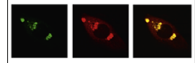


Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

ScienceDirect

[www.elsevier.com/locate/brainres](http://www.elsevier.com/locate/brainres)

Brain Research



## Research Report

# Internal and external spatial attention examined with lateralized EEG power spectra

Rob H.J. Van der Lubbe<sup>a,b,\*</sup>, Carsten Bundt<sup>a,c</sup>, Elger L. Abrahamse<sup>a,c</sup>

<sup>a</sup>Cognitive Psychology and Ergonomics, University of Twente, Enschede, The Netherlands

<sup>b</sup>Department of Cognitive Psychology, University of Finance and Management in Warsaw, Warsaw, Poland

<sup>c</sup>Department of Experimental Psychology, University of Ghent, Ghent, Belgium

## ARTICLE INFO

## Article history:

Accepted 6 August 2014

Available online 14 August 2014

## Keywords:

Visuospatial attention

Visual short term memory

PCN

Lateralized power spectra

Theta

Alpha

Simon effect

## ABSTRACT

Several authors argued that retrieval of an item from visual short term memory (internal spatial attention) and focusing attention on an externally presented item (external spatial attention) are similar. Part of the neuroimaging support for this view may be due to the employed experimental procedures. Furthermore, as internal spatial attention may have a more induced than evoked nature some effects may not have been visible in event related analyses of the electroencephalogram (EEG), which limits the possibility to demonstrate differences. In the current study, a colored frame cued which stimulus, one out of four presented in separate quadrants, required a response, which depended on the form of the cued stimulus (circle or square). Importantly, the frame occurred either before (precue), simultaneously with (simultaneous cue), or after the stimuli (postcue). The precue and simultaneous cue condition both concern external attention, while the postcue condition implies the involvement of internal spatial attention. Event-related lateralizations (ERLs), reflecting evoked effects, and lateralized power spectra (LPS), reflecting both evoked and induced effects, were determined. ERLs revealed a posterior contralateral negativity (PCN) only in the precue condition. LPS analyses on the raw EEG showed early increased contralateral theta power at posterior sites and later increased ipsilateral alpha power at occipito-temporal sites in all cue conditions. Responses were faster when the internally or externally attended location corresponded with the required response side than when not. These findings provide further support for the view that internal and external spatial attention share their underlying mechanism.

© 2014 Elsevier B.V. All rights reserved.

## 1. Introduction

In their review paper in 2011, Chun, Golomb and Turk-Browne proposed a new taxonomy regarding the operation

of attentional selection based on the source of information being selected (Chun et al., 2011). A distinction was made between external or perceptual attention, and internal or reflective attention. External attention refers to the selection

\*Corresponding author at: Cognitive Psychology and Ergonomics, Faculty of Behavioral Sciences, Universiteit Twente, Postbus 217, 7500 AE Enschede, The Netherlands.

E-mail address: [R.H.J.vanderLubbe@utwente.nl](mailto:R.H.J.vanderLubbe@utwente.nl) (R.H.J. Van der Lubbe).

and modulation of sensory induced activity, which may occur by directing attention at stimulus locations in the outer world. In contrast, internal attention refers to the selection of internally generated or maintained information, such as information that is temporarily kept in visual short-term memory.<sup>1</sup> In the last decade, many studies have addressed the question whether the underlying mechanisms of internal and external attentional selection are comparable (e.g., see Corbetta et al., 2002; Griffin and Nobre, 2003; Nobre et al., 2004; Kuo et al., 2009; Nee and Jonides, 2009; Theeuwes et al., 2011; Tamber-Rosenau et al., 2011; Tanoue et al., 2013). Several of them found support for overlapping neural mechanisms. For example, in conditions highlighting internal and external spatial attention comparable involvement of occipito-parietal and occipito-temporal areas brain areas was observed (Griffin and Nobre, 2003; Kuo et al., 2009; for a review see Gazzaley and Nobre, 2012; but see Tamber-Rosenau et al., 2011), whereas frontal brain areas seemed more relevant for internal than for external attention (Tanoue et al., 2013). In the current study, we further investigated the similarities between external and internal spatial attention by using different lateralized electroencephalographic (EEG) measures. One of the ideas explored concerns the possibility that the support for overlap may very well depend on the type of analyses, and the precise setup of the task. Namely, when employing lateralized event-related potentials (ERPs), often denoted as event-related lateralizations (ERLs, see Wascher and Wauschkuhn, 1996) internally induced neural activity, due to the averaging procedure used to compute ERPs, is likely to be canceled out (e.g., see Buszák, 2006), while stimulus-evoked activity remains. Thus, if the neural activity related to internal attention is not strongly bound to stimulus onset, then effects may not be visible in measures derived from ERPs, such as ERLs. This limitation can be overcome by using measures of lateralized activity derived from the raw EEG. Specifically, we here decided to compute lateralized power spectra (LPS; see Van der Lubbe and Utzerath, 2013), which is an extension of a method earlier proposed by Thut et al. (2006). Apart from the relevance of the precise type of analysis, some aspects of the tasks employed (detailed below) may induce unwanted similarities. Notwithstanding these concerns, the support for overlap between internal and external attention seems quite convincing.

At a more global level, the relation between attention and short-term memory has been addressed from various perspectives. For example, several studies revealed that keeping specific information in short-term memory biases attentional orienting (e.g., Downing, 2000; Klaver and Talsma, 2013; for a review see Olivers et al., 2011). Downing (2000) revealed that detection of a probe was faster when it occurred on the location of a previously presented stimulus that had to be remembered as compared to when it occurred on the location of another stimulus that did not require memorization. Other studies approached the relation from a neuropsychological

viewpoint by examining patients affected by perceptual or representational neglect. These patients appear not only to have problems with directing their attention in the left visual field but also with mental imagery concerning that field (Bisiach and Luzzatti, 1978; Loetscher and Brugger, 2007; Palermo et al., 2010), which has been linked to short-term memory (e.g., see Lückmann et al., 2014). Commonalities between attention and short-term memory have indeed been addressed in many recent studies (e.g., Awh et al., 2001, 2006; Ikkai and Curtis, 2011; Silk et al., 2010; for reviews see Cabeza et al., 2008, 2012; Gazzaley and Nobre, 2012; Lückmann et al., 2014; Kiyonaga and Egner, 2013). It is, however, quite difficult to examine short-term memory without the involvement of attention, and vice versa, which also depends on the precise definition of the various processes. Cowan related short-term memory with long-term memory and made a distinction between the activated part of long-term memory, and several items that are simultaneously kept in the focus of attention (Cowan, 1995; Cowan and Moray, 2006; Cowan, 2011). McElree (1998), however, claimed that only a single item can be in the focus of attention. The framework of Oberauer (2002, for a recent paper, see Oberauer, 2013) can be viewed as an integration of these ideas. He argued on the basis of behavioral data in a modified Sternberg task with active and passive memory sets that a distinction between three functional states is most appropriate. Selective interference with an arithmetic operation was only observed as a function of active but not as a function of passive memory set size, while at the same time a single item had to be selected for the required operation. Therefore, a trisection seems more appropriate. Several items can be simultaneously activated in long-term memory, a sub-set of them are represented in a direct-access region (DAR), and only one of them is in the focus of attention (FoA), which is the item that is used to select an (cognitive) action. So, only this specific item in the FoA is thought to be internally attended. Interestingly, the latter view corresponds with ideas on the role of attention in perception, to guide actions (“selection for action”, see also below) rather than to overcome the limitations of (visual) perception (e.g., see Allport, 1987; Van der Heijden, 1992, 2004). In the recent reviews by Nee and Jonides (2013) and LaRocque et al. (2014) the model of Oberauer was related to activation within specific brain regions as established with functional magnetic resonance imaging (fMRI) and EEG. For example, Nee and Jonides (2013) related the FoA with activity in ventral parietal cortex (VPC).

In this paper, we are mainly interested in contrasting external with internal spatial attention, so the question is whether directing attention at an item in the outer world is comparable to selection of an item from visual short-term memory to perform a certain (cognitive) action. The studies of Griffin and Nobre (2003), Nobre et al. (2004), and Kuo et al. (2009) seem most relevant with regard to this specific question. Griffin and Nobre (2003) used two variants of an endogenous orienting task in which spatial cues indicated the likely relevant location of an item in a 2 by 2 array that was presented either before or after the cue. In the standard precue condition, a directional cue indicated where a likely relevant stimulus would be presented in the array. After presenting the array, a probe stimulus was displayed and

<sup>1</sup>In line with several recent studies (e.g., see Nee and Jonides, 2013) we adopted the term short-term memory rather than working memory (e.g., Baddeley, 2003), as the former term is more theory-neutral.

participants had to indicate whether this probe was present in the array or not. On a large proportion of trials (80%) this probe was identical to the precued (externally attended) stimulus, and responses were faster on those trials than on trials in which another uncued item of the array was identical to the probe. In the retrocue condition, the cue was presented after the array, so now the relevant stimulus had to be retrieved from short-term memory and was therefore internally attended. Precisely the same pattern of results was obtained. A second experiment indicated that these findings were not due to different response criteria. These results fit with a common role for internal and external attention. Furthermore, as perceptual limitations are no longer at hand for the internally retrieved item, these data actually suggest that spatial attention may not be needed to overcome these limitations but rather plays a crucial role in guiding actions (see Allport, 1987; Van der Heijden, 1992, 2004).

