

Competitive Interactions of Attentional Resources in Early Visual Cortex during Sustained Visuospatial Attention within or between Visual Hemifields: Evidence for the Different-hemifield Advantage

Sabrina Walter¹, Clíodhna Quigley², and Matthias M. Mueller¹

Abstract

■ Performing a task across the left and right visual hemifields results in better performance than in a within-hemifield version of the task, termed the different-hemifield advantage. Although recent studies used transient stimuli that were presented with long ISIs, here we used a continuous objective electrophysiological (EEG) measure of competitive interactions for attentional processing resources in early visual cortex, the steady-state visual evoked potential (SSVEP). We frequency-tagged locations in each visual quadrant and at central fixation by flickering light-emitting diodes (LEDs) at different frequencies to elicit distinguishable SSVEPs. Stimuli were presented for several seconds, and participants were cued to attend to two LEDs either in one (Within) or distributed across left and right visual hemifields (Across). In addition, we introduced two reference measures: one for sup-

pressive interactions between the peripheral LEDs by using a task at fixation where attention was withdrawn from the periphery and another estimating the upper bound of SSVEP amplitude by cueing participants to attend to only one of the peripheral LEDs. We found significantly greater SSVEP amplitude modulations in Across compared with Within hemifield conditions. No differences were found between SSVEP amplitudes elicited by the peripheral LEDs when participants attended to the centrally located LEDs compared with when peripheral LEDs had to be ignored in Across and Within trials. Attending to only one LED elicited the same SSVEP amplitude as Across conditions. Although behavioral data displayed a more complex pattern, SSVEP amplitudes were well in line with the predictions of the different-hemifield advantage account during sustained visuospatial attention. ■

INTRODUCTION

In everyday life, we are confronted with multiple objects in the environment, of which only a subset is relevant to our current goals and actions. Attention helps to solve the competition of visual input for mental representation by selecting relevant over irrelevant stimuli to optimize our interaction with the environment. Prioritizing relevant from irrelevant information is considered an important step during perception because processing resources are thought to be capacity limited (Marois & Ivanoff, 2005; Luck & Vogel, 1997; Kahneman, 1973).

A consistent finding during spatial attentional selection (Posner, 1980) is that tasks are performed with greater accuracy and reduced RTs when task-relevant stimuli are presented in both left and right visual hemifields (referred to as “Across” from hereon) compared with presentation within one, that is, the left or right, hemifield (“Within”). Sereno and Kosslyn (1991) referred to that phenomenon as the different-hemifield advantage. Different-hemifield advantages have since been reported in numerous visuospatial attention paradigms such as motion object tracking (Harasawa & Shioiri, 2011; Alvarez

& Cavanagh, 2005), sustained multifocal spatial attention (Alvarez & Cavanagh, 2012), and split attention studies (Malinowski, Fuchs, & Müller, 2007; Kraft et al., 2005; Müller, Malinowski, Gruber, & Hillyard, 2003; Awh & Pashler, 2000). There is a difference only in terminology between the different-hemifield advantage and the bilateral advantage (Alvarez & Cavanagh, 2012; Reardon, Kelly, & Matthews, 2009; Brown & Jeeves, 1993; Norman, Jeeves, Milne, & Ludwig, 1992; Merola & Liederman, 1985) or bilateral field advantage (Kraft et al., 2007, 2013; Chakravarthi & VanRullen, 2011; Delvenne, Castronovo, Demeyere, & Humphreys, 2011; Kraft, Kehler, Hagedorf, & Brandt, 2011; Shipp, 2011; Chakravarthi & Cavanagh, 2009; Larson & Brown, 1997); all these terms describe the observed facilitation during performance across hemifields. A similarly named phenomenon, which does differ, is the bilateral distribution advantage (Welcome & Chiarello, 2008; Maertens & Pollmann, 2005; Pollmann, Zaidel, & Von Cramon, 2003; Banich, 1998; Belger, System, Haven, & Banich, 1998; Belger & Banich, 1992). Although the different-hemifield advantage mainly refers to (early) perceptual processes and the competition for attentional resources in spatial attention, the bilateral distribution advantage arises during more demanding tasks. Banich and colleagues (Banich, 1998) suggested that the bilateral distribution advantage

¹Leipzig University, ²German Primate Center, Göttingen

is predominantly found in tasks that these authors call “computationally complex.” Computationally simple tasks, such as the ones of the present experiments, will not benefit from that effect. It is noteworthy that the bilateral distribution advantage would yield the opposite prediction, that is, better performance when stimuli are presented within a visual hemifield under these circumstances (i.e., when one hemisphere can process these stimuli “alone”).

Here we focus exclusively on early perceptual processes. So how can these asymmetries between Within and Across hemifield performance be accounted for? On the basis of behavioral experiments in which participants were confronted with two briefly presented stimuli either in one visual hemifield or in the left and right visual hemifields, Sereno and Kosslyn (1991) argued that the different-hemifield advantage may result from separate, hemisphere-specific pools of attentional capacity operating during perceptual encoding, leading to twice as many resource pools being available during task performance across both hemifields. Processing multiple stimuli that are presented within one hemifield is suggested to lead to high intrahemispheric competition for common processing structures and low interhemispheric competition for representation and requires hemisphere-specific processes to take place in parallel (Sereno & Kosslyn, 1991).¹ The extent to which pools of processing resources act independently within each hemisphere has since been under debate (Kraft et al., 2013; Chakravarthi & VanRullen, 2011; Harasawa & Shioiri, 2011; Chakravarthi & Cavanagh, 2009; Alvarez & Cavanagh, 2005; Luck, Hillyard, Mangun, & Gazzaniga, 1989).

Resources and capacity limitations are constructs that are often discussed in the literature but are seldom defined in any detail. In a recent approach by Franconeri, Alvarez, and Cavanagh (2013), these constructs are thought of as temporary buffers for attention and working memory that are reified in cortex as competitive content maps, because map-like cortical representations are found in various sensory and motor areas. Competitive content maps take into account visual and cortical space—the external visual proximity of visual stimuli and their corresponding vicinity in retinotopically organized visual cortical areas—as well as competition between elements within the maps. Hence, these maps are considered flexible resources where capacity is dependent on the space consumed by activity requirements of individual elements, their interaction with other stimuli, as well as their alignment in the visual field. The account by Franconeri and colleagues thus provides a better understanding of what is meant by “limited resources” and offers an alternative way to explain the different-hemifield advantage. The model predicts that interitem competition will be reduced in across hemifield situations where “the hemifield boundary reduces competition across otherwise adjacent areas of a map” (Franconeri et al., 2013, p. 137) because of the brain’s anatomy.

In two experiments, we aimed to test the different-hemifield advantage during sustained spatial attention with objective electrophysiological (EEG) measures by instructing participants to either perform a stimulus discrimination task with two stimuli located within the left or right visual hemifield (Within) or in the upper or lower left and right visual hemifield (Across). Stimuli were presented concurrently for several seconds to study sustained effects of the deployment of attention to multiple stimuli and their competitive interactions as a function of hemifield arrangement. Furthermore, in contrast to several other studies (Welcome & Chiarello, 2008; Alvarez & Cavanagh, 2005; Banich, 1998; Belger et al., 1998; Larson & Brown, 1997; Belger & Banich, 1992; Sereno & Kosslyn, 1991), stimuli were always present at all locations and only deployment of attention to locations was manipulated, while participants kept their gaze fixated at the center of the display. Four light-emitting diodes (LEDs), each flickering at a different frequency, were located peripherally in the visual quadrants plus additional LEDs in the center of the display. As mentioned above, these central LEDs served as fixation point to prevent eye movements and moreover were used for a further experimental condition: Participants were cued to attend to central LEDs providing a reference measure for competitive interactions between LEDs in the respective quadrants when attention is drawn away from the periphery (Fuchs, Andersen, Gruber, & Müller, 2008; Beck & Kastner, 2007; Kastner, De Weerd, Desimone, & Ungerleider, 1998).

Each LED elicited a distinct steady-state visual evoked potential (SSVEP) in the recorded EEG. SSVEPs are cortical signals that oscillate at the same frequency as the driving stimulus (Regan, 1989) and whose generators have been located in early visual cortices (Quigley, Andersen, & Müller, 2012; Fuchs et al., 2008; Di Russo et al., 2007). The response elicited by each stimulus can be separated in the frequency domain, allowing analysis of the effects of experimental manipulations such as attentional selection on individual elements of multistimulus displays. SSVEP amplitudes have been found to increase with attention (Müller, Teder-Sälejärvi, & Hillyard, 1998; Morgan, Hansen, & Hillyard, 1996) and also provide an objective and reliable measure for studying competitive interactions for processing resources in early visual cortex between multiple stimuli in the visual field (cf. Andersen, Müller, & Hillyard, 2011).

Given the enhancement of SSVEP amplitudes when a flickering stimulus is attended compared with when that stimulus is unattended, one can calculate an amplitude modulation index (AMI; see Methods) that allows for a normalized estimation of the attention effect upon the steady-state signal (Walter, Quigley, Andersen, & Müller, 2012; Niebergall, Khayat, Treue, & Martinez-Trujillo, 2011; McAdams & Maunsell, 1999). Here we used the AMI to test attentional modulation of neural activity in early visual cortex as a function of attentional deployment to horizontally (Across) or vertically (Within) aligned

flickering stimuli. On the basis of earlier reports of the different-hemifield advantage (Serenio & Kosslyn, 1991) as well as on the model proposed by Franconeri and colleagues (2013), we expected a larger attention effect upon SSVEP amplitudes when participants attended to two stimuli in the left and right visual hemifield (horizontal arrangement or Across) compared with when they attended to two stimuli located within one visual hemifield (vertical arrangement or Within). Thus, we contrasted SSVEP amplitudes in conditions in which attention was deployed to two stimuli located peripherally across or within hemifields with SSVEP responses in conditions when peripheral stimuli were attended (e.g., Within: left hemifield attended [Attended Within] vs. right hemifield attended [Unattended Within] and vice versa; Across: upper left and right hemifields attended [Attended Across] vs. lower left and right hemifields attended [Unattended Across] and vice versa).

