should be sent to Iris Wiegand, Max-Planck Institute for Human Development, Lentzeallee 94, 14195 Berlin, Germany, or via e-mail: wiegand@mpib-berlin.mpg.de.

Notes

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 (although 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).
2. Recall that we analyzed only bilateral target-distractor 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 distractor stimuli, which permit the P_D and N_T to be distinguished (see Hickey et al., 2009).

REFERENCES

American Electroencephalographic Society. (1994). Guideline thirteen: American Electroencephalographic Society guidelines for standard electrode position nomenclature. *Journal of Clinical Neurophysiology*, *11*, 111–113.

Badzakova-Trajkov, G., Häberling, I. S., Roberts, R. P., & Corballis, M. C. (2010). Cerebral asymmetries: Complementary and independent processes. *PLoS One*, *5*, e9682.

Bäumler, G. (1985). *Farbe-Wort-Interferenztest (FWIT) nach J. R. Stroop*. Göttingen, Germany: Hogrefe.

Beck, A. T., Steer, R. A., & Brown, G. K. (1996). *Manual for the Beck Depression Inventory-II*. San Antonio, TX: Psychological Corporation.

Bell, A. J., & Sejnowski, T. J. (1995). An information-maximization approach to blind separation and blind deconvolution. *Neural Computation*, *7*, 1129–1159.

Bellgrove, M. A., Dockree, P. M., Aimola, L., & Robertson, I. H. (2004). Attenuation of spatial attentional asymmetries with poor sustained attention. *NeuroReport*, *15*, 1065–1069.

Benwell, C. S., Harvey, M., Gardner, S., & Thut, G. (2013). Stimulus- and state-dependence of systematic bias in spatial attention: Additive effects of stimulus-size and time-on-task. *Cortex*, *49*, 827–836.

Benwell, C. S., Thut, G., Learnmonth, G., & Harvey, M. (2013). Spatial attention: Differential shifts in pseudoneglect direction with time-on-task and initial bias support the idea of observer subtypes. *Neuropsychologia*, *51*, 2747–2756.

Bishop, S. J. (2008). Neural mechanisms underlying selective attention to threat. *Annals of the New York Academy of Sciences*, *1129*, 141–152.

Bowers, D., & Heilman, K. M. (1980). Pseudoneglect: Effects of hemispace on a tactile line bisection task. *Neuropsychologia*, *18*, 491–498.

Braver, T. S., Cole, M. W., & Yarkoni, T. (2010). Vive les differences! Individual variation in neural mechanisms of executive control. *Current Opinion in Neurobiology*, *20*, 242–250.

Brisson, B., & Jolicoeur, P. (2007). The N2pc component and stimulus duration. *NeuroReport*, *18*, 1163–1166.

Brosnan, M. B., Demaria, G., Petersen, A., Dockree, P. M., Robertson, I. H., & Wiegand, I. (2017). Plasticity of the right-lateralized cognitive reserve network in ageing. *Cerebral Cortex*, *24*, 1–11.

Bublak, P., Finke, K., Krummenacher, J., Preger, R., Kyllingsbæk, S., Müller, H. J., et al. (2005). Usability of a theory of visual attention (TVA) for parameter-based measurement of attention II: Evidence from two patients with frontal or parietal damage. *Journal of the International Neuropsychological Society*, *11*, 843–854.

Bundesen, C. (1990). A theory of visual attention. *Psychological Review*, *97*, 523–547.

Bundesden, C. (1998). A computational theory of visual attention. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *353*, 1271–1281.

Bundesden, C., & Habekost, T. (2008). *Principles of visual attention: Linking mind and brain*. Oxford: Oxford University Press.

Bundesden, C., Habekost, T., & Kyllingsbæk, S. (2005). A neural theory of visual attention: Bridging cognition and neurophysiology. *Psychological Review*, *112*, 291–328.

Bundesden, C., Habekost, T., & Kyllingsbæk, S. (2011). A neural theory of visual attention and short-term memory (NTVA). *Neuropsychologia*, *49*, 1446–1457.

Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science*, *315*, 1860–1862.