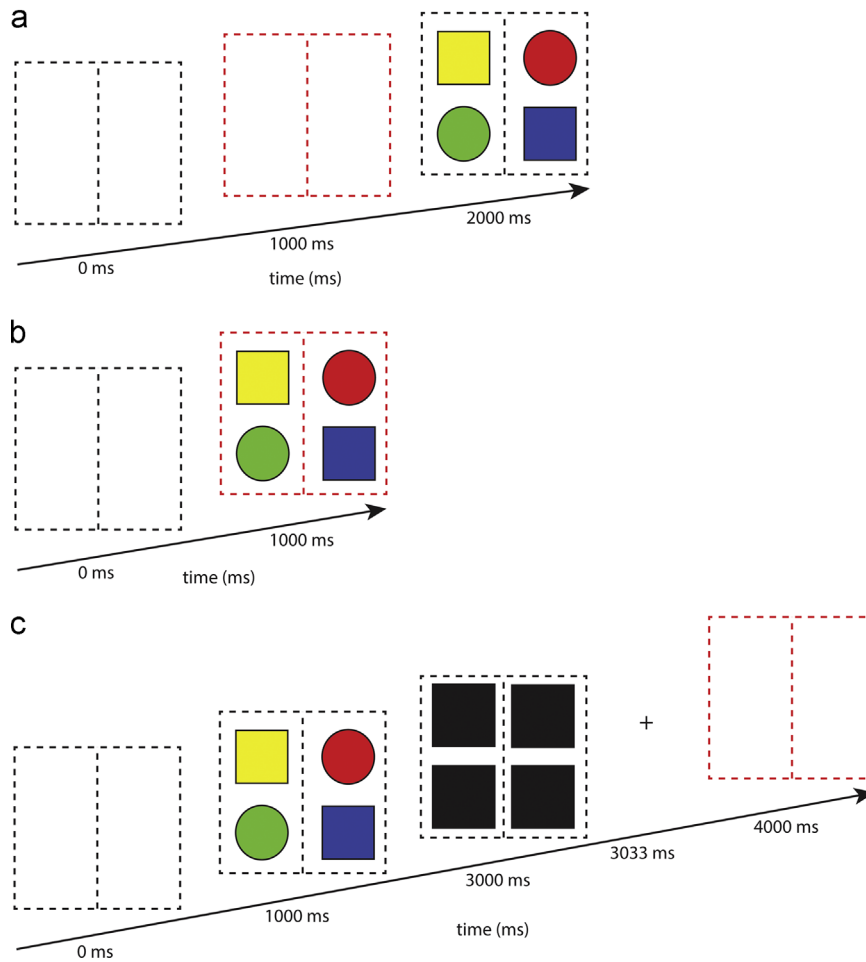
In a subsequent fMRI study of Nobre et al. (2004), a variant of the same task was employed (see also Nobre et al., 2008). External and internal spatial attention as examined with precues and retrocues, respectively, appeared both related to activity in parietal, frontal, and occipital areas, which are areas that are known to be activated in visual spatial orienting tasks (e.g., see Corbetta and Shulman, 2002; Kastner et al., 1999). The area that may serve both external and internal spatial attention was proposed to be posterior parietal cortex (PPC; the superior parietal lobule, and intraparietal sulcus). Right parietal cortex seemed more relevant for external spatial attention, while prefrontal cortex may be more selectively involved in the case of internal attention (see also Tanoue et al., 2013). It should be noted, however, that common activation in the case of precues and postcues may be related to automatic orienting effects (e.g., see Tipples, 2002) or participants may simply have had a tendency to focus their attention on the cued location (see the question addressed by McCollough et al., 2007).

Kuo et al. (2009) used another paradigm in which ERLs were derived to directly compare visual search with memory search. In their visual search task, involving external spatial attention, a centrally presented item had to be searched for in a subsequent symmetrical array of two or four items, with items being present in both visual fields. In the memory search task, first a symmetrical array of two or four items was presented. Subsequently, a single item was presented in the center and participants had to indicate whether this item was present in the memory set. So, in the latter case, attention had to be internally directed. In the visual search task, a posterior contralateral negativity (PCN, often denoted as N2pc, e.g., see Eimer, 1996), was observed after array onset, and in the memory search task, a PCN was observed at onset of the central item relative to the location of the identical item in the memory set. Similar time courses and scalp distributions were observed in both tasks. These findings accord with the idea that internal and external spatial attention overlap. The question may be raised, however, whether the observed pattern in the memory search condition is possibly related to repetition suppression (e.g., see Ward et al., 2013). Specifically, in the memory search task the central item might differentially activate

representations related to the left and right visual fields as one of the fields was already involved with processing this item. So, the lateralized effect might not be due to internal spatial attention but to different sensitivities of contralateral and ipsilateral neuronal representations. Furthermore, discrepancies between internal and external attention may have been absent due to the type of analyses as they will not pick up induced activity that is not time-locked to stimulus onset.

In the current paper we will also focus on ERLs but additionally used the LPS method (Van der Lubbe and Utzerath, 2013) to assess lateralized activity that is not strongly bound to an external event. The latter method may reveal discrepancies between external and internal attention that are not visible in ERLs. Van der Lubbe and Utzerath (2013) employed the LPS method in an endogenous cuing paradigm with symbolic cues. ERL analyses on the cue-target interval, which concerns the orienting phase, revealed the late directing attention negativity (LDAP) component, which has been interpreted as attentional modulation along the ventral visual processing stream (Hopf and Mangun, 2000). Interestingly, LPS analyses revealed that the LDAP may be related to lateralized effects (increased ipsilateral vs. contralateral power) in the theta ( $\theta$ ; 4–8 Hz) and the alpha ( $\alpha$ ; 8–13 Hz) bands. Furthermore, at the end of the orienting phase, increased lateralized  $\alpha$  power was observed at posterior sites (also increased ipsilateral vs. contralateral power), which may also reflect a modulation (i.e., ipsilateral inhibition) along the ventral processing stream. If external and internal spatial attention mechanisms are indeed closely related, then we may expect to observe effects in the very same frequency bands. Recent studies suggest that this may be the case. For example, in a study by Sauseng et al. (2009), increased ipsilateral vs. contralateral  $\alpha$  power was observed relative to the side of the to-be-memorized items, which was related to suppression of the irrelevant to-be-ignored items.

To contrast internal with external attention we employed a task developed by Hommel (2002). This task resembles the one used by Kuo et al. (2009) but avoids the need to repeat stimuli within a trial, which implies that repetition suppression is no issue. We used visual search or memory search displays containing four stimuli, two squares and two circles that were all presented in different colors (red, green, yellow and blue). Each stimulus is presented in one quadrant of a centrally positioned frame (see Fig. 1), with the restriction that each side of fixation always contains both a circle and a square. After some time the central frame (the cue) is colored (in one of the aforementioned colors) either before (precue), simultaneous with (simultaneous cue), or after the four stimulus display (postcue) thereby signaling the target stimulus – the one with the same color – that requires an action. Participants make a left or right button press depending on the form (square or circle) of this target stimulus. Importantly, the cues employed here do not induce automatic orienting effects, which have been observed with arrow cues (Tipples, 2002). Hommel observed that responses were faster when the stimulus and response sides corresponded as compared to no correspondence. This effect, known as the Simon effect (Simon, 1969, 1990), was not only observed in the case of precues and simultaneous cues, but also in the



**Fig. 1** – An example of the stimuli used in our experiment. For illustrational purposes black and white are reversed. In panels a, b, and c the order of events is indicated for the precue condition, the simultaneous cue condition, and the postcue condition, respectively. The moments of presenting the various stimuli are indicated along the time line and are relative to the start of a trial. The cue is the colored frame, which indicates what stimulus was the target (here, the red circle). Required left or right hand responses depended on the form of the target. The last stimulus in each condition remained present until a response was made.

case of postcues. Thus, the Simon effect depended on the memorized location of the relevant stimulus. As indicated in a number of recent studies (e.g., see [Abrahamse and Van der Lubbe, 2008](#); [Van der Lubbe et al., 2012](#)), this effect may reflect the operation of attention – in line with overlap between external and internal spatial attention. Most relevant for our purposes is lateralized EEG activity as it might confirm the similarity between internal and external attention. We decided to examine the presence of the PCN and determined the LPS in different frequency bands ranging from the lower  $\theta$  to the upper beta ( $\beta$ ; 13–20 Hz) range. The LPS method was also applied on individually obtained ERPs (LPS-ERP). This might reveal effects that are not visible in the ERLs due to individual differences (see [Van der Lubbe and Utzerath, 2013](#)). More interestingly, a comparison between effects on the LPS and the LPS-ERP might inform us on the more evoked or induced nature of observed effects (see [Herrmann et al., 2005](#)). Namely, in the case of an effect on the LPS but not on the LPS-ERP, it may be concluded that the LPS effect concerned induced activity.

## 2. Results

### 2.1. Behavioral measures

All trials with detectable eye movements within critical time intervals were removed (criteria:  $\pm 40 \mu\text{V}$  from 0 to 700 ms after onset of the relevant stimulus), which left on average 82% of the trials. Mean reaction times (RTs) and proportion of correct responses (PCs) are displayed in [Table 1](#). Analyses on RTs (ANOVA) with the factors cue condition and correspondence revealed that RTs were faster for corresponding than for noncorresponding trials (744 vs. 772 ms;  $F(1,14)=20.5$ ,  $p<0.001$ ,  $\eta_p^2=0.60$ ). An effect of cue condition was observed as well ( $F(2,28)=91.6$ ,  $p<0.001$ ,  $\epsilon=0.75$ ,  $\eta_p^2=0.87$ ), reflecting slowest responses in the simultaneous cue condition (1005 ms), fastest responses in the postcue condition (620 ms), and slightly slower responses in the precue condition (649 ms). The difference in RT between the precue and the postcue conditions was not significant ( $F(1,14)=1.8$ ,  $p=0.198$ ), but responses were always slower in the simultaneous cue condition than in the

other cue conditions ( $F(1,14) > 100.1, p < 0.001$ ). No interaction was observed between cue condition and correspondence ( $F < 0.4$ ). Separate *t*-tests per cue condition confirmed the presence of a correspondence effect in all cue conditions ( $t(14) > 2.4, p < 0.032$ ).

Analyses on PCs with the factors cue condition and correspondence revealed that more correct responses were made on corresponding than on noncorresponding trials (96.3 vs. 93.9%;  $F(1,14) = 13.9, p = 0.002, \eta_p^2 = 0.50$ ). The effect of cue condition was also significant ( $F(2,28) = 6.9, p = 0.006, \epsilon = 0.88, \eta_p^2 = 0.33$ ). Responses were more correct in the case of postcues (95.5%) and precues (96.6%) than in the case of simultaneous cues (93.2%;  $F(1,14) > 4.9, p < 0.05$ ), while no difference was observed between precues and postcues ( $F = 1.7$ ). No significant interaction was observed between cue condi-

tion and correspondence ( $F(2,28) = 1.8$ ). Separate *t*-tests per cue condition revealed that the correspondence effect was present in the precue and the simultaneous cue conditions, but no such effect was present in the postcue condition (precue:  $t(14) = 6.3, p < 0.001$ ; simultaneous cue:  $t(14) = 2.7, p = 0.017$ ; postcue:  $t(14) = 1.2, p = 0.39$ ).

2.2. EEG measures

2.2.1. ERLs

ERLs for relevant electrode pairs together with hEOG for the different cue conditions are presented in Fig. 2. Topographical maps covering the explored time range for the three conditions are displayed in Fig. 3.