Moreover, as a result of continuous stimulation at all locations of the display, we were able to study competitive suppressive interactions of the peripherally presented stimuli as a function of attentional deployment, that is, when the peripheral condition was attended Across or Within versus trials when attention was completely withdrawn from the periphery. Such suppressive interactions when multiple stimuli are presented in the visual field and are unattended compose one of the key elements of the biased competition account (Desimone & Duncan, 1995). Empirical evidence for these suppressive interactions has been found in animal single cell recordings (Reynolds, Chelazzi, & Desimone, 1999; Luck, Chelazzi, Hillyard, & Desimone, 1997; Moran & Desimone, 1985) as well as in noninvasive human recordings (cf. Fuchs et al., 2008; Beck & Kastner, 2007; Kastner et al., 1998). Here, the reference measure for estimating suppressive interactions was the condition when participants attended to the central LEDs and performed the task at fixation ("Fixation"). The analysis involved a contrast of the SSVEP elicited by a stimulus in peripheral conditions (i.e., that stimulus was Unattended in an Across or Within condition, respectively) with the SSVEP elicited by the stimulus when the central LEDs were attended (e.g., Within: left hemifield unattended during peripheral attentional deployment [Unattended Within] vs. center is attended [Attended Fixation]). In both cases, attention is withdrawn from the stimulus in question, but differing hypotheses regarding the distribution of attentional pools of resources lead to differing predictions. If one assumes that both cerebral hemispheres operate on separate resource pools, one would not expect any differences in SSVEP amplitudes for the to-be-ignored stimuli in Within conditions compared with when the central LEDs were attended. If, however, both hemispheres operate with a common pool, one should expect that, at least for conditions in which participants were cued to the left or right visual hemifield (Within), SSVEP amplitudes to unattended

stimuli would be smaller compared with amplitudes when participants attended central fixation, because resources needed to be shifted away from one visual hemifield to the to-be-attended one.

In Experiment II, as well as controlling for possible alternative explanations for the results in Experiment I, we introduced an additional condition where participants were cued to attend to one LED per visual quadrant only. This provided a reference measure for attentional effects, again based on the biased competition account (Desimone & Duncan, 1995), which predicts the release of the attended stimulus or stimuli from suppressive interactions. Importantly, the attentional response when two stimuli compete for processing resources and one is attended is predicted to be no larger compared with when that stimulus was presented and attended alone (Beck & Kastner, 2007; Kastner et al., 1998; Moran & Desimone, 1985). Although we never presented one LED alone, we believe that attending to one LED in Experiment II provided a good estimation of the upper limit of the SSVEP amplitude elicited by that location. In case of independent resources for each hemisphere, we expected that SSVEP amplitudes would not differ when participants attended to one LED compared with when they attended to two LEDs in the Across conditions. Furthermore, if attending to two LEDs in the same visual hemifield leads to more intrahemispheric competition compared with when attention is deployed across both hemifields, we would expect reduced SSVEP amplitudes for Within trials compared with when participants attended to one LED alone.

Overall we found supportive evidence for the different-hemifield advantage in the electrophysiological measurements that are also in line with some predictions of the competitive content maps account. Interestingly, behavioral data revealed a more complex pattern, in particular concerning the reference experimental conditions for competitive interactions in Experiments I and II. However, it is important to note that our findings did not result from a left visual field advantage, associated with a right hemisphere dominance, that is sometimes reported in the literature on visuospatial attention tasks in healthy individuals and in observers suffering from hemineglect (for a review, see Corbetta & Shulman, 2011).

EXPERIMENT I

Methods

Participants

Eighteen volunteers participated in the experiment (12 women; mean age = 23 years, $SD = 5.9$ years, range = 19–45 years; two left-handed). All reported normal or corrected-to-normal vision and gave written informed consent. The study was in accordance with the requirements of the Declaration of Helsinki and local and national ethics requirements. Participants received either financial compensation or course credits.

Stimulus Material

Six red LEDs with a size of $2.1^\circ \times 1.43^\circ$ of visual angle (height \times width) at a viewing distance of 60 cm were used. Two LEDs were mounted in the upper visual field, and two were mounted in the lower visual field. The two remaining LEDs with a size of $1.05^\circ \times 1.43^\circ$ were mounted in the middle of the display and together matched the size of a single peripheral LED. The distance between the middle LEDs and the four surrounding LEDs was 4.5° (center to center). The LED at each location flickered with a unique frequency. Driving frequencies were kept as close as possible to ensure equity of stimulus perception. Middle LEDs were tagged with 19 Hz, upper left with 11 Hz, upper right with 13 Hz, lower left with 15 Hz, and lower right with 17 Hz (Figure 1A). All frequencies were presented in a 50% on-off cycle.

Changing the luminance of the LEDs generated targets and distractors. The amount of increase and decrease was adjusted in a piloting phase (12 participants) to yield a hit rate of approximately 80%. The overall luminance of the resulting stimulus arrangement was measured with LEDs constantly on and corresponded to 105 cd/m^2 for ongoing flicker, 45 cd/m^2 during luminance decrements, and 245 cd/m^2 during luminance increments. LEDs were controlled using an external controlling device manufactured by Ulrich Krebs (Friedrich-Wilhelm-Bessel-Institute, Bremen, Germany). The experiment was programmed using Matlab (The MathWorks, Natick, MA) and Cogent Graphics (John Romaya, LON at the Wellcome Department of Imaging Neuroscience).

Experimental Paradigm

Figure 1 depicts a schematic overview of the stimulus configuration and experimental paradigm. The experiment consisted of five conditions. Participants were instructed to attend to the peripheral upper (“Up”; 11 Hz, 13 Hz) or lower LED pairs (“Down”; 15 Hz, 17 Hz). These two conditions formed the situation when participants attended

two LEDs simultaneously that were distributed across the left and right visual hemifields, referred to as “Across.” In conditions when participants had to attend LED pairs within one hemifield (“Within”), they were cued to the peripheral upper and lower LED in either the left (“Left”; 11 Hz, 15 Hz) or right visual hemifield (“Right”; 13 Hz, 17 Hz). A fifth condition, when attention was deployed to the middle LEDs at fixation (both at 19 Hz), served as a reference condition (“Fixation”) in which the four peripheral LEDs were unattended (see also Fuchs et al., 2008; Beck & Kastner, 2007; Kastner et al., 1998). Participants were cued trial by trial to covertly attend the respective LED pair in the periphery, while keeping fixation at the central LED pair, or to attend to the center LEDs, where location of fixation and location of attention coincided. They had to react by button press to simultaneous increments in luminance (targets) in the to-be-attended LED pair, whereas luminance decrements (distractors) had to be ignored. Another kind of distractor was luminance changes at task-irrelevant locations that could also involve one of the attended LEDs; this allowed confirmation that participants were attending to both LEDs of the instructed LED pair, because attention to only one of the cued LEDs could result in a false alarm to task-irrelevant events. As stated above, the central location contained two LEDs so that the discrimination task was performed comparably in all conditions.

Procedure

Each trial lasted 3200 msec and started with a spatial cue, consisting of a brief flash (50 msec) of the two task-relevant LEDs. All LEDs were then extinguished for 150 msec, followed by a stimulation period of 3000 msec. Trials contained zero or one event. Events were generated with random onsets between 500 and 2200 msec after stimulus onset and lasted 180 msec. These brief event durations were chosen to rule out the possibility that participants were attending to one location and then performed a rapid

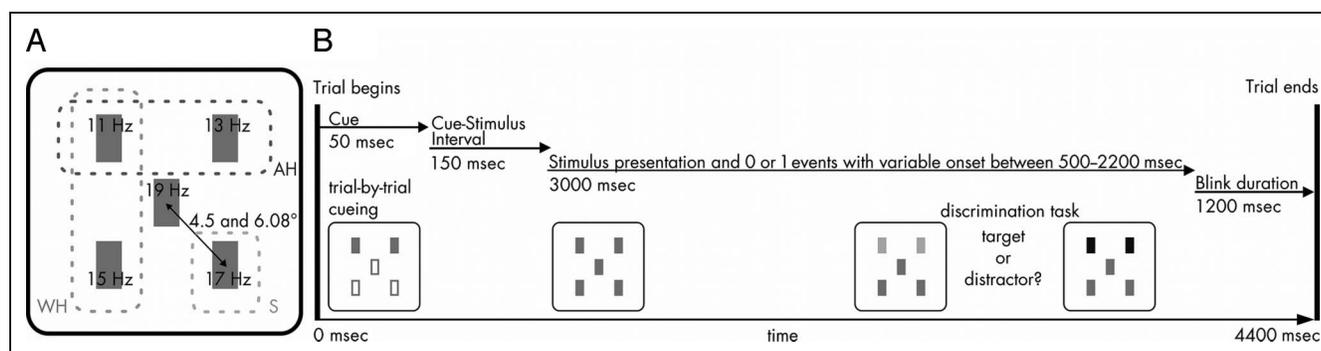


Figure 1. (A) Arrangement of LED stimuli and schematic overview of relevant stimuli for 2-LEDs across (AH) and within (WH) hemifield conditions, as well as 1-LED conditions (S). Numbers indicate flicker frequencies of respective LEDs. Eccentricities of LEDs from central fixation, indicated by the black arrow, were 4.5° for Experiment I and 6.08° for Experiment II. (B) Experimental paradigm exemplarily shown for conditions in which upper horizontal pairs of LEDs had to be attended. Participants were instructed to attend the cued LED pair while maintaining central fixation and had to react to discrete changes in luminance in the attended LED pair. Luminance increments (brighter) were defined as target stimuli, whereas luminance decrements (darker) had to be ignored.

switching to the other location, rather than attending to the cued locations concurrently (Müller et al., 2003; Duncan, Ward, & Shapiro, 1994; Weichselgartner & Sperling, 1987). Trials were followed by a 1200-msec break during which participants were allowed to blink (Figure 1B).

During the experiment, 12 blocks were run, each containing 40 trials. Half of the trials contained no luminance changes. Of the remaining 50% of the trials, 75% contained luminance increments and 25% contained luminance decrements. Distribution of events to attended and ignored LED pairs was pseudorandomized. Responding hand was changed midway through the experiment, and assignment of beginning hand was balanced across participants. Participants were instructed to respond as precisely and quickly as possible to luminance increments in the attended LED pair while ignoring luminance decrements and all kinds of events in the unattended LEDs. After each block, participants received feedback regarding overall hit rate (i.e., across all conditions within a respective block). Before the experiment, participants were trained in at least two training blocks of 40 trials, each of which contained either a target or any kind of distractor stimuli for more effective task learning.

Data Acquisition

EEG was recorded at 256 Hz in an electrically shielded chamber using an ActiveTwo amplifier system (BioSemi, Amsterdam, The Netherlands) and 64 Ag/AgCl cap-mounted electrodes. Four external electrodes measured vertical and horizontal EOG to monitor eye movements and blinks plus two reference electrodes affixed to the left and right earlobes.

Data Analysis

EEG Data. We used Matlab and EEGLab (Delorme & Makeig, 2004) for preprocessing and analysis of collected data. Epochs of 3000-msec duration, starting with stimulus onset, were extracted from the ongoing EEG and submitted to a variant of the statistical control of artifacts in dense array EEG/MEG (Junghöfer, Elbert, Tucker, & Rockstroh, 2000). Trials with eye movements exceeding a threshold of 25 μV ($\sim 1.5^\circ$ of visual angle) were excluded from SSVEP analysis, resulting in an average rejection rate of 9.47% with no significant difference between conditions, $F(4, 17) = 0.240$, $p = .91$. Artifact free trials were averaged for each experimental condition separately and converted to average reference off-line. We included epochs with and without events in the SSVEP analysis, given that luminance changes did not elicit a strong ERP that could distort the SSVEP (an approach also used by Müller, Picton, et al., 1998; Müller, Teder-Sälejärvi, et al., 1998).