Carlei, C., & Kerzel, D. (2018). Stronger interference from distractors in the right hemifield during visual search. *Laterality: Asymmetries of Body, Brain and Cognition*, *23*, 152–165.

Cassidy, S. M., Robertson, I. H., & O'Connell, R. G. (2012). Retest reliability of event-related potentials: Evidence from a variety of paradigms. *Psychophysiology*, *49*, 659–664.

Corbetta, M., Kincade, M. J., Lewis, C., Snyder, A. Z., & Sapir, A. (2005). Neural basis and recovery of spatial attention deficits in spatial neglect. *Nature Neuroscience*, *8*, 1603–1610.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215.

Corbetta, M., & Shulman, G. L. (2011). Spatial neglect and attention networks. *Annual Review of Neuroscience*, *34*, 569–599.

- Corriveau, I., Fortier-Gauthier, U., Pomerleau, V. J., McDonald, J., Dell'Acqua, R., & Jolicoeur, P. (2012). Electrophysiological evidence of multitasking impairment of attentional deployment reflects target-specific processing, not distractor inhibition. *International Journal of Psychophysiology*, *86*, 152–159.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222.
- Duncan, J., Bundesen, C., Olson, A., Humphreys, G., Chavda, S., & Shibuya, H. (1999). Systematic analysis of deficits in visual attention. *Journal of Experimental Psychology: General*, *128*, 450–478.
- Dyrholm, M., Kyllingsbæk, S., Espeseth, T., & Bundesen, C. (2011). Generalizing parametric models by introducing trial-by-trial parameter variability: The case of TVA. *Journal of Mathematical Psychology*, *55*, 416–429.
- Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, *99*, 225–234.
- Eimer, M. (2014). The neural basis of attentional control in visual search. *Trends in Cognitive Sciences*, *18*, 526–535.
- Eimer, M. (2015). EPS Mid-Career Award 2014: The control of attention in visual search: Cognitive and neural mechanisms. *Quarterly Journal of Experimental Psychology*, *68*, 2437–2463.
- Finke, K., Bublak, P., Krummenacher, J., Kyllingsbæk, S., Müller, H. J., & Schneider, W. X. (2005). Usability of a theory of visual attention (TVA) for parameter-based measurement of attention I: Evidence from normal subjects. *Journal of the International Neuropsychological Society*, *11*, 832–842.
- Finke, K., Matthias, E., Keller, I., Müller, H. J., Schneider, W. X., & Bublak, P. (2012). How does phasic alerting improve performance in patients with unilateral neglect? A systematic analysis of attentional processing capacity and spatial weighting mechanisms. *Neuropsychologia*, *50*, 1178–1189.
- Fortier-Gauthier, U., Dell'Acqua, R., & Jolicoeur, P. (2013). The “red-alert” effect in visual search: Evidence from human electrophysiology. *Psychophysiology*, *50*, 671–679.
- Found, A., & Müller, H. J. (1996). Searching for unknown feature targets on more than one dimension: Investigating a “dimension-weighting” account. *Attention, Perception, & Psychophysics*, *58*, 88–101.
- Gokce, A., Geyer, T., Finke, K., Müller, H. J., & Töllner, T. (2014). What pops out in positional priming of pop-out: Insights from event-related EEG lateralizations. *Frontiers in Psychology*, *5*, 688.
- Gold, J. M., Fuller, R. L., Robinson, B. M., Braun, E. L., & Luck, S. J. (2007). Impaired top-down control of visual search in schizophrenia. *Schizophrenia Research*, *94*, 148–155.
- Gross, M. M. (1972). Hemispheric specialization for processing of visually presented verbal and spatial stimuli. *Attention, Perception, & Psychophysics*, *12*, 357–363.
- Habekost, T. (2015). Clinical TVA-based studies: A general review. *Frontiers in Psychology*, *6*, 290.