Statistical analyses confirmed that an early PCN was present in the precue condition from 200 to 280 ms after array onset (PO7/8,  $t(14) > 3.8, p < 0.003$ ; P7/8,  $t(14) > 3.0, p < 0.01$ ; PO3/4,  $t(14) > 3.8, p < 0.003$ ; P3/4;  $t(14) > 3.5, p < 0.004$ ; C3/4,  $t(14) > 3.0, p < 0.02$ ). Analyses on the hEOG revealed that small eye movements were present, starting in the 240–280 ms time window ( $t(14) > 3.0, p < 0.01$ ). Control analyses (bivariate correlations with hEOG) revealed that the observed effects on the posterior electrodes were not related to the detected eye movements ( $p > 0.2$ ). A fronto-central contralateral negativity was visible from 320 to 440 ms (FC5/6,  $t(14) > 3.1, p < 0.01$ ), but this effect appeared to be related to small horizontal eye movements from 320 to 400 ms ( $p < 0.002$ ). Finally, an occipito-parietal contralateral positivity was

**Table 1 – Mean RTs and PCs as a function of cue condition and correspondence with standard errors in between brackets. corr = corresponding; ncorr = noncorresponding.**

Cue condition	RT (ms)		PC (%)	
	corr	ncorr	corr	ncorr
Precue	637(23)	661(26)	98.2(0.6)	94.9(0.8)
Simultaneous cue	987(35)	1023(40)	94.6(1.4)	91.7(1.4)
Postcue	607(19)	632(20)	96.2(0.7)	94.9(0.9)

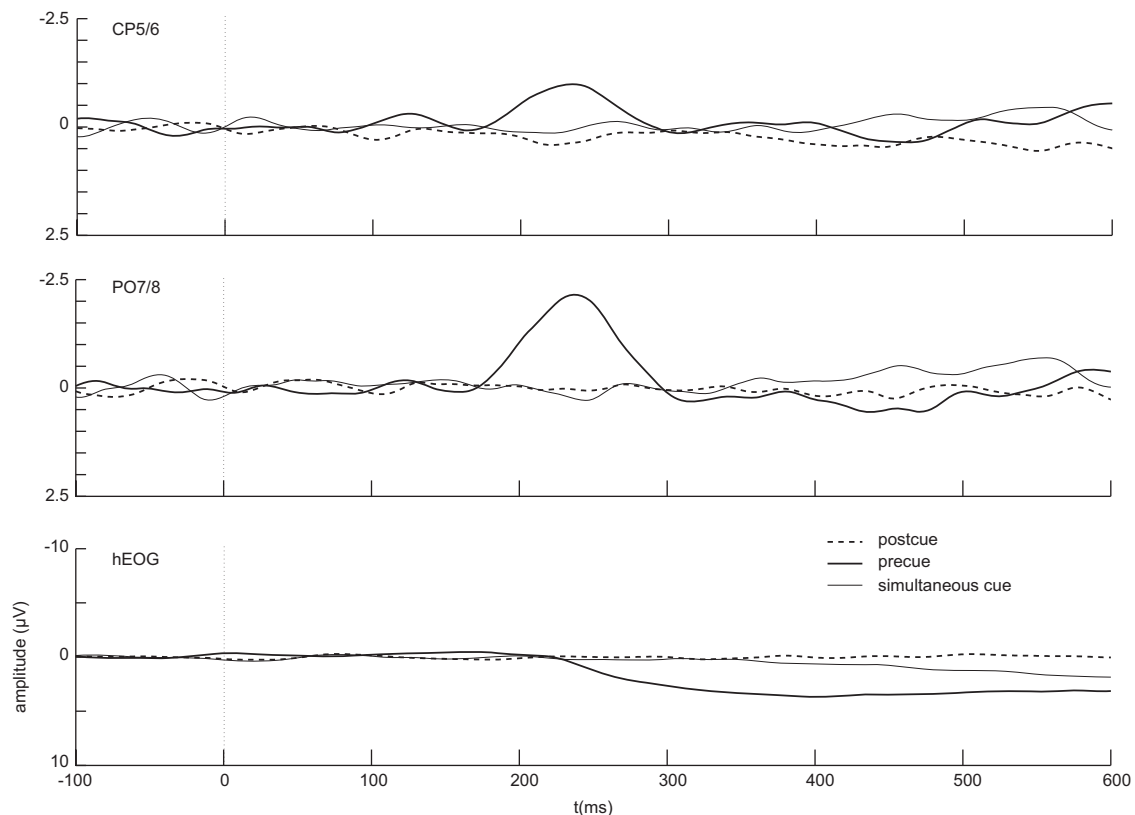
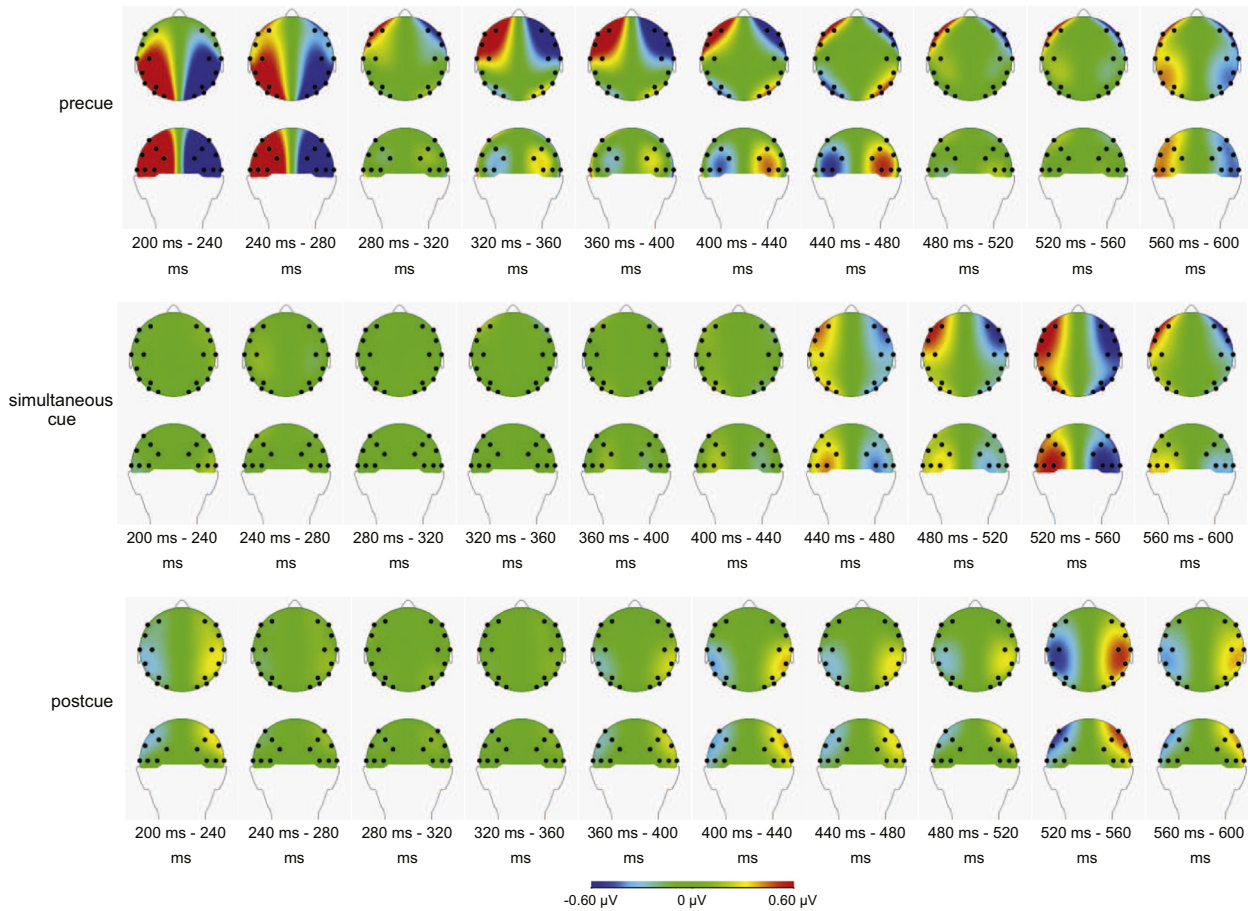


Fig. 2 – ERLs for the three different cue conditions at occipito-temporal (PO7/8) and centro-parietal electrodes (CP5/6). For the displayed hEOG, polarity was recoded depending on the relevant stimulus side.



**Fig. 3 – Topographical maps of the ERLs for the precue, simultaneous cue, and the postcue conditions, which were created by using spherical splines. The right hemisphere represents the contra-ipsilateral difference, while the left hemisphere reflects the ipsi-contralateral differences. Negativity on the right hemisphere implies that activity was more negative on contralateral than on ipsilateral electrodes.**

present from 400 to 480 ms ( $PO3/4$ ,  $t(14) > 3.4$ ,  $p < 0.005$ ), which was not related to small eye movements ( $p > 0.099$ ).

No early PCN could be detected in the simultaneous cue condition. Small eye movements could be detected, starting from 360 to 400 ms ( $t(14) > 2.4$ ,  $p < 0.04$ ). A posterior contralateral negativity seemed present from 520 to 560 ms ( $PO7/8$ ,  $t(14) = 3.4$ ,  $p = 0.004$ ;  $P7/8$ ,  $t(14) = 2.7$ ,  $p = 0.017$ ;  $PO3/4$ ,  $t(14) = 3.1$ ,  $p = 0.007$ ), but it did not meet our significance criterion of two successive time windows with  $p < 0.025$ .

No PCN was present in the postcue condition, but we also did not observe any sign of small eye movements in the explored time windows ( $p > 0.28$ ). A centro-parietal contralateral positivity was present from 360 to 480 ms ( $CP5/6$ ,  $t(14) > 2.8$ ,  $p < 0.016$ ).