SSVEP amplitudes were estimated by extraction of Fourier components of corresponding driving frequencies in the window from 500 to 3000 msec after stimulus onset. The first 500 msec after stimulus onset were not

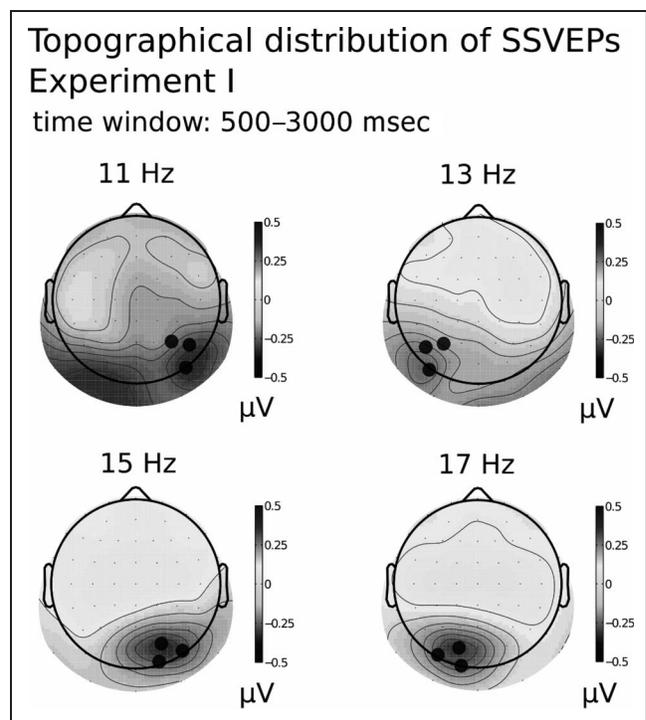


Figure 2. Isocontour voltage maps of the grand average for the 2-LEDs task during the first experiment for frequencies 11 Hz, 13 Hz, 15 Hz, and 17 Hz. Voltage maps are derived from data in the time window of 500–3000 msec after stimulus onset. Black dots at posterior electrode sites highlight the electrode clusters chosen for statistical analysis based on the amplitude maxima as revealed by the maps.

included in the analysis to avoid contamination by the ERP to stimulus onset and to allow for the SSVEP to build up. To identify the electrodes with the largest SSVEP amplitudes for statistical analysis, we inspected the grand mean voltage map averaged across all experimental conditions within 500–3000 msec after stimulus onset (see Figure 2). As expected, topographies revealed the SSVEP amplitude maxima for the peripheral stimuli (11 Hz, 13 Hz, 15 Hz, and 17 Hz) to be at occipital sites contralateral to the driving stimulus and a central-occipital cluster for centrally located stimuli (19 Hz). Because the central stimulus served only as a reference for the investigation of suppressive interactions between the covertly attended peripheral stimuli and the task involved overt attention to the central LEDs, which modulates the SSVEP more strongly than covert attention (Walter et al., 2012), the 19-Hz SSVEP was excluded from further analysis. Based on findings from the isocontour voltage maps, we selected clusters of three electrodes for the analysis of each frequency of interest, namely 11 Hz: P4, P6, PO8; 13 Hz: P5, P7, PO7; 15 Hz: O2, PO4, PO8; and 17 Hz: O1, PO3, PO7 (see Figure 2). For further statistical analysis, we averaged across these electrodes, respectively. We additionally averaged the conditions Up and Down to Across and Left and Right to Within. These averages were statistically tested using repeated-measures ANOVAs with the factors

of Attention (Attended/Unattended) and Hemisphere Competition (Across/Within). Follow-up planned comparisons were realized using paired *t* tests.

To further estimate attentional modulation of SSVEP amplitudes, we calculated an AMI. The AMI was calculated according to

$$\text{AMI} = (\text{Attended} - \text{Unattended}) / (\text{Attended} + \text{Unattended}) \quad (1)$$

and, similar to a normalization procedure, gives a relative measure for the impact of attention on amplitudes. AMIs were tested by means of paired *t* tests between conditions and *t* tests against zero to test for significant attentional SSVEP amplitude modulation.

As mentioned above, the Fixation task served as a reference comparable to an amplitude baseline for competitive interactions when attention is withdrawn from all four LEDs. For a direct comparison between this reference value and attend and ignore conditions, we calculated the same averages as mentioned above, that is, Across and Within and tested the derived data using paired *t* tests.

Behavioral data. Button presses to luminance changes within the period 200–800 msec after event onset were considered as correct responses (hits) when occurring after a target presentation. Button presses to distractors were considered as false alarms. Incorrect responses were excluded from the analyses of RTs. In line with the SSVEP analysis conditions, Up, Down, Left, and Right were collapsed into Across and Within and compared using paired *t* tests. To make sure there was no difference between task performance in the left compared with the right hemifield, conditions Within Left and Within Right were additionally compared using paired *t* tests. For comparisons of the performance during the Fixation task with behavioral performance in Across and Within conditions, we calculated paired *t* tests.

Results

Behavioral Data

Behavioral data are summarized in Table 1. There was no difference in task performance in the left compared with the right hemifield (RTs Within Left vs. Within Right:

Table 1. RTs and Accuracy Measure *d'* for Experiments I and II for Both 2-LEDs and 1-LED Tasks during Across and Within Conditions

Experiment	Task	Condition	Mean <i>d'</i>	<i>p</i>	Mean RT (msec)	<i>p</i>
I	2-LEDs	Left	3.94 (0.23)	<i>p</i> = .778	476.52 (8.68)	<i>p</i> = .587
		Right	3.87 (0.28)		480.50 (9.78)	
I	2 LEDs	Across	4.28 (0.12)	<i>p</i> = .044	468.86 (8.01)	<i>p</i> = .015
		Within	3.91 (0.22)		478.51 (8.52)	
I	2-LEDs	Fixation	4.22 (0.22)	<i>p</i> = .746	502.48 (10.35)	<i>p</i> = .001
		Across	4.28 (0.14)		468.86 (8.01)	
I	2-LEDs	Fixation	4.22 (0.22)	<i>p</i> = .285	502.48 (10.35)	<i>p</i> = .008
		Within	3.9 (0.22)		478.51 (8.52)	
II	2-LEDs	Left	4.06 (0.26)	<i>p</i> = .217	509.77 (10.87)	<i>p</i> = .986
		Right	3.78 (0.27)		509.87 (9.51)	
I	1-LED	Left	3.91 (0.31)	<i>p</i> = .479	503.77 (10.71)	<i>p</i> = .660
		Right	4.13 (0.24)		506.18 (10.28)	
II	2-LEDs	Across	4.12 (0.20)	<i>p</i> = .315	495.07 (9.94)	<i>p</i> = .046
		Within	3.92 (0.24)		509.82 (9.76)	
II	2-LEDs	Fixation	4.78 (0.73)	<i>p</i> = .027	512.31 (11.22)	<i>p</i> = .032
		Across	4.12 (0.20)		495.07 (9.94)	
II	2-LEDs	Fixation	4.78 (0.73)	<i>p</i> = .005	512.31 (11.22)	<i>p</i> = .799
		Within	3.92 (0.24)		509.82 (9.76)	
II	1-LED	Fixation	4.70 (0.66)	<i>p</i> < .001	508.98 (11.51)	<i>p</i> = .473
		Periphery	3.76 (0.82)		513.46 (9.36)	
II	2-LEDs	All cond.	4.02 (0.20)	<i>p</i> = .02	502.44 (9.22)	<i>p</i> = .002
	1-LED	All cond.	3.76 (0.18)		513.46 (9.36)	

SEM are in parentheses.

Data from Fixation tasks (Fixation) are contrasted with the mean over Across and Within conditions at peripheral LEDs (Periphery). For comparison of 1-LED and 2-LEDs tasks, the mean over conditions Up, Down, Left, Right, and Middle (All cond.) is taken and compared using paired *t* tests.

$t(17) = -0.554, p = .587$; d' Within Left vs. Within Right: $t(17) = 0.287, p = .778$). Participants were faster and more precise when responding to luminance changes across hemifields (RTs Across vs. Within: $t(17) = -2.69, p = .015$; d' Across vs. Within: $t(17) = 2.173, p = .044$). When performing the task at the central LEDs, participants were significantly slower compared with both peripheral conditions (Fixation vs. Across: $t(17) = 3.985, p = .001$; Fixation vs. Within $t(17) = 3.000, p = .008$). No significant differences were found for d' (Fixation vs. Across: $t(17) = -.329, p = .746$; Fixation vs. Within $t(17) = 1.104, p = .285$).

SSVEP Amplitudes

Figure 2 depicts isocontour voltage maps for the respective attention conditions of Experiment I at peripheral LEDs in the left and right visual hemifield. Electrode clusters are indicated by black dots at posterior electrode sites.

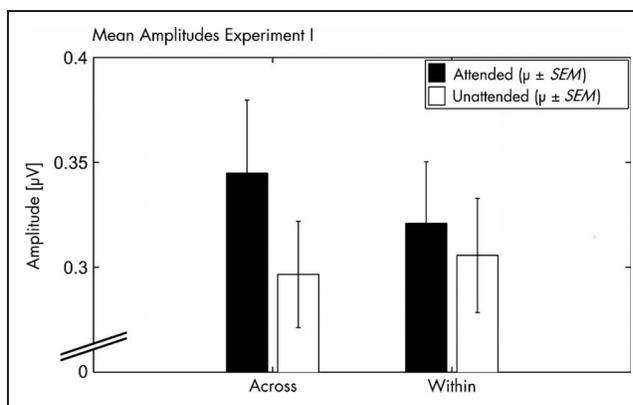


Figure 3. Mean amplitudes (μV) for conditions Across (left bars) and Within (right bars) when stimuli are attended (black) and unattended (white) in Experiment I. Amplitudes were significantly modulated by attention only during Across conditions. Error bars depict SEM.

Table 2. SSVEP Mean Amplitudes (in μV) with SEM

Experiment	Task	Condition	Mean Amplitudes (μV)	p
I	2-LEDs	Across +	0.34 (0.034)	$p = .010$
		Across -	0.29 (0.025)	
I	2-LEDs	Within +	0.32 (0.029)	$p = .247$
		Within -	0.30 (0.027)	
I	2-LEDs	Fixation -	0.29 (0.023)	$p = .813$
		Across -	0.29 (0.025)	
I	2-LEDs	Fixation -	0.29 (0.023)	$p = .287$
		Within -	0.30 (0.027)	
II	2-LEDs	Across +	0.25 (0.022)	$p = .026$
		Across -	0.22 (0.024)	
II	2-LEDs	Within +	0.23 (0.020)	$p = .142$
		Within -	0.25 (0.025)	
II	2-LEDs	Across +	0.25 (0.022)	$p = .231$
		1-LED Across +	0.26 (0.010)	
II	2-LEDs	Within +	0.23 (0.020)	$p = .020$
		1-LED Within +	0.26 (0.010)	
II	2-LEDs	Fixation -	0.21 (0.025)	$p = .150$
		Across -	0.22 (0.024)	
II	2-LEDs	Fixation -	0.21 (0.025)	$p < .001$
		Within -	0.25 (0.025)	
II	1-LED	Fixation -	0.23 (0.028)	$p = .431$
		Across -	0.22 (0.020)	
II	1-LED	Fixation -	0.23 (0.028)	$p = .591$
		Within -	0.22 (0.026)	

SEM are in parentheses.