- Habekost, T., Petersen, A., & Vangkilde, S. (2014). Testing attention: Comparing the ANT with TVA-based assessment. *Behavior Research Methods*, *46*, 81–94.
- Harvey, M., Milner, A. D., & Roberts, R. C. (1995). An investigation of hemispatial neglect using the Landmark Task. *Brain and Cognition*, *27*, 59–78.
- Heilman, K. M., & Van Den Abell, T. (1980). Right hemisphere dominance for attention: The mechanism underlying hemispheric asymmetries of inattention (neglect). *Neurology*, *30*, 327–330.
- Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience*, *21*, 760–775.
- Hopf, J.-M., Boelmans, K., Schoenfeld, A. M., Heinze, H.-J., & Luck, S. J. (2002). How does attention attenuate target-distractor interference in vision?: Evidence from magnetoencephalographic recordings. *Cognitive Brain Research*, *15*, 17–29.
- Hopf, J.-M., Luck, S. J., Boelmans, K., Schoenfeld, M. A., Boehler, C. N., Rieger, J., et al. (2006). The neural site of attention matches the spatial scale of perception. *Journal of Neuroscience*, *26*, 3532–3540.
- Jannati, A., Gaspar, J. M., & McDonald, J. J. (2013). Tracking target and distractor processing in fixed-feature visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, *39*, 1713–1730.
- Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia*, *38*, 93–110.
- Jung, T.-P., Makeig, S., Westerfield, W., Townsend, J., Courchesne, E., & Sejnowski, T. J. (2000). Removal of eye activity artifacts from visual event-related potentials in normal and clinical subjects. *Clinical Neurophysiology*, *111*, 1745–1758.
- Kane, M. J., Poole, B. J., Tuholski, S. W., & Engle, R. W. (2006). Working memory capacity and the top-down control of visual search: Exploring the boundaries of “executive attention”. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *32*, 749–777.
- Kraft, A., Dyrholm, M., Kehler, S., Kaufmann, C., Bruening, J., Kathmann, N., et al. (2015). TMS over the right precuneus reduces the bilateral field advantage in visual short term memory capacity. *Brain Stimulation*, *8*, 216–223.
- Kyllingsbæk, S. (2006). Modeling visual attention. *Behavior Research Methods*, *38*, 123–133.
- Luck, S. J. (2005). *An introduction to the event-related potential technique*. Cambridge, MA: MIT Press.
- Luck, S. J. (2012). Electrophysiological correlates of the focusing of attention within complex visual scenes: N2pc and related electrophysiological correlates. In S. J. Luck & E. S. Kappenmann (Eds.), *The Oxford handbook of event-related potential components* (pp. 329–360). Oxford: Oxford University Press.
- Luck, S. J., Girelli, M., McDermott, M. T., & Ford, M. A. (1997). Bridging the gap between monkey neurophysiology and human perception: An ambiguity resolution theory of visual selective attention. *Cognitive Psychology*, *33*, 64–87.
- Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, *20*, 1000–1014.
- Luck, S. J., & Hillyard, S. A. (1995). The role of attention in feature detection and conjunction discrimination: An electrophysiological analysis. *International Journal of Neuroscience*, *80*, 281–297.
- Luck, S. J., Woodman, G. F., & Vogel, E. K. (2000). Event-related potential studies of attention. *Trends in Cognitive Sciences*, *4*, 432–440.
- Luh, K. E. (1995). Line bisection and perceptual asymmetries in normal individuals: What you see is not what you get. *Neuropsychology*, *9*, 435–448.
- Madden, D. J. (2007). Aging and visual attention. *Current Directions in Psychological Science*, *16*, 70–74.
- Matthias, E., Bublak, P., Costa, A., Müller, H. J., Schneider, W. X., & Finke, K. (2009). Attentional and sensory effects of lowered levels of intrinsic alertness. *Neuropsychologia*, *47*, 3255–3264.