### 2.2.2. LPS

Results for the LPS analyses (and the LPS-ERP analyses) that fulfilled our significance criteria (two consecutive time windows,  $p < 0.01$ ) are depicted in Table 2. Separate analyses for the different frequency bands in the precue condition revealed a significant deviation from zero in the  $\theta_1$  band (3.2–4.8 Hz) at posterior electrode pairs, starting at 200 ms after array onset, being most pronounced, long-lasting, and most significant at the  $PO3/4$  electrode pair (from 240 to

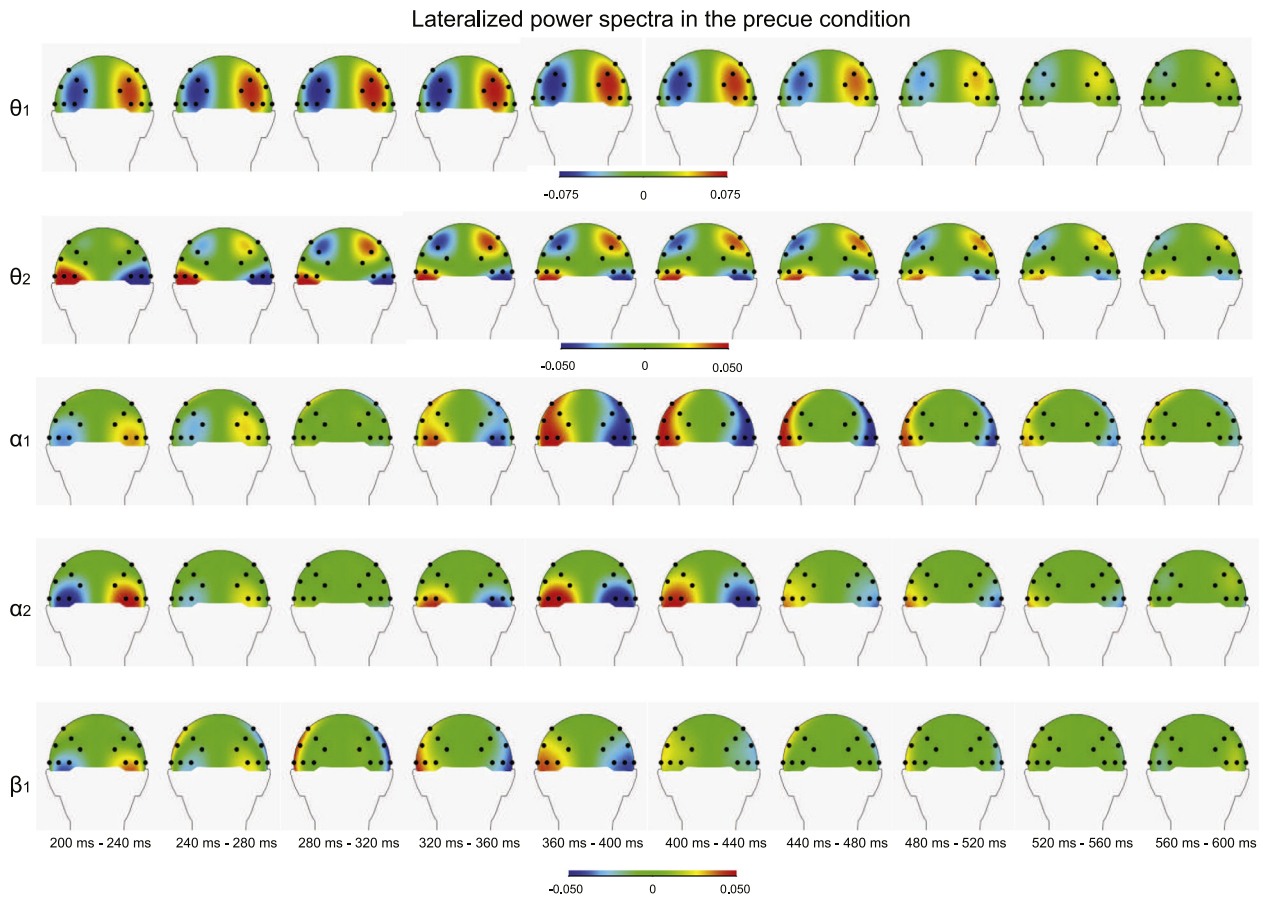
320 ms,  $t(14) = 4.5$ ,  $p < 0.0005$ ). This effect reflected increased contralateral as compared to ipsilateral power (see Fig. 4). Comparable effects were present in the  $\theta_2$  band (4.2–6.3 Hz) above parietal sites. These effects seem not related to small eye movements ( $p > 0.08$ ). Opposite effects, increased ipsilateral vs. contralateral power were observed in the  $\alpha_1$  (7.2–10.7 Hz),  $\alpha_2$  (9.4–14.0 Hz), and  $\beta_1$  (12.2–18.4 Hz) bands at centroparietal, occipito-temporal, and centroparietal sites. This effect seemed partly (see Table 2) related to small eye movements, as a significant correlation between hEOG and lateralized  $\alpha_2$  power at  $PO7/8$  was observed from 320 to 360 ms after array onset ( $p = 0.017$ ), and also between hEOG and lateralized  $\beta_1$  power at  $CP5/6$  from 360 to 400 ms ( $p = 0.047$ ).

In the simultaneous cue condition we observed a significant deviation from zero in the  $\theta_2$  band at the  $P3/4$  electrode pair from 280 to 360 ms ( $t(14) > 3.2$ ,  $p < 0.006$ ), which concerned increased contralateral vs. ipsilateral power (see Fig. 5). This effect seemed unrelated to small eye movements ( $p > 0.07$ ). We also noticed a very late (560–600 ms) opposite effect (increased ipsilateral vs. contralateral power) in the  $\alpha_1$  band at the  $P7/8$  electrode pair ( $t(14) = 3.8$ ,  $p = 0.002$ ) and the  $\theta_3$  band (5.5–8.2 Hz) at the  $PO7/8$  electrode pair ( $t(14) = 3.4$ ,  $p = 0.004$ ), but this effect (which was not related to small eye movement,  $p > 0.4$ ) did not fulfill our criteria as it was only

**Table 2 – LPS and LPS-ERP results for the different frequency bands for the precue, simultaneous cue, and the postcue conditions. LPS=lateralized power spectra. ERP=event related potential. <sup>eye</sup> means that the effect seems related to small eye movements.**

Condition	Band (site)	LPS time window	Polarity	LPS-ERP band (site)	Time window	Polarity
Precue	$\theta_1$ (P3)	200–440 ms	neg	$\theta_2$ (P7)	200–280 ms	pos
	$\theta_1$ (PO3)	200–520 ms	neg	$\theta_3$ (P3)	240–320 ms	neg
	$\theta_1$ (PO7)	280–480 ms	neg	$\theta_3$ (PO3)	240–320 ms	neg
	$\theta_1$ (P7)	280–400 ms	neg	$\theta_1$ (PO3)	400–560 ms	neg
	$\theta_2$ (P3)	320–400 ms	neg	$\theta_1$ (P3)	480–600 ms	neg
	$\alpha_2$ (PO7) <sup>eye</sup>	320–440 ms	pos			
	$\alpha_1$ (CP5)	360–480 ms	pos			
	$\beta_1$ (CP5) <sup>eye</sup>	360–440 ms	pos			
Simultaneous cue	$\theta_2$ (P3)	280–360 ms	neg	–	–	–
	$\alpha_1$ (P7)	560–640 ms	pos			
	$\theta_3$ (PO7)	560–640 ms	pos			
Postcue	$\theta_3$ (P7)	240–320 ms	neg	–	–	–
	$\alpha_1$ (P7)	480–560 ms	pos			

pos = ipsilateral > contralateral power.  
 neg = contralateral > ipsilateral power.



**Fig. 4 – Topographical maps of the LPS results for the relevant frequency bands in the precue condition. Here, the left hemisphere reflects ipsi vs. contralateral power, whereas the right hemisphere reflects contra vs. ipsilateral power. Thus, negativity at the left hemisphere means that power in a specific frequency band (e.g., the  $\theta_1$  band) was higher above contralateral than above ipsilateral sites.**

observed for the 560–600 ms time window. Therefore, we examined the subsequent time window (600–640 ms), and confirmed a continuation of the observed effect ( $t(14) > 3.6$ ,  $p < 0.004$ ); see Fig. 5).

In the postcue condition, we observed increased contralateral vs. ipsilateral power in the  $\theta_3$  band at the P7/8 electrode pair from 240 to 320 ms after frame onset (see Fig. 6). This effect was most significant from 280 to 320 ms ( $t(14) = 3.7$ ,  $p = 0.003$ ). Slightly later, we observed an opposite effect (increased ipsilateral vs. contralateral power) at the same electrode pair from 480 to 560 ms in the  $\alpha_1$  band, being most pronounced from 520 to 560 ms, ( $t(14) = 3.4$ ,  $p = 0.004$ ).

Although we found support for early increased contralateral vs. ipsilateral  $\theta$  power in all cue conditions, there may be subtle differences as the topographies and effects in the specific sub- $\theta$  bands are not identical (see Table 2 and Figs. 4–6). To further explore this, we decided to focus on the 280–320 ms interval as increased contralateral activity in the  $\theta$  band was present within this interval in all three conditions.

An ANOVA was performed with the factors cue condition, band ( $\theta_1$ ,  $\theta_2$ , and  $\theta_3$ ), and electrode pair (P3/4, PO3/4, PO7/8, and P7/8). An interaction between cue condition and band was observed ( $F(4,56) = 4.6$ ,  $p = 0.005$ ,  $\epsilon = 0.89$ ,  $\eta_p^2 = 0.25$ ).

Inspection of Table 2 suggests that there may be differences between cue conditions concerning the involved bands. Separate comparisons between cue conditions revealed a cue condition–band interaction for the comparisons between the precue and the simultaneous cue condition, and between the precue and the postcue condition ( $F(2,28) > 6.3$ ,  $p < 0.006$ ,  $\eta_p^2 > 0.31$ ), but not between the simultaneous cue and the postcue condition ( $F = 1.6$ ). This reflects the presence of lateralized  $\theta_1$  activity in the precue condition, while effects in the simultaneous cue and postcue conditions concern the higher  $\theta_2$  and  $\theta_3$  bands. Further interactions were observed between cue condition and electrode pair ( $F(6,84) = 5.9$ ,  $p = 0.001$ ;  $\epsilon = 0.57$ ,  $\eta_p^2 = 0.30$ ), and between cue condition, band, and electrode pair ( $F(12,168) = 2.7$ ,  $p = 0.038$ ,  $\epsilon = 0.36$ ,  $\eta_p^2 = 0.16$ ). To ensure an adequate interpretation of observed interactions with the factor electrode pair (e.g., due to general differences in signal strength between conditions, see McCarthy and Wood, 1985), we made separate comparisons between two conditions. We applied a method recommended by Jing et al. (2006), which circumvents some problems that remain with the vector normalization method of McCarthy and Wood (1985). With this method, data in one condition (A) is rescaled as a function of another condition (B) to A' in such a way that amplitude differences between conditions are