Plus and minus signs in the Condition row indicate amplitude responses to attended (+) and unattended (-) peripheral stimuli. Amplitudes evoked at irrelevant locations during the Fixation task serve as a reference condition to investigate between-stimulus suppressive effects when attention is completely withdrawn from the peripheral LEDs. Data were subjected to paired t tests.

Table 3. AMIs with SEM Derived from SSVEP Mean Amplitudes of Experiments I and II

Experiment	Task	Condition	AMI	<i>p</i>
I	2-LEDs	Across	0.07 (0.017)	<i>p</i> = .039
	2-LEDs	Within	0.03 (0.020)	
II	2-LEDs	Across	0.04 (0.020)	<i>p</i> = .036
	2-LEDs	Within	−0.02 (0.025)	
II	2-LEDs	Across	0.048 (0.020)	<i>p</i> = .125
	1-LED	Across	0.096 (0.027)	
II	2-LEDs	Within	−0.029 (0.025)	<i>p</i> = .006
	1-LED	Within	0.095 (0.023)	

SEM are in parentheses.

As described in Data Analysis (Experiment II), 1-LED SSVEP responses to single stimuli were averaged according to conditions Up, Down, Left, and Right. Hereafter, conditions from 2-LEDs and 1-LED tasks were collapsed identically for the generation of AMIs. Data were subjected to paired *t* tests.

Mean and SEM of SSVEP amplitudes are summarized in Table 2 and depicted in Figure 3; AMIs are listed in Table 3. Analysis of SSVEP amplitudes revealed a main effect of Attention, $F(1, 17) = 5.584$, $p = .03$, and an interaction between Attention and Hemisphere Competition, $F(1, 17) = 6.8$, $p = .018$, but no effect of Hemisphere Competition, $F(1, 17) = 1.012$, $p = .329$. Planned comparisons confirmed a significant amplitude modulation in the Across condition (Attended vs. Unattended: $t(17) = 2.895$, $p = .010$), which is absent during the Within condition (Attended vs. Unattended: $t(17) = 1.198$, $p = .247$). With respect to the AMI, significant differences between the two conditions Across and Within were found (Across vs. Within: $t(17) = 2.238$, $p < .039$; see also Figure 6). Further testing of AMIs against zero revealed a significant amplitude modulation for the Across, $t(17) = 3.999$, $p = .001$, but not for the Within condition, $t(17) = 1.461$, $p = .162$.

Comparing SSVEP amplitudes of the reference condition (i.e., attend Fixation) with the responses when participants had to ignore the LED pairs during Across and Within conditions revealed no significant differences (Attended Fixation vs. Unattended Across: $t(17) = -.24$, $p = .81$; Attended Fixation vs. Unattended Within: $t(17) = -1.09$, $p = .28$).²

Discussion

Attention significantly modulated SSVEP amplitudes when attended stimuli were distributed across but not within visual hemifields. Behavioral data matched EEG data with faster RTs and higher sensitivity in Across conditions. No advantage for left visual field performance (i.e., right hemisphere dominance) was detected. Thus, our behavioral findings are in line with previous reports of facilitation whenever a task is performed across both hemifields (Kraft et al., 2005, 2007, 2011, 2013; Alvarez & Cavanagh, 2005, 2012; Chakravarthi & Cavanagh, 2009;

Sereno & Kosslyn, 1991) and thus conform to the different-hemifield account (Sereno & Kosslyn, 1991) and to the idea of competitive content maps (Franconeri et al., 2013). As hypothesized, comparisons of SSVEP amplitudes to the reference measure of suppressive interactions, that is, when participants attended to the central LEDs, exhibited no significant differences for both conditions.

To our surprise, we found no significant SSVEP amplitude modulation with attention during Within trials. There are two explanations for that result. First, LEDs were very bright and might have produced a ceiling or saturation effect with respect to SSVEP amplitudes. However, such an effect seems unlikely, given the attentional modulation of SSVEP amplitudes in the Across condition. Second, the separation of LEDs was smaller in the vertical compared with the horizontal arrangement because of the rectangular shape of the LEDs. Although the distance between the borders of adjacent LEDs was about 5° of visual angle in the horizontal arrangement, it was only about 4.2° for the vertical arrangement. Given that attentional foci are linked to a suppressive surround (Tomblu & Tsotsos, 2008; Boehler, Tsotsos, Schoenfeld, Heinze, & Hopf, 2009; Schwartz et al., 2005; Cutzu & Tsotsos, 2003; Plainis, Murray, & Chauhan, 2001; Bahcall & Kowler, 1999; Tsotsos, Culhane, Wai, Davis, & Nuflo, 1995) that operates at the level of the receptive field (Kastner & Pinsk, 2004), it might be the case that the suppressive surround has overridden the attentional modulation. According to the model by Franconeri and colleagues (2013), a horizontal arrangement benefits from a stronger blocking of the suppressive surround in spatial selection maps along the hemifield boundary compared with a vertical arrangement. In the present and in previous studies in which SSVEPs to various different stimuli were source localized, attentional modulation was reported in early visual cortex including V4 and human MT complex (Quigley et al., 2012; Fuchs et al., 2008; Di Russo et al., 2007). Cells in these areas have receptive field sizes of around 5° of visual angle (Kastner & Ungerleider, 2001), which would include both stimuli in the receptive fields of retinotopically activated cells, at least in the vertical arrangement. Thus, it might be the case that the weaker blockage of surround suppression in the vertical arrangement (perhaps in addition to the brightness of LEDs) was responsible for the “null-finding” in the Within condition. To control for these possible confounds, we conducted Experiment II, in which we flickered LEDs with a lower luminance and increased their spatial separation.

EXPERIMENT II

As outlined above, we made two changes regarding the physical properties of the stimulation device. First, we expanded the eccentricity by about 1.6° of visual angle, and second, we reduced the luminance (see Methods). As mentioned above, we introduced a further experimental condition, that is, participants were cued to attend to one

LED only to estimate an upper bound of amplitude magnitude, as stated by the biased competition account.

Methods

For the sake of brevity, only those methods that differ from Experiment I will be detailed in the following.

Participants

We collected data from 24 participants, three of whom had to be excluded from analysis because of excessive eye movements, leaving 21 participants (15 women; mean age = 25.5 years, $SD = 6.6$ years, range = 20–45 years; three left-handed).

Stimulus Material

We increased eccentricities of the peripheral LEDs by 1.58° to 6.08° of visual angle. Luminance was adjusted to 70 cd/m^2 for the ongoing flicker, 30 cd/m^2 during luminance decrements, and 160 cd/m^2 during luminance increments. The relative changes in perceived luminance between increments and decrements were similar to

those in the first experiment and again optimized during a piloting phase with nine participants.

Experimental Paradigm

In addition to the experimental conditions in Experiment I, participants were instructed to covertly attend to one LED only. That resulted in six additional experimental conditions, that is, attending to the upper or lower LED in either the left or right hemifield during peripheral tasks (Figure 1A) or attending to the upper or lower LED at central fixation. Again the latter conditions served as a reference baseline to get a measure of competitive interactions between the LEDs at the periphery when attention was totally withdrawn from any peripheral LED. 2-LEDs and 1-LED tasks were pseudorandomized equiprobably across blocks and predetermined by the experimenter at the beginning of each block. As in the first experiment, participants were cued in a trial-by-trial fashion to covertly attend randomly chosen LED pairs or single LEDs, respectively.

Procedure

During the experiment, again 12 blocks were run. In order not to extend the duration of the entire experiment

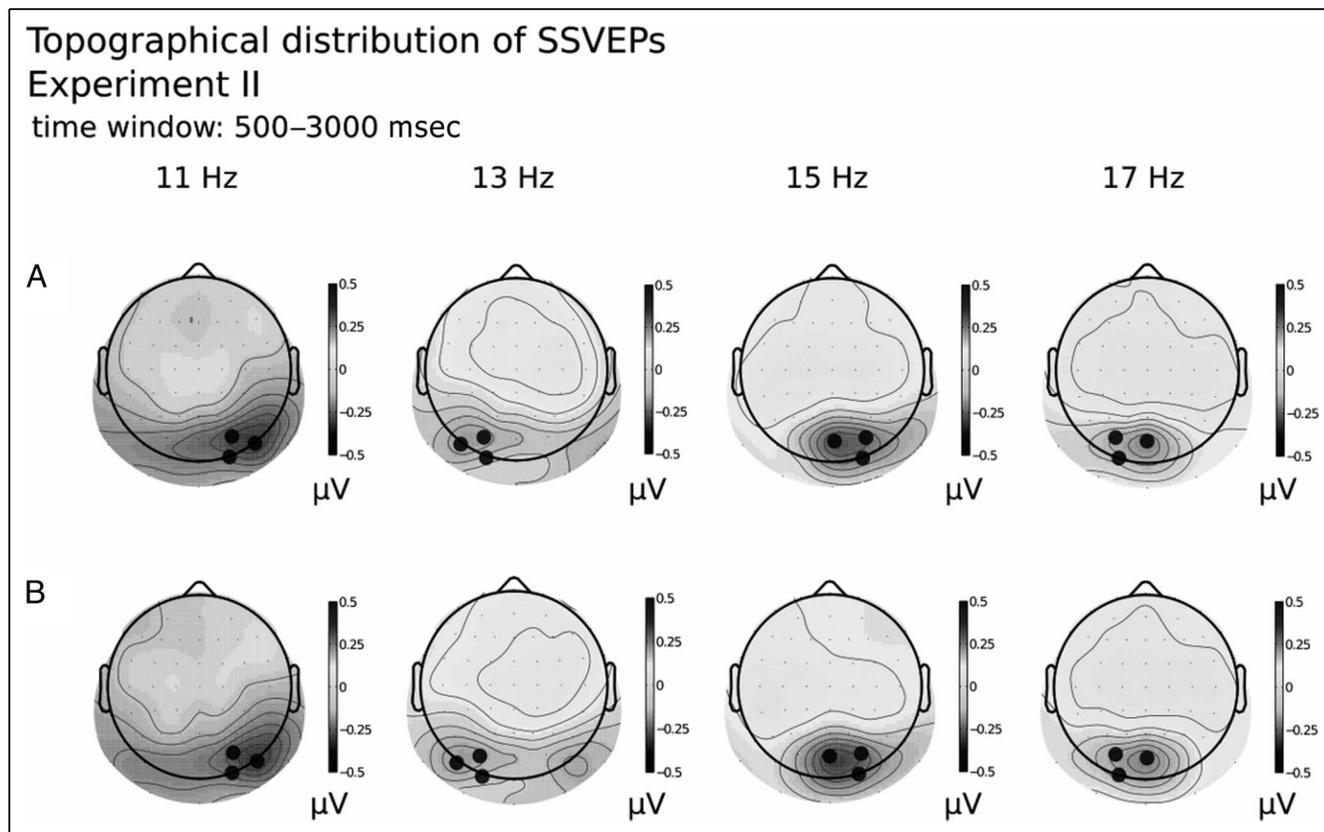


Figure 4. Isocontour voltage maps of the grand average for (A) the 2-LEDs task during the second experiment and (B) the 1-LED task during the second experiment. Voltage maps are derived from data in the time window of 500–3000 msec after stimulus onset. Columns from left to right depict topographies for 11, 13, 15, and 17 Hz SSVEP amplitudes, respectively. Black dots at posterior electrode sites highlight the electrode clusters chosen for statistical analysis based on the amplitude maxima as revealed by the maps.