- Mazza, V., & Pagano, S. (2017). Electroencephalographic asymmetries in human cognition. In L. Rogers & G. Vallortigara (Eds.), *Lateralized brain functions: Neuromethods* (Vol. 122, pp. 407–439). New York: Humana Press.
- McAvinue, L. P., Habekost, T., Johnson, K. A., Kyllingsbæk, S., Vangkilde, S., Bundesen, C., et al. (2012). Sustained attention, attentional selectivity, and attentional capacity across the lifespan. *Attention, Perception, & Psychophysics*, *74*, 1570–1582.
- McLoughlin, G., Makeig, S., & Tsuang, M. T. (2014). In search of biomarkers in psychiatry: EEG-based measures of brain function. *American Journal of Medical Genetics Part B: Neuropsychiatric Genetics*, *165*, 111–121.
- Müller, H. J., Heller, D., & Ziegler, J. (1995). Visual search for singleton feature targets within and across feature dimensions. *Perception & Psychophysics*, *57*, 1–17.
- Müller, H. J., & Krummenacher, J. (2006). Locus of dimension weighting: Preattentive or postselective? *Visual Cognition*, *14*, 490–513.
- Nicholls, M. E., Bradshaw, J. L., & Mattingley, J. B. (1999). Free-viewing perceptual asymmetries for the judgement of brightness, numerosity and size. *Neuropsychologia*, *37*, 307–314.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.
- Parasuraman, R., & Haxby, J. V. (1993). Attention and brain function in Alzheimer's disease: A review. *Neuropsychology*, *7*, 242–272.
- Pomerleau, V. J., Fortier-Gauthier, U., Corriveau, I., Dell'Acqua, R., & Jolicœur, P. (2014). Colour-specific differences in attentional deployment for equiluminant pop-out colours: Evidence from lateralised potentials. *International Journal of Psychophysiology*, *91*, 194–205.
- Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42.
- Sawaki, R., & Luck, S. J. (2013). Active suppression after involuntary capture of attention. *Psychonomic Bulletin & Review*, *20*, 296–301.
- Sheremata, S. L., Bettencourt, K. C., & Somers, D. C. (2010). Hemispheric asymmetry in visuotopic posterior parietal cortex emerges with visual short-term memory load. *Journal of Neuroscience*, *30*, 12581–12588.
- Sheremata, S., & Shomstein, S. (2014). Hemifield asymmetries differentiate VSTM for single and multiple-feature objects. *Attention, Perception, & Psychophysics*, *76*, 1609–1619.
- Śmigajewicz, K., Asanowicz, D., Westphal, N., & Verleger, R. (2015). Bias for the left visual field in rapid serial visual presentation: Effects of additional salient cues suggest a critical role of attention. *Journal of Cognitive Neuroscience*, *27*, 266–279.
- Śmigajewicz, K., Liebrand, M., Landmesser, J., & Verleger, R. (2017). How handedness influences perceptual and attentional processes during rapid serial visual presentation. *Neuropsychologia*, *100*, 155–163.
- Spielberger, C. D., Gorsuch, R. L., & Lushene, R. E. (1970). *Test manual for the State-Trait Anxiety Inventory*. Palo Alto, CA: Consulting Psychologists Press.
- Szczepanski, S. M., & Kastner, S. (2013). Shifting attentional priorities: Control of spatial attention through hemispheric competition. *Journal of Neuroscience*, *33*, 5411–5421.
- Thiebaut de Schotten, M., Ffytche, D. H., Bizzi, A., Dell'Acqua, F., Allin, M., Walshe, M., et al. (2011). Atlasing location, asymmetry and inter-subject variability of white matter tracts in the human brain with MR diffusion tractography. *Neuroimage*, *54*, 49–59.
- Töllner, T., Conci, M., & Müller, H. J. (2015). Predictive distractor context facilitates attentional selection of high, but not intermediate and low, salience targets. *Human Brain Mapping*, *36*, 935–944.
- Töllner, T., Gramann, K., Müller, H. J., Kiss, M., & Eimer, M. (2008). Electrophysiological markers of visual dimension changes and response changes. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 531–542.