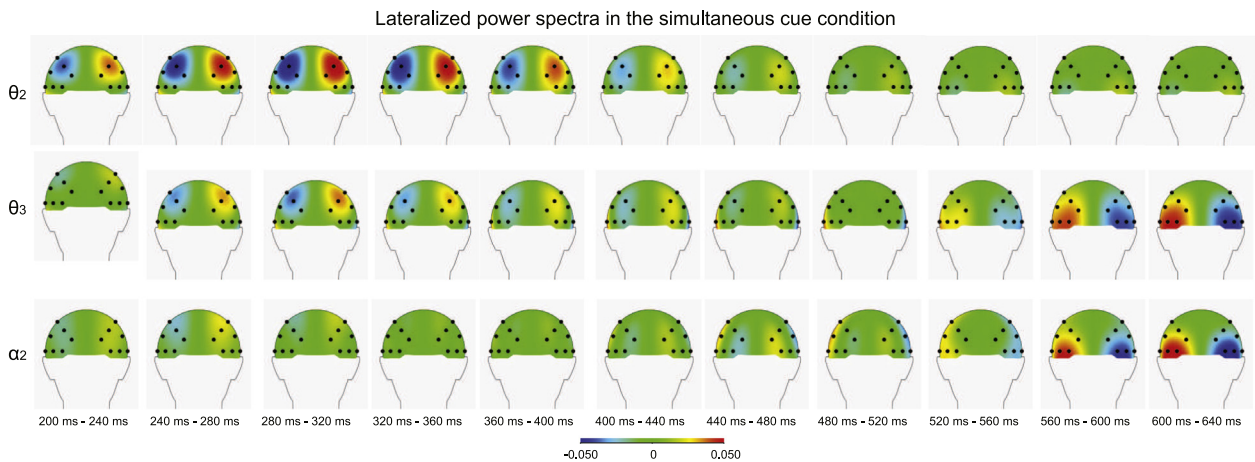


Fig. 5 – Topographical maps of the LPS results for the relevant frequency bands in the simultaneous cue condition (further details, see Fig. 4).

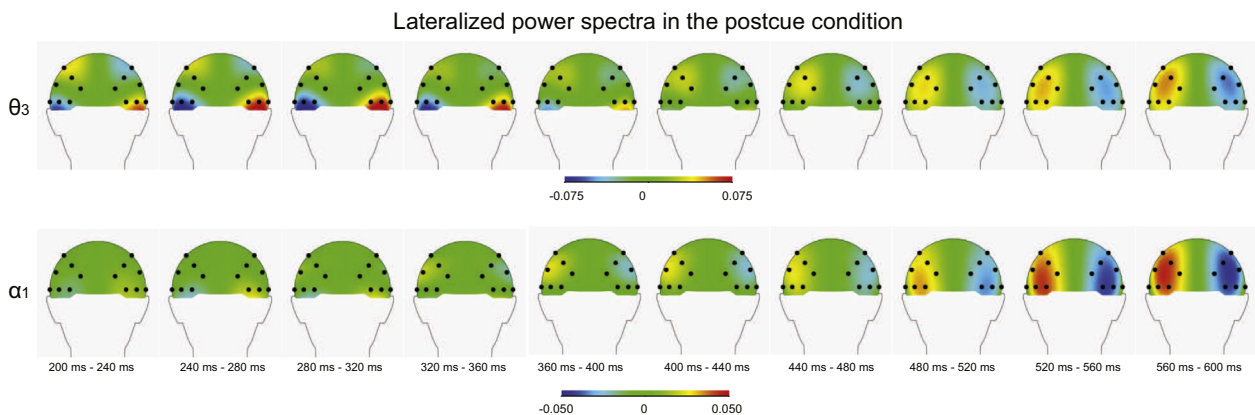
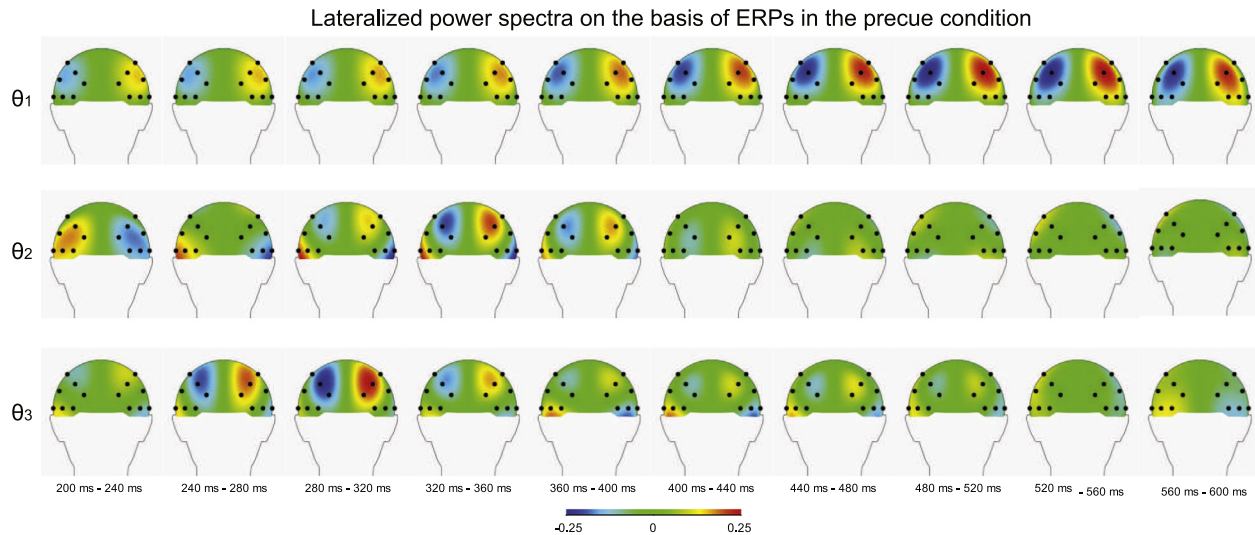


Fig. 6 – Topographical maps of the LPS results for the relevant frequency bands in the postcue condition (further details, see Fig. 4).





**Fig. 7 – Topographical maps of the LPS–ERP results for the relevant frequency bands in the precue condition (further details, see Fig. 4).**

removed. This rescaling is also done the other way round, for condition B relative to condition A, leading to B'. Subsequently, ANOVAs can be carried out to test for topographical differences between the conditions B and A', and A and B'. After application of this method, no interactions could be detected involving the factors task and electrode ( $F < 1.5$ ).

We did not compare the cue conditions concerning the later increased ipsilateral posterior  $\alpha$  power as the time windows in which these effects occurred do not really overlap, and as the topography in the simultaneous cue and the postcue condition seem rather comparable (occipito-temporal, see Table 2 and Figs. 5 and 6).

### 2.2.3. LPS–ERP

Results for these analyses that fulfilled our significance criteria are displayed in Table 2. Performing the LPS procedure on the ERPs in the precue condition revealed increased contralateral vs. ipsilateral power in the  $\theta_3$  band at parietal electrodes from 240 until 320 ms (see Fig. 7), being most pronounced at the PO3/4 electrode pair (280–320 ms,  $t(14)=5.6$ ,  $p < 0.0001$ ). An opposite effect, increased ipsilateral vs. contralateral  $\theta_2$  power, was present at the P7/8 electrode pair, being most pronounced from 200 to 240 ms ( $t(14)=5.5$ ,  $p < 0.0001$ ). A later increase in contralateral vs. ipsilateral power in the  $\theta_1$  band was also present at parietal electrodes, being most pronounced at the PO3/4 electrode pair (480–520 ms,  $t(14)=3.5$ ,  $p < 0.005$ ). None of these effects were related to small eye movements ( $p > 0.08$ ). Furthermore, no effects in any of the frequency bands (from the lower  $\theta$  to the upper  $\beta$  band) were observed in the simultaneous cue and the postcue condition.

## 3. Discussion

Previous EEG research showed remarkable similarities between ERLs indicative of external and internal spatial attention, providing support for a common underlying mechanism. However, as we indicated in our introduction, part of the neuroimaging support may be due to the type of analyses

performed (which favors evoked activity) and/or specific details of the used tasks. In the present study, a design and set of analyses were employed that avoids such potential confounding. A colored frame was used that indicated which item out of four colored items, being presented in each quadrant of the visual field, was the target. Depending on the form of the target, a left or right button press was required. The frame occurred either before (i.e., precue), simultaneously with (simultaneous cue) or after the items (postcue), thereby creating conditions involving external (precue and simultaneous cue) and internal spatial attention (postcue). Apart from ERLs to determine changes in lateralized evoked activity related to the target position, we also computed the LPS (Van der Lubbe and Utzerath, 2013) which includes lateralized activity that is not strictly bound to a certain event (induced activity). By applying the same procedure to ERPs, we could explore whether observed effects have a more evoked or induced nature.

Behavioral results in the precue condition showed a Simon effect on RT and PCs; responses were faster and more accurate when the stimulus and response sides corresponded than when they did not correspond. A clear PCN was observed from 200 to 280 ms after array onset (see Figs. 2 and 3), which was unrelated to eye movements. A later frontal effect seemed related with small (below threshold) eye movements, while a later posterior contralateral positivity (PCP) was present from 400 to 480 ms.<sup>2</sup> The LPS analyses (see Fig. 4) showed posterior increased contralateral vs. ipsilateral power in the  $\theta_1$  band starting from 200 ms, appearing slightly later in the  $\theta_2$  band, with a maximum at occipito-parietal sites. Comparable, though not completely identical effects were found in the LPS–ERP analyses (see Fig. 7). These findings suggest that the PCN may be characterized as a reflection of evoked posterior increased contralateral  $\theta$  power. The PCN has been interpreted as attentional selection of the relevant item (e.g., see Töllner et al., 2013), while studies on the  $\theta$  band suggest that activity reflects the encoding (and retrieval) of

<sup>2</sup>This PCP might very well be identical to the LDAP commonly observed in endogenous orienting paradigms (see Van der Lubbe et al., 2006; Van der Lubbe and Utzerath, 2013).

new information in the contralateral hemifield (e.g., see [Staudigl and Hanslmayr, 2013](#)). These interpretations appear strongly related. The LPS analyses also revealed a slightly later effect in the  $\alpha$  bands (360–480 ms), with posterior increased ipsilateral vs. contralateral power. This effect may be related to the PCP visible in the ERL analyses, although no effect was visible in the LPS–ERP analyses. The effect in the  $\alpha$  band is commonly interpreted as reduced inhibition of the contralateral hemifield and/or increased inhibition of the ipsilateral hemifield (e.g., see [Jokisch and Jensen, 2007](#); [Klimesch et al., 2011](#); [Van der Lubbe and Utzerath, 2013](#)) but no straightforward conclusion can be drawn here as a part of the effect was related to small eye movements (but see below).