because of six additional experimental conditions, we decided to keep the total number of blocks identical to Experiment I. As a consequence, in comparison with the first experiment, in Experiment II only 50% of trials per condition when participants attended two LEDs were available for analysis. Given the different number of experimental conditions (2-LEDs: five conditions; 1-LED: six conditions), the amount of trials per block was slightly different for the two tasks (2-LEDs blocks contained 40 trials each, 1-LED blocks 42 trials). As in Experiment I, before the experiment, participants performed training with at least three training blocks (2×2 -LEDs and 1×1 -LED). Training blocks consisted of 40 trials for the 2-LEDs task and 42 trials for the 1-LED task, and each trial contained either a target or distractor for more effective task learning.

Data Analysis

EEG Data. Given the reduction in the absolute number of trials per experimental condition compared with Experiment I, we corrected for eye blinks using independent component analysis (Bell & Sejnowski, 1995) to keep as many trials as possible in the final analysis. Independent components detected by the source separation algorithm were inspected visually, and components associated with eye blinks were removed. Data sets were then processed further as in Experiment I. Overall rejection rates were 9.5% for the 2-LEDs condition and 5.1% for the 1-LED condition. The number of trials per condition (Up, Down, Left, Right, Middle) did not differ in either the 2-LEDs task, $F(4, 20) = 1.247, p = .29$, or 1-LED task, $F(4, 20) = 0.865, p = .48$.

Figure 4 depicts grand average voltage maps for conditions Across and Within during 1-LED and 2-LEDs tasks. Grand average topographies were similar to those of Experiment I (Figure 2), but in comparison, maximum SSVEP amplitudes for peripheral responses were shifted slightly, presumably because of adjustments to stimulus eccentricity. As in Experiment I, based on the topographical distribution we selected three electrodes (11 Hz: PO8, PO4, O2; 13 Hz: PO7, PO3, O1; 15 Hz: PO8, O2, POz; and 17 Hz: PO7, O1, POz; see Figure 4), and the average across the respective three electrodes entered statistical analysis.

As in Experiment I, we collapsed SSVEPs of conditions Up, Down, Left, and Right from the 2-LEDs tasks into Across and Within conditions. For analysis of 1-LED task, we treated the data in the same way by assigning single LEDs to positions in the four quadrants. We could then average SSVEP responses to single stimuli into conditions Up, Down, Left, and Right and subsequently collapsed into conditions Across and Within to allow for comparison with 2-LEDs tasks.

2-LEDs and 1-LED tasks were compared using repeated-measures ANOVAs with factors of Task (2-LEDs/1-LED), Attention (Attended/Unattended), and Hemisphere Competition (Across/Within). Planned comparisons were realized using paired t tests.

The amplitude modulation indices for tasks comprising 2-LEDs (Across and Within) were calculated as described for Experiment I with Equation 1. AMIs Across and Within for 1-LED tasks were calculated with averaged SSVEP amplitudes, as described above, collapsed in the same way as AMIs for 2-LEDs tasks and also calculated with Equation 1. AMIs derived from 2-LEDs and 1-LED tasks were tested using repeated-measures ANOVAs with factors of Task (1-LED/2-LEDs) and Hemisphere Competition (Across/Within) and paired t tests.

As in Experiment I, data from Fixation tasks served as a reference measure for interstimulus competition. As for Experiment I, we contrasted SSVEP amplitudes from conditions Across and Within with conditions when participants attended to both centrally located LEDs (2-LEDs tasks) or to one of the centrally located LEDs (1-LED tasks). These values were subjected to paired t tests.

Finally, we directly compared SSVEP amplitudes between Experiments I and II with a mixed-model ANOVA with within-subject factors of Attention (Attended/Unattended) and Hemisphere Competition (Across/Within) and between-subject factor Experiment (Experiment I/Experiment II) for the 2-LEDs tasks. Furthermore, we tested AMIs between Experiments I and II by means of unpaired t tests.

Behavioral data. Behavioral data derived from the 2-LEDs tasks were analyzed following the procedures of Experiment I and were tested statistically using paired t tests. In

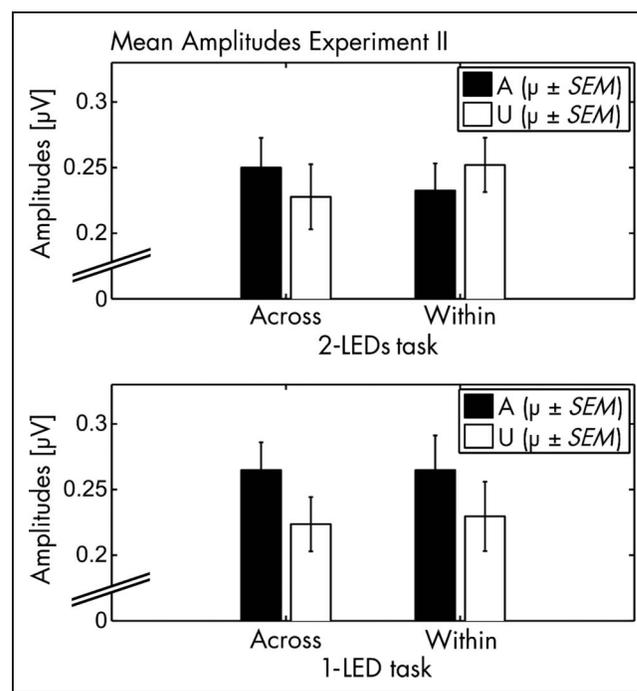
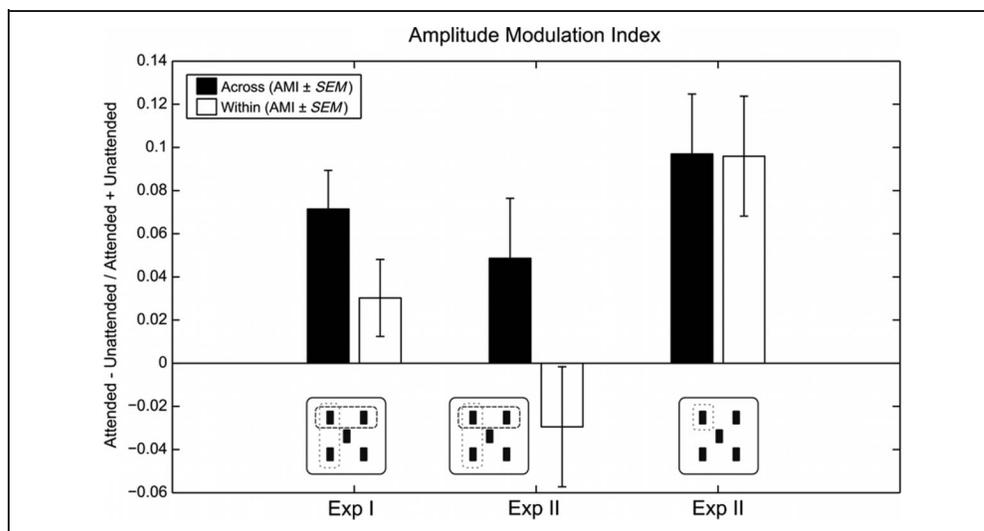


Figure 5. Mean SSVEP amplitudes for conditions Across (left bars) and Within (right bars) during 2-LEDs tasks (top) and 1-LED tasks (bottom) when respective stimuli were attended (black bars) versus unattended (white bars) in Experiment II. Error bars indicate SEM.

Figure 6. Grand mean AMIs for Experiment I (left) and the 2-LEDs (middle) and 1-LED tasks (right) of Experiment II. Participants attended LEDs distributed across hemifields (Across conditions: dashed black line, black bars) or within hemifields (Within conditions: dotted gray line, white bars). See Methods for information of how these values were obtained. Error bars indicate *SEM*.



line with the SSVEP analysis, we averaged responses to single stimuli during the 1-LED task into conditions Up, Down, Left, and Right and subsequently calculated averages for Across and Within to allow for comparison with 2-LEDs tasks. These averages were tested statistically using paired *t* tests. Also for 1-LED conditions, we investigated possible differences between task performance in the left compared with the right hemifield by comparing conditions Within Left and Within Right using paired *t* tests.

Results

Behavioral Data

Mean and *SEM* of all behavioral measures are listed in Table 1. A difference in task performance for stimuli in the left compared with the right hemifield was not found in either the 2-LEDs task (RTs Within Left vs. Within Right: $t(20) = -0.018, p = .986$; d' Within Left vs. Within Right: $t(20) = 1.274, p = .217$) or for the 1-LED task (RTs Within Left vs. Within Right: $t(20) = -0.446, p = .660$; d' Within Left vs. Within Right: $t(20) = -0.721, p = .479$). For the 2-LEDs task, RTs between Across and Within conditions again differed significantly (2-LEDs Across vs. Within: $t(20) = -2.129, p = .046$). The comparison with the Fixation task revealed that participants were only significantly slower in the Fixation task compared with Across, $t(20) = 2.308, p = .032$, but not compared with Within, $t(20) = 0.258, p = .79$. With regard to d' there was no significant difference between Across vs. Within, $t(20) = 1.03, p = .315$. However, accuracy was significantly greater in the Fixation task compared with both tasks in the periphery (Fixation vs. Across: $t(20) = 2.387, p = .027$; Fixation vs. Within $t(20) = 3.190, p = .005$).

Mean RTs in the 2-LEDs versus 1-LED tasks showed that participants were faster when responding to luminance changes in the 2-LEDs task (2-LEDs vs. 1-LED: $t(20) = 3.51,$

$p = .002$) and more precise (d' 2-LEDs vs. 1-LED: $t(20) = 2.51, p = .02$).

SSVEP Amplitudes

Mean and *SEM* of all SSVEP amplitudes are listed in Table 2; AMIs are listed in Table 3. Figure 5 depicts SSVEP amplitudes of Experiment II, and Figure 6 shows AMIs from Experiments I and II.