- Töllner, T., Müller, H. J., & Zehetleitner, M. (2012). Top-down dimensional weight set determines the capture of visual attention: Evidence from the PCN component. *Cerebral Cortex*, *22*, 1554–1563.
- Töllner, T., Rangelov, D., & Müller, H. J. (2012). How the speed of motor-response decisions, but not focal-attentional selection, differs as a function of task set and target prevalence. *Proceedings of the National Academy of Sciences, U.S.A.*, *109*, E1990–E1999.
- Töllner, T., Zehetleitner, M., Gramann, K., & Müller, H. J. (2010). Top-down weighting of visual dimensions: Behavioral and electrophysiological evidence. *Vision Research*, *50*, 1372–1381.
- Töllner, T., Zehetleitner, M., Gramann, K., & Müller, H. J. (2011). Stimulus saliency modulates pre-attentive processing speed in human visual cortex. *PLoS One*, *6*, e16276.
- Tomer, R., Slagter, H. A., Christian, B. T., Fox, A. S., King, C. R., Murali, D., et al. (2013). Dopamine asymmetries predict orienting bias in healthy individuals. *Cerebral Cortex*, *23*, 2899–2904.
- Vangkilde, S., Coull, J. T., & Bundesen, C. (2012). Great expectations: Temporal expectation modulates perceptual processing speed. *Journal of Experimental Psychology: Human Perception and Performance*, *38*, 1183–1191.
- Verleger, R., Sprenger, A., Gebauer, S., Fritzmanna, M., Friedrich, M., Kraft, S., et al. (2009). On why left events are the right ones: Neural mechanisms underlying the left-hemifield advantage in rapid serial visual presentation. *Journal of Cognitive Neuroscience*, *21*, 474–488.
- Wiegand, I., Finke, K., Töllner, T., Starman, K., Müller, H. J., & Conci, M. (2015). Age-related decline in global form suppression. *Biological Psychology*, *112*, 116–124.
- Wiegand, I., Hennig-Fast, K., Kilian, B., Müller, H. J., Töllner, T., Möller, H. J., et al. (2016). EEG correlates of visual short-term memory as neuro-cognitive endophenotypes of ADHD. *Neuropsychologia*, *85*, 91–99.
- Wiegand, I., Lauritzen, M. J., Osler, M., Mortensen, E. L., Rostup, E., Rask, L., et al. (2018). EEG correlates of visual short-term memory in older age vary with adult lifespan cognitive development. *Neurobiology of Aging*, *62*, 210–220.
- Wiegand, I., Petersen, A., Bundesen, C., & Habekost, T. (2017). Phasic alerting increases visual attention capacity in younger but not in older individuals. *Visual Cognition*, *25*, 343–357.
- Wiegand, I., Petersen, A., Finke, K., Bundesen, C., Lansner, J., & Habekost, T. (2017). Behavioral and brain measures of phasic alerting effects on visual attention. *Frontiers in Human Neuroscience*, *11*, 176.
- Wiegand, I., Töllner, T., Dyrholm, M., Müller, H. J., Bundesen, C., & Finke, K. (2014). Neural correlates of age-related decline and compensation in visual attention capacity. *Neurobiology of Aging*, *35*, 2161–2173.
- Wiegand, I., Töllner, T., Habekost, T., Dyrholm, M., Müller, H. J., & Finke, K. (2014). Distinct neural markers of TVA-based visual processing speed and short-term storage capacity parameters. *Cerebral Cortex*, *24*, 1967–1978.
- Williams, L., & Drew, T. (2017). Electrophysiological correlates of individual differences in visual search. *Journal of Vision*, *17*, 1140.

- Wolfe, J. M. (1994). Guided Search 2.0 A revised model of visual search. *Psychonomic Bulletin & Review*, *1*, 202–238.
- Wolfe, J. M. (2007). Guided search 4.0. In W. D. Gray (Ed.), *Integrated models of cognitive systems* (pp. 99–119). Oxford: Oxford University Press.
- Wolfe, J. M., Cave, K. R., & Franzel, S. L. (1989). Guided search: An alternative to the feature integration model for visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *15*, 419–433.
- Woodman, G. F., & Luck, S. J. (1999). Electrophysiological measurement of rapid shifts of attention during visual search. *Nature*, *400*, 867–869.
- Zimmermann, P. & Fimm, B. (1993). *Test of Attentional Performance (TAP)*. Herzogenrath, Germany: Psytest.