Behavioral data for the simultaneous cue condition also revealed a Simon effect both for RTs and PCs. The ERL data showed a tendency to a very late PCN (520–560 ms; see [Fig. 3](#)), but the effect was too short-lasting to meet our significance criteria. LPS analyses revealed early posterior increased contralateral vs. ipsilateral power in the  $\theta_2$  band starting from 280 ms, being maximal at parietal sites (see [Fig. 4](#)). Furthermore, very late posterior increased ipsilateral vs. contralateral power in the  $\theta_3$  and  $\alpha_1$  band was observed (560–640 ms), which may concern the same effect as in the precue condition. This effect was not related to small eye movements. This result may be interpreted as reduced inhibition of the contralateral hemifield and/or increased inhibition of the ipsilateral hemifield. As no effects were found with the LPS–ERP analyses, the observed effects in this condition may be considered as induced rather than evoked.

In the postcue condition, a Simon effect was present on RT, but not on PC. ERLs showed no early PCN, although late centroparietal positivity was observed (360–480 ms). This effect may be related to the PCP visible in the precue condition, although here, the effect seems to be more parietal. The LPS analyses revealed early posterior increased contralateral vs. ipsilateral power in the  $\theta_3$  band (240–320 ms) and a later opposite effect in the  $\alpha_1$  band (480–560 ms). The former effect (see [Fig. 6](#)) may reflect attentional selection of internally maintained representations, while the latter points at reduced inhibition of internal representations of the contralateral hemifield and/or increased inhibition of the ipsilateral hemifield. These findings provide further support for the view that internal spatial attention involves visual areas (e.g., see [Munneke et al., 2010](#); [Postle et al., 2004](#)).

With regard to the discussed methodological issues in the studies of [Nobre et al. \(2004\)](#) and [Kuo et al. \(2009\)](#), we may conclude that our results resemble their findings and therefore the current study provides important new support for common underlying mechanisms regarding internal and external spatial attention. Interestingly, inspection of the topographies of the early posterior increased contralateral  $\theta$  power in the conditions highlighting external and internal spatial attention suggests that there are actually some subtle differences between these processes that may be related to a different involvement of the dorsal and ventral visual pathways. If we consider the way in which the relevant representation may be selected with our color cue, then this may actually occur in two ways ([Van der Heijden, 1993](#)). The first mechanism is based on the idea that “position is special”. Here the order of selection would be [color>location>form].

This selection by means of location selection would involve the dorsal path in which spatial information is preserved (see [Van der Heijden, 1992](#); [Van der Lubbe and Woestenburg, 2000](#)). An alternative mechanism would be non-spatial: [color>form]. This selection might be more related to the ventral pathway as spatial information is not required for target selection. Given the observed topographical differences between the conditions, one might propose that external spatial attention concerns the dorsal pathway while internal spatial attention mainly involves the ventral pathway. As elaborated below, our analyses comparing the different cue conditions provide relevant clues regarding this possibility.

Our behavioral data revealed fastest responses in the postcue and the precue conditions, and slowest responses in the simultaneous cue condition (983 ms). The latter result seems not so surprising as both the cue has to be identified and the relevant item has to be retrieved to select the appropriate response, whereas in the other conditions one of these processes can already be carried out in advance. The Simon effect on RT was observed in all cue conditions, thereby replicating the results of [Hommel \(2002\)](#), which points to a shared underlying process (i.e., attentional selection) in all the three conditions. Regarding PCs, Simon effects were present in the precue and simultaneous cue condition, but not in the postcue condition, which might reflect some subtle difference between the processes involved. However, the overall analysis on PC could not confirm that the effect differed between cue conditions. The observed discrepancies in early posterior increased contralateral  $\theta$  power were evaluated with ANOVAs, and an initial statistical analysis suggested that the pattern might be the way as described above, with a more dorsal maximum in the case of external spatial attention in the precue and simultaneous cue condition, and a more ventral maximum in the case of internal spatial attention in the postcue condition. However, the observed interaction effect may be due to general differences between the conditions (see [McCarthy and Wood, 1985](#)). An analysis performed on rescaled data according to a procedure advocated by [Jing et al. \(2006\)](#) indeed revealed that we cannot conclude that there are topographical differences between the different conditions, supporting the idea that external and internal spatial attention share a common underlying mechanism. This view is underlined by the observed effect on  $\alpha$  power in all cue conditions. Nevertheless, a follow-up study using a more fine-grained approach with a larger number of electrodes seems needed to give a more definite answer.

If external and internal spatial attention shares a common process then the question arises what the common role of this process actually is. According to us, our results, like the findings of [Griffin and Nobre \(2003\)](#), fit very well with the view that attentional selection should be considered as “selection for action” and not as a way to deal with limitations of the visual system or by inhibiting interfering memory traces (e.g., see [Waldhauser et al., 2012](#)). Apart from the commonalities between external and internal spatial attention it has also been observed that attending to a location, and preparing an action (e.g., a saccade) concerning that location is similar (e.g., [Van der Lubbe et al., 2006](#)), and comparable findings have been observed when attending to forthcoming tactile stimuli ([Eimer and Van Velzen, 2002](#)). Furthermore, it has been proposed that the Simon effect may very well be related

to a spatial map that is shared by external spatial attention and the coding of stimulus-response links in memory (see [Wühr and Ansorge, 2007](#); [Van der Lubbe et al., 2012](#)). This overall pattern points to an overarching mechanism that plays a crucial role in linking perception with action (e.g., see [Bisley and Goldberg, 2010](#)). Thus, increased posterior contralateral  $\theta$  power might concern extraction of those features or objects that are relevant for guiding an action, which may also apply to an internal action or mental simulation, while increased posterior ipsilateral  $\alpha$  power might reflect inhibition of specific perception to action links.

The current study suggests that it may be a great advantage to focus not only on standard lateralized components that can be derived from ERPs that are related to attentional selection (the PCN and the LDAP), or short-term memory but also to use methods that avoid the cancellation of effects due to phase differences between trials and participants, like the LPS and wavelet analyses on individual ERPs. Combined use of these measures additionally improves our understanding of effects. For example, the clear PCN that we observed in our precue condition could be understood in terms of changes in the lower  $\theta$  range, which could be related to the encoding and retrieval of new information in the contralateral hemifield ([Staudigl and Hanslmayr, 2013](#)), and not with reduced inhibition of the contralateral hemifield. Furthermore, if we would have limited ourselves to the more standard ERL analyses, then we would have faced a problem, as in the precue condition a PCN was found, while no such effect seemed present in the other cue conditions. This neither fits with a conclusion that internal and external concern a different or a shared mechanism. Fortunately, the LPS analyses solved this problem.

A final issue to be addressed concerns the presence of small below threshold saccades that sometimes can account for observed lateralized effects in the case of external spatial attention. In an earlier study ([Van der Lubbe and Utzerath, 2013](#)) we also observed that small eye movements may sometimes partly explain observed effects. Obviously, this underlines the need for assessing the potential relation. Furthermore, it seems also in line with the aforementioned ideas of an overarching mechanism that links perception with action.

---

## 4. Conclusions

Our results show a strong resemblance in lateralized EEG power spectra measures between conditions that involve external spatial attention and conditions that require internal spatial attention. The presence of a Simon effect in all cue conditions additionally underlines the idea that a comparable process is involved. Together, these data provide support for the idea that internal and external spatial attention shares an underlying mechanism.

---

## 5. Experimental procedures

### 5.1. Participants

Eighteen participants (all students from the University of Twente; 13 women, 5 men; mean age 19.1 years, two

left-handed, 16 right-handed) received course credits for the participation in our experiment. All of them had normal or corrected-to-normal vision and no neurological or psychiatric disorder. None of our participants reported to be color-blind. They were naïve with regard to the purpose of the experiment. Every participant was informed about the procedure and signed an informed consent before electrode application. Three participants were excluded from the final analyses, one because of technical problems with the EEG measurements, and two others because of too many eye movements during the critical intervals (for criteria, see below). The study was approved by the ethics committee at the Faculty of Behavioral Sciences at the University of Twente.

### 5.2. Stimuli, task and procedure

On every trial a sequence of stimuli was presented on a black background (see [Fig. 1](#)) consisting of a frame (height  $\times$  width:  $10.2^\circ \times 8.8^\circ$ ), which was subdivided by a vertical line, and four objects appearing in every quadrant of the frame. The center of the frame was presented at a to-be fixated fixation point. The objects were two squares and two circles ( $2.5^\circ \times 2.5^\circ$ ). The centers of the objects were located at  $2.3^\circ$  and  $2.5^\circ$  from the horizontal and vertical midlines from the frame. The objects were colored blue, yellow, green, and red. At a certain moment, depending on the type of condition, the color of the frame changed from white to one of the aforementioned four colors, thereby signaling what object was the target on a specific trial. There was always one type of object (circle or square) on each side of the frame, but locations and color of the objects varied pseudo-randomly.

Three different cue conditions were used, the order of which was counterbalanced between participants. Each condition consisted of 32 test trials and 192 experimental trials (672 trials in total). All conditions started with a white frame on a black background being presented for 1000 ms. In the precue condition the frame was subsequently colored in one of the aforementioned colors, and after another 1000 ms, the four stimuli were displayed until a response was made. In the simultaneous cue condition, the white frame was followed by both a colored frame and the four stimuli, which also stayed until a response was made. In the postcue condition, the four stimuli were presented for 2000 ms after the white frame, which were followed by four squared white masks for 33 ms, whereafter the fixation remained for another 967 ms. Subsequently, the colored frame was presented until a response was made.

Participants had to react as fast as possible by indicating the stimulus (square or circle) that was cued by the colored frame. To prevent any effects of stimulus shape, half of the participants had to press the left control button when the frame color-cued a square and with the right control button when the frame cued a circle. The other half of the participants used the opposite mapping. The left and right index fingers were placed at the left and right control buttons. A trial finished when the participant gave a response. Erroneous responses evoked a short textual feedback (“wrong”). Correct responses elicited no feedback. Instructions and descriptions of the task were provided before the start of the experiment. Participants were allowed to take a short break

between the conditions, and between the test and experimental blocks.

### 5.3. Apparatus and data recording

Participants were seated in an armchair in a darkened room at a distance of approximately 50 cm in front of a 17 in. CRT monitor. The monitor was running at 60 Hz, and had a screen resolution of 1024 × 768 pixels. A standard QWERTY keyboard was used to register the responses. Stimuli were presented using Presentation software (Neurobehavioral Systems, Inc., version 11.0) installed on a personal computer (Intel P640, 3.2 GHz). Reaction time was measured using event-markers that were registered together with the EEG, the electro-oculogram (EOG), and other relevant event markers using Brainvision Recorder (version 1.05) software.