As in the first experiment, SSVEP analysis revealed a significant amplitude modulation during 2-LEDs Across but not Within conditions (Attended Across vs. Unattended Across: $t(20) = 2.412, p = .026$; Attended Within vs. Unattended Within: $t(20) = -1.529, p = .142$) further quantified by analysis of AMIs (AMI Across vs. Within: $t(20) = 2.251, p = .036$; *t* tests against zero, Across: $t(20) = 2.367, p = .028$, Within: $t(20) = -1.173, p = .225$).

Comparison of mean amplitudes during the 1-LED task with the 2-LEDs task resulted in a main effect for the factor Attention, $F(1, 20) = 6.23, p = .021$, as well as a significant interaction of factors Task \times Attention, $F(1, 20) = 8.55, p = .008$, and Attention \times Hemisphere Competition, $F(1, 20) = 7.308, p = .014$. Although the first interaction was driven by the greater attentional modulations for 1-LED compared with 2-LEDs tasks, the latter was the consequence of larger attentional modulation for Across conditions when averaged across 1-LED and 2-LEDs trials (see Figure 5). The factor Hemisphere Competition, $F(1, 20) = 0.68, p = .419$, and the interaction of all three factors were not significant (Task \times Attention \times Hemisphere Competition, $F(1, 20) = 3.16, p = .091$). There was no difference between SSVEP amplitudes evoked during the attend 1-LED task Across and the attend 2-LEDs task Across, $t(20) = 1.235, p = .231$, but a significant difference was found between attend 1-LED task Within and attend 2-LEDs task Within, $t(20) = 2.524, p = .020$.

In the next step, we compared the AMIs for 1-LED versus 2-LEDs tasks. Analysis revealed a main effect for Task, $F(1,$

20) = 9.478, $p = .006$. When we compared the 1-LED with the 2-LEDs task for Across conditions, we found no significant difference, $t(20) = 1.602$, $p = .125$. In contrast the comparison for Within trials was significant, $t(20) = 3.096$, $p = .006$. The main effect Hemisphere Competition became significant, $F(1, 20) = 5.511$, $p = .029$, with no significant difference between Across versus Within for the 1-LED task, $t(20) = 0.055$, $p = .956$, but for the 2-LEDs task, $t(20) = 2.251$, $p = .036$. The interaction Task \times Hemisphere Competition was not significant, $F(1, 20) = 3.103$, $p = .093$. As depicted in Figure 5 and similar to Experiment I, we found only the AMI Across to be significantly greater than zero (Across: $t(20) = 2.367$, $p = .028$; Within: $t(20) = -1.173$, $p = .255$) in the 2-LEDs tasks. As expected for the respective 1-LED task, AMIs were greater than zero for both Across and Within conditions (Across: $t(20) = 3.487$, $p = .002$; Within: $t(20) = 4.057$, $p = .001$).

The comparison of SSVEP amplitudes when participants attended to both centrally located LEDs (reference measure) with the SSVEP amplitudes in to-be-ignored conditions during Across or Within revealed no significant differences for the Across conditions (Attend Fixation vs. Unattended Across: $t(20) = -1.499$, $p = .15$). In contrast, a significant difference for the Within conditions was evident (Attend Fixation vs. Unattended Within: $t(20) = -4.391$, $p < .001$) with larger SSVEP amplitudes when participants had to ignore opposite hemifield LEDs during Within trials. No such differences were found in the 1-LED task (Attend Fixation vs. Unattended Across: $t(20) = 0.8$, $p = .431$; Attend Fixation vs. Unattended Within: $t(20) = 0.546$, $p = .591$).

In a last step, we directly compared SSVEP amplitudes between Experiments I and II, for tasks with 2-LEDs. We found a main effect for Attention, $F(1, 37) = 4.778$, $p = .035$, and an interaction of Attention \times Hemisphere Competition, $F(1, 37) = 13.38$, $p = .001$, as a result of greater attentional SSVEP amplitude modulation in the Across condition compared with Within. In fact, across both experiments, there was a negligible attentional modulation of SSVEP amplitudes during Within conditions. The between-subject factor Experiment was significant, $F(1, 37) = 4.567$, $p = .039$, with smaller SSVEP amplitudes in Experiment II compared with Experiment I. The interaction of Attention \times Experiment just slightly failed to reach the significance level, $F(1, 37) = 4.039$, $p = .052$; given greater SSVEP amplitudes in Experiment II for the condition in which participants had to ignore the vertically located LEDs (Within) compared with when they had to attend them, the overall attention effect is very small (see Figures 5 and 6) compared with Experiment I (see Figures 3 and 6). No further factors were significant, namely main effects of Hemisphere Competition, $F(1, 37) = 0.18$, $p = .674$, and interactions Hemisphere Competition \times Experiment, $F(1, 37) = 1.315$, $p = .259$, and Attention \times Hemisphere Competition \times Experiment, $F(1, 37) = 0.188$, $p = .667$. A direct comparison of the AMIs revealed no significant differences

between the two experiments (Across: $t(40) = 0.885$, $p = .345$; Within: $t(40) = 1.943$, $p = .086$).

Discussion

In Experiment II, we replicated the main findings of Experiment I, including the null finding for attentional amplitude modulation in within-hemifield conditions. Overall, we found smaller SSVEP amplitudes in Experiment II, as we had intended by changing luminance and increasing eccentricity. However, these changes did not produce a different pattern of results, clearly indicating that our findings from Experiment I cannot be explained by a saturation of response because of the brightness of LEDs. In addition, the increased eccentricity in Experiment II further rules out that the null effect for Within conditions in Experiment I was because of a suppressive surround. A direct AMI comparison also found no significant differences between Experiments I and II.

In Experiment II we introduced the experimental conditions in which participants were cued to attend to one LED only. On the basis of the biased competition account (Desimone & Duncan, 1995), attending to one LED can serve as a reference point for the upper bound of amplitude changes when multiple stimuli are simultaneously presented in the visual field and enter competition for attentional resources. A direct comparison of SSVEP amplitudes between the attend 1-LED and attend 2-LEDs tasks showed that, for Within conditions, SSVEP amplitudes were significantly smaller in the 2-LEDs compared with the 1-LED task. That was not the case for Across conditions. Again, these results support the idea of greater intrahemispheric competition in Within conditions. Testing of AMIs further supported that idea. We found significantly reduced AMIs in the 2-LEDs Within compared with the 1-LED situation, but that was not the case for the Across comparison. With respect to our second reference measure of competitive interactions between stimuli provided by Fixation conditions, in Experiment II we replicated the findings from the first study with respect to the Across condition, indicating no difference between peripheral and central conditions. That was not so for Within conditions; given larger SSVEP amplitudes when participants had to ignore two vertically located LEDs compared with when they had to attend them, here SSVEP amplitudes were significantly larger compared with when participants performed the task at fixation. Besides that unexpected difference, overall we can conclude that Experiment II replicated all major findings from Experiment I.

GENERAL DISCUSSION

In two experiments, we investigated competition for attentional processing resources when two stimuli were

either attended in one or in the left and right visual hemifield. A common finding in previous studies using across/within hemifield paradigms is better performance for across-hemifield tasks in spatial attention paradigms (Kraft et al., 2005, 2007, 2011, 2013; Alvarez & Cavanagh, 2005, 2012; Chakravarthi & Cavanagh, 2009). That effect has been attributed to the different-hemifield advantage (Serenó & Kosslyn, 1991), with the idea that each cortical hemisphere acts with an independent pool of attentional resources. As a consequence, intrahemispheric competition for processing resources is much greater and contributes to costs in behavioral performance when stimuli are located within one visual hemifield. A more recent approach suggested competitive content maps that take spatial properties of external stimuli and their proximity in cortical space into account (Franconeri et al., 2013). Spatial proximity and stimulus crowding influence behavioral performance, because overlapping suppressive surrounds of nearby stimuli have an impact on stimulus representation. Importantly, the vertical meridian eliminates competition; this results in better performance in tasks with stimuli that are distributed across the left and right visual hemifields.

Our behavioral results replicated previous reports of the different-hemifield advantage (Serenó & Kosslyn, 1991) and are largely in line with the predictions of the competitive content map idea (Franconeri et al., 2013). In both experiments, we found faster RTs when participants attended two horizontally aligned LEDs compared with when they were cued to two vertically aligned LEDs. Accuracy was greater in Across trials, although a direct comparison failed to be significant in Experiment II possibly because of the increased eccentricity, which also resulted in overall slower RTs (Yeshurun & Carrasco, 1999). However, that increase of eccentricity with the consequence of no significant differences in accuracy between Across and Within would nicely fit with the competitive content map idea, because greater spatial separation of the vertical LEDs resulted in better stimulus representation. Moreover, to make sure that the lack of an advantage in Within conditions were not driven by a right hemisphere dominance for visuospatial attention tasks (cf. Corbetta & Shulman, 2011), we additionally tested for this possibility in behavioral data. However, a left visual field advantage was not found in either experiment.

Electrophysiological data were in accordance with the predictions of the two accounts. In both experiments, we found significantly increased SSVEP amplitude modulation when stimuli were attended versus unattended during Across but not during Within conditions (also confirmed by the direct comparison of the two experiments). That was additionally supported by the attentional effect upon SSVEP amplitudes as indicated by the AMI. In both experiments, these indices were significantly larger than zero in the Across but not in the Within conditions. Consequently, a direct comparison of AMIs between these conditions confirmed significantly larger attentional mod-

ulation of SSVEP amplitudes for Across compared with Within. Interestingly, the increased spatial separation of vertical LEDs in Experiment II did not result in an enhancement of modulation for within conditions, although, as argued above, increasing separation should have resulted in a better stimulus representation on the respective hemispheric content map. As hypothesized, comparisons of SSVEP amplitudes to the reference measure for suppressive interactions (i.e., when participants attended to the central LEDs) exhibited no significant differences compared with the amplitude of to-be-ignored LEDs in the periphery. Furthermore, comparison with the reference measure of an upper bound of SSVEP amplitude (i.e., when participants attended to one LED) were also supportive of the idea of separate attentional processing resources in cortical hemispheres or different competitive interactions within content maps with no significant differences found in the 1-LED compared with 2-LEDs Across trials. Attention effects in SSVEP amplitudes quantified by the AMI also supported this view.

Our electrophysiological results are in line with a recent fMRI study (Kraft et al., 2011), which analyzed BOLD responses in predefined ROIs in human visual cortex (V1–V4v). Participants split their attention to two locations separated by an intermediate distractor position and performed a discrimination task at two nonadjacent positions that were either distributed within one hemifield or across both hemifields. The authors reported higher integration of interposed distractor positions within compared with across visual hemifields, indexed by changes in BOLD response. In other words, distractors' competition for representation was weaker across than within the hemifields. In a near infrared spectroscopy study on motion object tracking, Harasawa and Shioiri (2011) observed increased activity in visual and posterior parietal cortex when participants attended to two compared with one stimulus within one hemifield. That was not the case when they tracked two objects in the left and right visual hemifield compared with one object alone. This finding matches our comparison of Across trials in 1-LED and 2-LEDs tasks, in which we did not find a significant difference in Attended amplitude or AMI. When we look at studies that investigated spatial shifting, some studies found faster shifting times from one location to another within compared with across hemifield shifts (Kraft et al., 2011; Ibos, Duhamel, & Ben Hamed, 2009). This faster shifting time was explained by the idea of larger stimulus integration in within hemifield spatial arrangements (Large, Culham, Kuchinad, Aldcroft, & Vilis, 2008; Murray, Foxe, Higgins, Javitt, & Schroeder, 2001). However, some other results exist that make the picture less conclusive (see e.g., Chakravarthi & VanRullen, 2011).