EEG was recorded according to the extended 10/20 system from 25 Ag/AgCl ring electrodes located at Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, PO7, PO3, PO4, PO8 and Oz. Vertical EOG was recorded from electrodes placed above and below the left eye, horizontal EOG from electrodes placed at the outer canthi of both eyes. EEG and EOG were amplified with a Quick-Amp amplifier (72 channels, DC), which implies an online average reference. Electrode impedance was kept below 10 k $\Omega$ . EEG and EOG were continuously recorded with a sample rate of 1000 Hz. A high-cutoff filter was set at 200 Hz and a notch filter of 50 Hz was used.

### 5.4. Behavioral measures

Trials with detectable eye movements (exceeding  $\pm 40 \mu\text{V}$  from 0 to 700 ms relative to the onset of the four stimulus display in the precue and simultaneous cue conditions, and relative to the coloring of the frame in the postcue condition) were removed. Premature (RT < 150 ms) and too slow responses (> 2000 ms) as well as erroneous responses were excluded from RT analysis. Reaction times (RT) and proportion of correct responses (PC) were computed as a function of correspondence (corr/ncorr) between stimulus and response side, and cue condition (precue, simultaneous cue, postcue). A repeated measures ANOVA was used to analyze these results. Greenhouse–Geisser  $\epsilon$  correction was performed. Separate paired-samples *t* tests were additionally performed per cue condition.

### 5.5. EEG measures

The continuously recorded EEG was analyzed with Brain Vision Analyzer 2.0.4 (Brain Products GmbH, 2012). The data was first partitioned in  $-500$  to  $2500$  ms intervals relative to the markers that signaled the relevant stimulus and the specific condition. In the postcue and the simultaneous cue condition this marker coincided with the cues, whereas in the precue condition, this marker coincided with the onset of the four stimuli. After a baseline correction, independent component analysis (ICA) was used to correct the EEG for eye movement-related artifacts. Trials with detectable horizontal eye movements and EEG channels with artifacts (gradient criterion: 100  $\mu\text{V}/\text{ms}$ , min–max: 150  $\mu\text{V}$ , low activity: 0.1  $\mu\text{V}$  for

50 ms) were removed. Subsequently, three different analyses were carried out.

For the ERLs, we first computed ERPs per relevant cue condition and side of the target stimulus. Then a double subtraction was carried out to determine contra-ipsilateral difference waves (see Van der Lubbe et al., 2006). Polarity of the horizontal (h)EOG was inverted when the side of the relevant stimulus was at the right. The PCN was expected to be most prominent at the PO7/8 electrode pair. To provide a broader picture, we decided to explore activity for several electrode pairs (FC5/6, C3/4, CP5/6, P3/4, PO3/4, PO7/8, P7/8) as they overlay the potentially relevant brain areas like the frontal eye fields, hand motor areas, parietal areas, occipito-parietal areas, and occipito-temporal areas. Amplitudes were determined per individual in 40 ms time windows from 200 ms to 600 ms after onset of the relevant stimulus. Separate paired-samples *t* tests were performed per cue condition to determine whether activity deviated from zero. To reduce the possibility of a Type I error, we applied a procedure comparable to one described by Talsma et al. (2001), which implies to use a critical *p*-value ( $p_{\text{crit}}$ ) for two consecutive time windows. To have a corrected *p*-value of 0.05 per group of analyses,  $p_{\text{crit}}$  can be computed as  $p_{\text{crit}} < \sqrt{(0.05 / ((\text{windows} - 1) \times \text{electrodes}))}$ . With seven electrode pairs and 10 time windows this implies:  $p_{\text{crit}} < 0.02817$ . We decided to use a significance criterion of 0.025 for two consecutive time windows. Control analyses were performed on the hEOG to determine whether observed effects might be related to small eye movements below the detection threshold.

For the LPS, we first extracted the power of different frequency bands starting from the lower theta ( $\theta_1$ ) to the upper beta ( $\beta_2$ ) band (4–20 Hz), separated in seven steps, by performing a wavelet analysis on the raw EEG. A complex Morlet wavelet ( $c=5$ ) was chosen with Gabor normalization. The following seven frequency bands were specified:  $\theta_1$  (3.2–4.8 Hz; Gaussian lower and upper band, respectively),  $\theta_2$  (4.2–6.3 Hz),  $\theta_3$  (5.5–8.2 Hz),  $\alpha_1$  (7.2–10.7 Hz),  $\alpha_2$  (9.4–14.0 Hz),  $\beta_1$  (12.2–18.4 Hz), and  $\beta_2$  (16.0–24.0 Hz). Individual averages of these estimates were computed for all cue conditions, per side of the relevant condition. Next, normalized lateralization indices ( $(\text{ipsilateral} - \text{contralateral}) / (\text{ipsilateral} + \text{contralateral})$ ) were calculated for the different frequency bands, both for the left and right relevant side. These power indices were computed for all symmetrical electrode pairs. Furthermore, an average was computed across the indices for both relevant sides, thereby constructing the LPS (see Van der Lubbe and Utzerath, 2013). Values of the LPS vary from  $-1$  to  $+1$ . A positive sign indicates that the power within a specific frequency band was larger above the hemisphere ipsilateral to the cued side than contralateral, whereas a negative sign indicates the opposite pattern. A value of zero signifies the absence of hemispherical differences. An increase in power of 5% corresponds with a value of 0.024, whereas an increase in power of 10% corresponds with a value of 0.048. The obtained estimates were evaluated per frequency band for the same time intervals as the ERLs. Finally, we determined the LPS for the individual ERPs (LPS–ERP) with the same parameters as the previous analysis. By comparing these results with the LPS findings we may determine whether observed LPS findings are more likely to have an induced than an evoked nature, and we might also observe some evoked effects that did not show up

in the ERLs due to individual differences. The same procedure to determine the significance criterion was employed but now the number of electrodes was additionally multiplied with the number of frequency bands that we explored. This results in a  $p_{\text{crit}} < 0.01065$ . We decided to adopt a significance criterion of 0.01 for two consecutive time windows.

## Acknowledgments

Our research was supported by the Institute of Behavioral Research (IBR) and the Institute for Biomedical Technology and Technical Medicine (MIRA) at the University of Twente, the Netherlands. Elger Abrahamse was additionally supported by the Netherlands Organization for Scientific Research (NWO, the Netherlands) by Grant no. 446-10-025 and by the Research Foundation – Flanders (FWO, Belgium) by Grant no. 12C4712N. The work described was carried out in accordance with the code of ethics of the world medical association (Declaration of Helsinki) for experiments involving humans. We want to thank Durk Talsma and another reviewer for their helpful comments on a previous draft of this manuscript.

## REFERENCES

- Abrahamse, E.L., Van der Lubbe, R.H.J., 2008. Endogenous orienting modulates the Simon effect: critical factors in experimental design. *Psychol. Res.* 72, 261–272, <http://dx.doi.org/10.1007/s00426-007-0110-x>.
- Allport, D.A., 1987. Selection for action: some behavioral and neurophysiological considerations of attention and action. In: Heuer, H., Sanders, A.F. (Eds.), *Perspectives on Perception and Action*. Erlbaum, Hillsdale, NJ.
- Awh, E., Jonides, J., 2001. Overlapping mechanisms of attention and spatial working memory. *Trends Cogn. Sci.* 5, 119–126.
- Awh, E., Vogel, E.K., Oh, S.-H., 2006. Interaction between attention and working memory. *Neuroscience* 139, 201–208, <http://dx.doi.org/10.1016/j.neuroscience.2005.08.023>.
- Baddeley, A., 2003. Working memory: looking back and looking forward. *Nat. Rev. Neurosci.* 4, 829–839, <http://dx.doi.org/10.1038/nrn1201>.
- Bisiach, E., Luzzatti, C., 1978. Unilateral neglect of representational space. *Cortex* 14, 129–133.
- Bisley, J.W., Goldberg, M.E., 2010. Attention, intention, and priority in the parietal lobe. *Annu. Rev. Neurosci.* 33, 1–21, <http://dx.doi.org/10.1146/annurev-neuro-060909-152823>.
- Buszák, G., 2006. *Rhythms of the Brain*. Oxford University Press, New York.
- Cabeza, R., Ciaramelli, E., Olson, I.R., Moscovitch, M., 2008. Parietal cortex and episodic memory: an attentional account. *Nat. Rev. Neurosci.* 9, 613–625, <http://dx.doi.org/10.1038/nrn2459>.
- Cabeza, R., Ciaramelli, E., Moscovitch, M., 2012. Cognitive contributions of the ventral parietal cortex: an integrative theoretical account. *Trends Cognit. Sci.* 16, 338–352, <http://dx.doi.org/10.1016/j.tics.2012.04.008>.
- Chun, M.M., Golomb, J.D., Turk-Browne, N.B., 2011. A taxonomy of external and internal attention. *Annu. Rev. Psychol.* 62, 73–101, <http://dx.doi.org/10.1146/annurev.psych.093008.100427>.
- Corbetta, M., Shulman, G., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3, 201–215.
- Corbetta, M., Kincade, J.M., Shulman, G.L., 2002. Neural systems for visual orienting and their relationships to spatial working memory. *J. Cognit. Neurosci.* 14, 508–523.
- Cowan, N., 1995. *Attention and Memory: an Integrated Framework*. Oxford University Press, New York.
- Cowan, N., 2011. The focus of attention as observed in visual working memory tasks: making sense of competing claims. *Neuropsychologia* 49, 1401–1406, <http://dx.doi.org/10.1016/j.neuropsychologia.2011.01.035>.
- Cowan, N., Moray, C.C., 2006. Visual working memory depends on attentional filtering. *Trends Cognit. Sci.* 10, 139–141, <http://dx.doi.org/10.1016/j.tics.2006.02.001>.
- Downing, P.E., 2000. Interactions between visual working memory and selective attention. *Psychol. Sci.* 11, 467–473, <http://dx.doi.org/10.1111/1467-9280.00290>.
- Eimer, M., 1996. The N2pc component as an indicator of attentional selectivity. *Electroencephalogr. Clin. Neurophysiol.* 99, 225–234.
- Eimer, M., Van Velzen, J., 2002. Crossmodal links in spatial attention are mediated by supramodal control processes: evidence from event-related potentials. *Psychophysiology* 39, 437–449.
- Gazzaley, A., Nobre, A.C., 2012. Top-down modulation: bridging selective attention and working memory. *Trends Cognit. Sci.* 16, 129–135, <http://dx.doi.org/10.1016/j.tics.2011.11.014>.
- Griffin, I.C., Nobre, A.C., 2003. Orienting attention to locations in internal representations. *J. Cognit. Neurosci.* 15, 1176–1194.
- Herrmann, C., Grigutsch, M., Busch, N.A., 2005. EEG oscillations and wavelet analysis. In: Handy, Todd C. (Ed.), *Event-Related Potentials. A Methods Handbook*. MIT Press, Cambridge.
- Hopf, J.M., Mangun, G.R., 2000. Shifting visual attention in space: an electrophysiological analysis using high spatial resolution mapping. *Clin. Neurophysiol.* 111, 1241–1257.
- Hommel, B., 2002. Responding to object files: automatic integration of spatial information revealed by stimulus-response compatibility effects. *Q. J. Exp. Psychol.* 55A, 567–580.
- Ikkai, A., Curtis, C.E., 2011. Common neural mechanisms supporting working memory, attention and motor intention. *Neuropsychologia* 49, 1428–1434, <http://dx.doi.org/10.1016/j.neuropsychologia.2010.12.020>.
- Jing, H., Pivik, R.T., Dykman, R., 2006. A new scaling method for topographical comparisons of event-related potentials. *J. Neurosci. Methods* 151, 239–249, <http://dx.doi.org/10.1016/j.jneumeth.2005.08.002>.
- Jokisch, D., Jensen, O., 2007. Modulation of gamma and alpha activity during a working memory task engaging the dorsal or ventral stream. *J. Neurosci.* 27, 3244–3251, <http://dx.doi.org/10.1523/JNEUROSCI.5399-06.2007>.
- Kastner, S., Pinsk, M., De Weerd, P., Desimone, R., Ungerleider, L., 1999. Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron* 22, 751–761.
- Kiyonaga, A., Egner, T., 2013. Working memory as internal attention: toward an integrative account of internal and external selection processes. *Psychon. Bull. Rev.* 20, 228–242, <http://dx.doi.org/10.3758/s13423-012-0359-y>.
- Klaver, P., Talsma, D., 2013. Behind the scenes: how visual memory load biases selective attention during processing of visual streams. *Psychophysiology* 50, 1133–1146, <http://dx.doi.org/10.1111/psyp.12126>.
- Klimesch, W., Fellinger, R., Freunberger, R., 2011. Alpha oscillations and early stages of visual encoding. *Front. Psychol.* 2, 118, <http://dx.doi.org/10.3389/fpsyg.2011.00118>.
- Kuo, B.C., Rao, A., Lepsien, J., Nobre, A.C., 2009. Searching for targets within the spatial layout of visual short-term memory. *J. Neurosci.* 29, 8032–8038, <http://dx.doi.org/10.1523/JNEUROSCI.0952-09.2009>.
- LaRocque, J.J., Lewis-Peacock, J.A., Postle, B.R., 2014. Multiple neural states of representation in short-term memory? It's a matter of attention. *Front. Hum. Neurosci.* 8, 5, <http://dx.doi.org/10.3389/fnhum.2014.00005>.