A closer look at our results, in particular with respect to the reference measures, shows that the picture is not so straightforward for behavioral data. Interestingly, we found significantly slower RTs to targets in the central

LEDs in three of four comparisons (Across and Within). Only the comparison between Fixation and Within in Experiment II showed no significant difference. The short presentation time of 180 msec made it impossible for participants to attend to one LED in one visual quadrant and then shift attention rapidly to the other LED to detect a match in luminance enhancement in both LEDs (Müller et al., 2003; Duncan et al., 1994; Weichselgartner & Sperling, 1987). Furthermore, this would have resulted in slower RTs in the periphery. Thus, the faster RTs for the peripheral tasks might rather be because of grouping effects resulting from synchrony (for a review, see Wagemans et al., 2012). On the other hand, taking into account the idea of competitive content maps (Franconeri et al., 2013), LEDs in the center were not spatially separated at all, resulting in a much greater (vertical) overlap of suppressive surrounds, which might have caused the slowing of responses. In opposition to that argument stands the finding of significantly greater accuracy for central targets compared with peripheral targets across or within hemifields in Experiment II. Also, given that accuracy did not differ between these conditions in Experiment I, where eccentricity was smaller, it is possible that the spatial proximity between central and peripheral LEDs has caused an overlap of suppressive surrounds and a classical flanker interference (Eriksen & Eriksen, 1974), with costs evident in accuracy and speed in Experiment I but only in speed in Experiment II.

Whether or not participants adopted a strategy to stress speed for peripheral tasks at the cost of accuracy is hard to judge. However, we believe that four reasons argue against that alternative. First, we instructed participants to react as fast and as precisely as possible, and it is very unlikely that they changed their strategy for different tasks on a trial-by-trial basis. Second, participants received general feedback about performance after each block; thus, they did not get any feedback regarding performance in central compared with peripheral tasks. Third, we found no differences in accuracy in Experiment I but again slower RTs for the central task, and fourth, no differences in RTs were found when participants attended to one LED in the periphery compared with one central LED, but again a significantly greater accuracy was found at the central LED.

Another consistent finding in the literature is the so-called central performance drop (e.g., Yeshurun & Carrasco, 1998; Kehrner, 1987, 1989), with better performance as a function of increasing eccentricity (about 3–6° of visual angle) than in the fovea for early visual perception. This effect was recently demonstrated for luminance tasks in and beyond the eccentricity range of the stimuli used here (Meinecke & Kehrner, 2007). Other studies mainly reported a central performance drop in texture segregation defined by orientation stimuli that form texture targets (Yeshurun & Carrasco, 1998, 2000). That effect has been attributed to the spatial integration hypothesis (Meinecke & Kehrner, 2007; Meinecke & Donk, 2002) with the idea of

larger spatial sampling units (based on receptive field sizes) in the periphery compared with the fovea, allowing for better integration of low-level perceptual information. The matching luminance task used in our study is well suited to allow for such a mechanism to operate during task performance.

It should be mentioned that we did not control whether the behavioral findings supporting the different-hemifield advantage are because of the horizontal alignment of stimuli. However, we can rule out that possibility based on previous studies that have failed to find a causal relationship between observed responses and stimulus alignment (Delvenne et al., 2011; Chakravarthi & Cavanagh, 2009; Alvarez & Cavanagh, 2005).

Turning back to our results regarding SSVEP amplitudes in relation to our reference measures, attending to the centrally located LEDs provided a reference measure for suppressive interactions between the LEDs in the periphery (Fuchs et al., 2008; Beck & Kastner, 2007; Kastner et al., 1998) without attentional resources being allocated across or within visual hemifields. If perceptual processes were limited by a single resource governing the entire visual field, one would expect that attending to the left or right visual hemifield results in a shift of resources away from the to-be-ignored visual hemifield and in favor of the to-be-attended one. The consequence would be a reduction in SSVEP amplitudes elicited by LEDs in the to-be-ignored visual hemifield compared with the reference measure. That was not what we found; in fact, no significant difference was found for either Across or Within conditions compared with when participants attended to the central LEDs. For the Within comparisons in both experiments, our results clearly point to the control of separate resources in both cortical hemispheres and nicely fit the findings of a previous spatial shifting experiment (Müller, Teder-Sälejärvi, et al., 1998). In that experiment, we flickered LEDs in the left and right visual hemifield, and participants were cued to shift attention to the left or right visual hemifield about 1 sec after flicker onset of stimuli in both hemifields. We found an increase in SSVEP amplitude only for the to-be-attended hemifield with no difference in amplitudes of the to-be-ignored hemifield compared with a baseline before the presentation of the spatial cue. Thus, the spatial shifting experiment also indicated that shifting attention to one hemifield will not result in withdrawal of resources from the to-be-ignored hemifield. The only unexpected finding in this study was the larger SSVEP amplitudes in Experiment II for ignore Within conditions. At present, we have no explanation for that reversed effect. A closer inspection on the individual subject level showed that the reversed attention effect is neither restricted to one hemifield nor that participants (except one) exhibit that effect equally strongly in both visual hemifields. Although the results with respect to the Within conditions are in line with predictions of the different-hemifield advantage account, the comparison of amplitudes of to-be-ignored stimuli in Across compared with Fixation is

noteworthy here as well. Again we found no significant differences. Even under the assumption of separate resources in each hemisphere, one could expect that shifting attention to the upper or lower horizontally located LEDs should occur at the cost of withdrawing resources from the to-be-ignored horizontally located LEDs, resulting in reduced amplitudes compared with the reference measure. However, this was not the case.

The experimental conditions in which participants had to attend to one LED in Experiment II were included to allow an estimation of an upper bound of SSVEP amplitudes. SSVEP amplitudes were significantly smaller when participants attended to a member of vertically distributed task-relevant LED pairs compared with when they attended that LED alone, indicating competitive intrahemispheric interactions as proposed by the different-hemifield advantage. No such competitive interactions seem to act when participants were attending to horizontally aligned stimuli, because we found no significant amplitude differences during 1-LED and 2-LEDs tasks, which is also in line with assumptions of the different-hemifield advantage.

To summarize, we found supportive experimental evidence for the different-hemifield advantage and hemisphere-specific attentional processing resources in early visual cortex. Our results largely correspond to the recently introduced idea of competitive content maps (Franconeri et al., 2013). The innovative extension compared with previous studies is the frequency-tagging of stimuli, which allows measurement of competitive interactions between stimuli during sustained visual spatial attention and the introduction of reference measures that have not been reported before. Interestingly, behavioral data resulted in a more complex pattern, in particular in comparison with the reference measures.

Acknowledgments

We thank Renate Zahn, Karolin Meiss, and Karen Krause for their valuable help during EEG recordings. We also thank Ed Vogel and a second anonymous reviewer for helpful comments. We thank Ulrich Krebs (Friedrich-Wilhelm-Bessel-Institute, Bremen, Germany), who provided technical equipment and support for the LED stimulation apparatus. This experiment was realized using Cogent Graphics, developed by John Romaya at the LON at the Wellcome Department of Imaging Neuroscience. The research leading to these results has received funding from Deutsche Forschungsgemeinschaft (DFG, Grant MU972/20-1) as well as from Forschungsvereinigung DFMRs via AiF and the German Federal Ministry of Economics and Technology (BMW, Grant sBCI, 16136BG).

Reprint requests should be sent to Matthias M. Mueller, Institute of Psychology, Leipzig University, Neumarkt 9-19, 04109 Leipzig, Germany, or via e-mail: m.mueller@rz.uni-leipzig.de.

Note

1. Again it is important to notice that earlier accounts such as the ones by Herdman and Friedman (1985) or Kinsbourne and

Hicks (1978) were dealing with much higher cognitive functions in claiming that cerebral hemispheres have functionally distinct sets of resources.

REFERENCES

- Alvarez, G. A., & Cavanagh, P. (2005). Independent resources for attentional tracking in the left and right visual hemifields. *Psychological Science, 16*, 637–643.
- Alvarez, G. A., & Cavanagh, P. (2012). Anatomical constraints on attention: Hemifield independence is a signature of multifocal spatial selection. *Journal of Vision, 12*, 1–20.
- Andersen, S. K., Müller, M. M., & Hillyard, S. A. (2011). Tracking the allocation of attention in visual scenes with steady-state evoked potentials. In M. I. Posner (Ed.), *Cognitive neuroscience of attention* (2nd ed., pp. 197–216). New York: Guilford.
- Awh, E., & Pashler, H. (2000). Evidence for split attentional foci. *Journal of Experimental Psychology: Human Perception and Performance, 26*, 834–846.
- Bahcall, D. O., & Kowler, E. (1999). Attentional interference at small spatial separations. *Vision Research, 39*, 71–86.
- Banich, M. T. (1998). The missing link: The role of interhemispheric interaction in attentional processing. *Brain and Cognition, 36*, 128–157.
- Beck, D. M., & Kastner, S. (2007). Stimulus similarity modulates competitive interactions in human visual cortex. *Journal of Vision, 7*, 1–12.
- Belger, A., & Banich, M. T. (1992). Interhemispheric interaction affected by computational complexity. *Neuropsychologia, 30*, 923–929.
- Belger, A., System, H., Haven, W., & Banich, M. T. (1998). Costs and benefits of integrating information between the cerebral hemispheres: A computational perspective. *Neuropsychology, 12*, 380–398.
- Bell, A. J., & Sejnowski, T. J. (1995). An information-maximization approach to blind separation and blind deconvolution. *Neural Computation, 7*, 1129–1159.
- Boehler, C. N., Tsotsos, J. K., Schoenfeld, M. A., Heinze, H.-J., & Hopf, J.-M. (2009). The center-surround profile of the focus of attention arises from recurrent processing in visual cortex. *Cerebral Cortex, 19*, 982–991.
- Brown, W. S., & Jeeves, M. A. (1993). Bilateral visual field processing and evoked potential interhemispheric transmission time. *Neuropsychologia, 31*, 1267–1281.
- Chakravarthi, R., & Cavanagh, P. (2009). Bilateral field advantage in visual crowding. *Vision Research, 49*, 1638–1646.
- Chakravarthi, R., & VanRullen, R. (2011). Bullet trains and steam engines: Exogenous attention zips but endogenous attention chugs along. *Journal of Vision, 11*, 1–12.
- Corbetta, M., & Shulman, G. L. (2011). Spatial neglect and attention networks. *Annual Review of Neuroscience, 34*, 569–599.
- Cutzu, F., & Tsotsos, J. K. (2003). The selective tuning model of attention: Psychophysical evidence for a suppressive annulus around an attended item. *Vision Research, 43*, 205–219.
- Delvenne, J.-F., Castronovo, J., Demeyere, N., & Humphreys, G. W. (2011). Bilateral field advantage in visual enumeration. *PloS One, 6*, e17743.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18*, 193–222.
- Di Russo, F., Pitzalis, S., Aprile, T., Spitoni, G., Patria, F., Stella, A., et al. (2007). Spatiotemporal analysis of the cortical sources of the steady-state visual evoked potential. *Human Brain Mapping, 28*, 323–334.

- Duncan, J., Ward, R., & Shapiro, K. (1994). Direct measurement of attentional dwell time in human vision. *Nature*, *369*, 313–315.
- Eriksen, B., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception & Psychophysics*, *16*, 143–149.
- Franconeri, S. L., Alvarez, G. A., & Cavanagh, P. (2013). Flexible cognitive resources: Competitive content maps for attention and memory. *Trends in Cognitive Sciences*, *17*, 134–141.
- Fuchs, S., Andersen, S. K., Gruber, T., & Müller, M. M. (2008). Attentional bias of competitive interactions in neuronal networks of early visual processing in the human brain. *Neuroimage*, *41*, 1086–1101.
- Harasawa, M., & Shioiri, S. (2011). Asymmetrical brain activity induced by voluntary spatial attention depends on the visual hemifield: A functional near-infrared spectroscopy study. *Brain and Cognition*, *75*, 292–298.
- Herdman, C. M., & Friedman, A. (1985). Multiple resources in divided attention: A cross-modal test of the independence of hemispheric resources. *Journal of Experimental Psychology: Human Perception and Performance*, *11*, 40–49.
- Ibos, G., Duhamel, J.-R., & Ben Hamed, S. (2009). The spatial and temporal deployment of voluntary attention across the visual field. *PLoS One*, *4*, e6716.
- Jungthöfer, M., Elbert, T., Tucker, D. M., & Rockstroh, B. (2000). Statistical control of artifacts in dense array EEG/MEG studies. *Psychophysiology*, *37*, 523–532.
- Kahneman, D. (1973). *Attention and effort*. Englewood Cliffs, NJ: Prentice-Hall.
- Kastner, S., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science*, *282*, 108–111.
- Kastner, S., & Pinsk, M. A. (2004). Visual attention as a multilevel selection process. *Cognitive, Affective & Behavioral Neuroscience*, *4*, 483–500.
- Kastner, S., & Ungerleider, L. G. (2001). The neural basis of biased competition in human visual cortex. *Neuropsychologia*, *39*, 1263–1276.
- Kehrer, L. (1987). Perceptual segregation and retinal position. *Spatial Vision*, *2*, 247–261.
- Kehrer, L. (1989). Central performance drop on perceptual segregation tasks. *Spatial Vision*, *4*, 45–62.
- Kinsbourne, M., & Hicks, R. E. (1978). Functional cerebral space: A model for overflow, transfer and interference effects in human performance: A tutorial review. In J. Requin (Ed.), *Attention and performance VII* (pp. 345–362). Hillsdale, NJ: Erlbaum.
- Kraft, A., Dyrholm, M., Bundesen, C., Kyllingsbæk, S., Kathmann, N., & Brandt, S. A. (2013). Visual attention capacity parameters covary with hemifield alignment. *Neuropsychologia*, *51*, 876–885.
- Kraft, A., Kehrer, S., Hagendorf, H., & Brandt, S. A. (2011). Hemifield effects of spatial attention in early human visual cortex. *The European Journal of Neuroscience*, *33*, 2349–2358.
- Kraft, A., Müller, N. G., Hagendorf, H., Schira, M. M., Dick, S., Fendrich, R. M., et al. (2005). Interactions between task difficulty and hemispheric distribution of attended locations: Implications for the splitting attention debate. *Cognitive Brain Research*, *24*, 19–32.
- Kraft, A., Pape, N., Hagendorf, H., Schmidt, S., Naito, A., & Brandt, S. A. (2007). What determines sustained visual attention? The impact of distracter positions, task difficulty and visual fields compared. *Brain Research*, *1133*, 123–135.
- Large, M.-E., Culham, J., Kuchinad, A., Aldcroft, A., & Vilis, T. (2008). fMRI reveals greater within- than between-hemifield integration in the human lateral occipital cortex. *The European Journal of Neuroscience*, *27*, 3299–3309.
- Larson, E. B., & Brown, W. S. (1997). Bilateral field interactions, hemispheric specialization and evoked potential interhemispheric transmission time. *Neuropsychologia*, *35*, 573–581.
- Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology*, *77*, 24–42.
- Luck, S. J., Hillyard, S. A., Mangun, G. R., & Gazzaniga, M. S. (1989). Independent hemispheric attentional systems mediate visual search in split-brain patients. *Nature*, *342*, 543–545.
- Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, *390*, 279–281.
- Maertens, M., & Pollmann, S. (2005). Interhemispheric resource sharing: Decreasing benefits with increasing processing efficiency. *Brain and Cognition*, *58*, 183–192.
- Malinowski, P., Fuchs, S., & Müller, M. M. (2007). Sustained division of spatial attention to multiple locations within one hemifield. *Neuroscience Letters*, *414*, 65–70.
- Marois, R., & Ivanoff, J. (2005). Capacity limits of information processing in the brain. *Trends in Cognitive Sciences*, *9*, 296–305.
- McAdams, C. J., & Maunsell, J. H. R. (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *The Journal of Neuroscience*, *19*, 431–441.
- Meinecke, C., & Donk, M. (2002). Detection performance in pop-out tasks: Nonmonotonic changes with display size and eccentricity. *Perception*, *31*, 591–602.
- Meinecke, C., & Kehrer, L. (2007). A central performance drop with luminance. *Perception & Psychophysics*, *69*, 923–929.
- Merola, J. L., & Liederman, J. (1985). Developmental changes in hemispheric independence. *Child Development*, *56*, 1184–1194.
- Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science*, *229*, 782–784.
- Morgan, S. T., Hansen, J. C., & Hillyard, S. A. (1996). Selective attention to stimulus location modulates the steady-state visual evoked potential. *Proceedings of the National Academy of Sciences, U.S.A.*, *93*, 4770–4774.
- Müller, M. M., Malinowski, P., Gruber, T., & Hillyard, S. A. (2003). Sustained division of the attentional spotlight. *Nature*, *424*, 309–312.
- Müller, M. M., Picton, T. W., Valdés-Sosa, P., Riera, J., Teder-Sälejärvi, W. A., & Hillyard, S. A. (1998). Effects of spatial selective attention on the steady-state visual evoked potential in the 20–28 Hz range. *Cognitive Brain Research*, *6*, 249–261.
- Müller, M. M., Teder-Sälejärvi, W. A., & Hillyard, S. A. (1998). The time course of cortical facilitation during cued shifts of spatial attention. *Nature Neuroscience*, *1*, 631–634.
- Murray, M. M., Foxe, J. J., Higgins, B. A., Javitt, D. C., & Schroeder, C. E. (2001). Visuospatial neural response interactions in early cortical processing during a simple reaction time task: A high-density electrical mapping study. *Neuropsychologia*, *39*, 828–844.
- Niebergall, R., Khayat, P. S., Treue, S., & Martinez-Trujillo, J. C. (2011). Expansion of MT neurons excitatory receptive fields during covert attentive tracking. *Journal of Neuroscience*, *31*, 15499–15510.
- Norman, W. D., Jeeves, M. A., Milne, A., & Ludwig, T. (1992). Hemispheric interactions: The bilateral advantage and task difficulty. *Cortex*, *28*, 623–642.

- Plainis, S., Murray, I. J., & Chauhan, K. (2001). Raised visual detection thresholds depend on the level of complexity of cognitive foveal loading. *Perception*, *30*, 1203–1212.
- Pollmann, S., Zaidel, E., & Von Cramon, D. Y. (2003). The neural basis of the bilateral distribution advantage. *Experimental Brain Research*, *153*, 322–333.
- Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*, 3–25.
- Quigley, C., Andersen, S. K., & Müller, M. M. (2012). Keeping focused: Sustained spatial selective visual attention is maintained in healthy old age. *Brain Research*, *1469*, 24–34.
- Reardon, K. M., Kelly, J. G., & Matthews, N. (2009). Bilateral attentional advantage on elementary visual tasks. *Vision Research*, *49*, 691–701.
- Regan, D. (1989). *Human brain electrophysiology: Evoked potentials and evoked magnetic fields in science and medicine*. New York: Elsevier.
- Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *The Journal of Neuroscience*, *19*, 1736–1753.
- Schwartz, S., Vuilleumier, P., Hutton, C., Maravita, A., Dolan, R. J., & Driver, J. (2005). Attentional load and sensory competition in human vision: Modulation of fMRI responses by load at fixation during task-irrelevant stimulation in the peripheral visual field. *Cerebral Cortex*, *15*, 770–786.
- Sereno, A. B., & Kosslyn, S. M. (1991). Discrimination within and between hemifields: A new constraint on theories of attention. *Neuropsychologia*, *29*, 659–675.
- Shipp, S. (2011). Interhemispheric integration in visual search. *Neuropsychologia*, *49*, 2630–2647.
- Tombu, M., & Tsotsos, J. K. (2008). Attending to orientation results in an inhibitory surround in orientation space. *Perception & Psychophysics*, *70*, 30–35.
- Tsotsos, J. K., Culhane, S. M., Wai, W. Y. K., Davis, N., & Nuflo, F. (1995). Modeling visual attention via selective tuning. *Artificial Intelligence*, *78*, 507–545.
- Wagemans, J., Elder, J. H., Kubovy, M., Palmer, S. E., Peterson, M. A., Singh, M., et al. (2012). A century of Gestalt psychology in visual perception I. Perceptual grouping and figure-ground organization. *Psychological Bulletin*, *138*, 1172–1217.
- Walter, S., Quigley, C., Andersen, S. K., & Müller, M. M. (2012). Effects of overt and covert attention on the steady-state visual evoked potential. *Neuroscience Letters*, *519*, 37–41.
- Weichselgartner, E., & Sperling, G. (1987). Dynamics of automatic and controlled visual attention. *Science*, *238*, 778–780.
- Welcome, S. E., & Chiarello, C. (2008). How dynamic is interhemispheric interaction? Effects of task switching on the across-hemisphere advantage. *Brain and Cognition*, *67*, 69–75.
- Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature*, *396*, 72–75.
- Yeshurun, Y., & Carrasco, M. (1999). Spatial attention improves performance in spatial resolution tasks. *Vision Research*, *39*, 293–306.
- Yeshurun, Y., & Carrasco, M. (2000). The locus of attentional effects in texture segmentation. *Nature Neuroscience*, *3*, 622–627.