- Loetscher, T., Brugger, P., 2007. A disengagement deficit in representational space. *Neuropsychologia* 45, 1299–1304, <http://dx.doi.org/10.1016/j.neuropsychologia.2006.09.020>.
- Lückmann, H.C., Jacobs, H.I.L., Sack, A.T., 2014. The cross-functional role of frontoparietal regions in cognition: internal attention as the overarching mechanism. *Prog. Neurobiol.* 116, 66–86, <http://dx.doi.org/10.1016/j.pneurobio.2014.02.002>.
- McCarthy, G., Wood, C.C., 1985. Scalp distributions of event-related potentials: an ambiguity associated with analysis of variance models. *Electroencephalogr. Clin. Neurophysiol.* 62, 203–208.
- McCullough, A.W., Machizawa, M.G., Vogel, E.K., 2007. Electrophysiological measures of maintaining representations in visual working memory. *Cortex* 43, 77–94.
- McElree, B., 1998. Attended and non-attended states in working memory: accessing categorized structures. *J. Mem. Lang.* 38, 225–252.
- Munneke, J., Heslenfeld, D.J., Theeuwes, J., 2010. Spatial working memory effects in early visual cortex. *Brain Cognit.* 72, 368–377, <http://dx.doi.org/10.1016/j.bandc.2009.11.001>.
- Nee, D.E., Jonides, J., 2009. Common and distinct neural correlates of perceptual and memorial selection. *NeuroImage* 45, 963–975, <http://dx.doi.org/10.1016/j.neuroimage.2009.01.005>.
- Nee, D.E., Jonides, J., 2013. Trisecting representational states in short-term memory. *Front. Hum. Neurosci.* 7, 796, <http://dx.doi.org/10.3389/fnhum.2013.00796>.
- Nobre, A.C., Coull, J.T., Maquet, P., Frith, C.D., Vandenberghe, R., Mesulam, M.M., 2004. Orienting attention to locations in perceptual versus mental representations. *J. Cognit. Neurosci.* 16, 363–373.
- Nobre, A.C., Griffin, I.C., and Rao, A., 2008. Spatial attention can bias search in visual short-term memory. *Front. Hum. Neurosci.*, 1, a4. <http://dx.doi.org/10.3389/neuro.09.004.2007>.
- Oberauer, K., 2002. Access to information in working memory: exploring the focus of attention. *J. Exp. Psychol. Learn. Mem. Cognit.* 28, 411–421, <http://dx.doi.org/10.1037//0278-7393.28.3.411>.
- Oberauer, K., 2013. The focus of attention in working memory—from metaphors to mechanisms. *Front. Hum. Neurosci.* 7, 673, <http://dx.doi.org/10.3389/fnhum.2013.00673>.
- Olivers, C.L., Peters, J., Houtkamp, R., Roelfsema, P.R., 2011. Different states in visual working memory: when it guides attention and when it does not. *Trends Cognit. Sci.* 15, 327–334, <http://dx.doi.org/10.1016/j.tics.2011.05.004>.
- Palermo, L., Piccardi, L., Nori, R., Giusberti, F., Guariglia, C., 2010. Does hemineglect affect visual mental imagery? Imagery deficits in representational and perceptual neglect. *Cognit. Neuropsychol.* 27, 115–133, <http://dx.doi.org/10.1080/02643294.2010.503478>.
- Postle, B.R., Awh, E., Jonides, J., Smith, E.E., D'Esposito, M., 2004. The where and how of attention-based rehearsal in spatial working memory. *Cognit. Brain Res.* 20, 194–205, <http://dx.doi.org/10.1016/j.cogbrainres.2004.02.008>.
- Sauseng, P., Klimesch, W., Heise, K.F., Gruber, W.R., Holz, E., Karim, A.A., Glennon, M., et al., 2009. Brain oscillatory substrates of visual short-term memory capacity. *Curr. Biol.* 19, 1846–1852, <http://dx.doi.org/10.1016/j.cub.2009.08.062>.
- Silk, T.J., Bellgrove, M.A., Wrafter, P., Mattingley, J.B., Cunnington, R., 2010. Spatial working memory and spatial attention rely on common neural processes in the intraparietal sulcus. *NeuroImage* 53, 718–724, <http://dx.doi.org/10.1016/j.neuroimage.2010.06.068>.
- Simon, J.R., 1969. Reactions toward the source of stimulation. *J. Exp. Psychol.* 81, 174–176.
- Simon, J.R., 1990. The effects of an irrelevant directional cue on human information processing. In: Proctor, R.W., Reeve, T.G. (Eds.), *Stimulus-Response Compatibility: An Integrated Perspective*. North Holland, Amsterdam, pp. 31–86.
- Staudigl, T., Hanslmayr, S., 2013. Theta oscillations at encoding mediate the context-dependent nature of human episodic memory. *Curr. Biol.* 23, 1101–1106, <http://dx.doi.org/10.1016/j.cub.2013.04.074>.
- Talsma, D., Wijers, A.A., Klaver, P., Mulder, G., 2001. Working memory shows different degrees of lateralization: evidence from event-related potentials. *Psychophysiology* 38, 425–439.
- Tamber-Rosenau, B.J., Esterman, M., Chiu, Y., Yantis, S., 2011. Cortical mechanisms of cognitive control for shifting attention in vision and working memory. *J. Cognit. Neurosci.* 23, 2905–2919, <http://dx.doi.org/10.1162/jocn.2011.21608>.
- Tanoue, R.T., Jones, K.T., Peterson, D.J., Berryhill, M.E., 2013. Differential frontal involvement in shifts of internal and perceptual attention. *Brain Stimul.* 6, 675–682, <http://dx.doi.org/10.106/j.brs.2012.11.003>.
- Tipples, J., 2002. Eye gaze is not unique: automatic orienting in response to uninformative arrows. *Psychon. Bull. Rev.* 9, 314–318.
- Theeuwes, J., Kramer, A.F., Irwin, D.E., 2011. Attention on our mind: the role of spatial attention in visual working memory. *Acta Psychol.* 137, 248–251, <http://dx.doi.org/10.1016/j.actpsy.2010.06.011>.
- Thut, G., Nietzel, A., Brandt, S.A., Pascual-Leone, A., 2006. Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *J. Neurosci.* 26, 9494–9502, <http://dx.doi.org/10.1523/JNEUROSCI.0875-06.2006>.
- Töllner, T., Conci, M., Rusch, T., Müller, H.J., 2013. Selective manipulation of target identification demands in visual search: the role of stimulus contrast in CDA activations. *J. Vis.* 13, 1–13, <http://dx.doi.org/10.1167/13.3.23>.
- Van der Heijden, A.H.C., 1992. *Selective Attention in Vision*. Routledge, London.
- Van der Heijden, A.H., 1993. The role of position in object selection in vision. *Psychol. Res.* 56, 44–58.
- Van der Heijden, A.H.C., 2004. *Attention in Vision. Perception, Communication, and Action*. Psychology Press, New York, NY.
- Van der Lubbe, R.H.J., Abrahamse, E.L., De Kleine, E., 2012. The premotor theory of attention as an account for the Simon effect. *Acta Psychol.* 140, 25–34, <http://dx.doi.org/10.1016/j.actpsy.2012.01.011>.
- Van der Lubbe, R.H.J., Neggers, S.F.W., Verleger, R., Kenemans, J.L., 2006. Spatiotemporal overlap between brain activation related to saccade preparation and attentional orienting. *Brain Res.* 1072, 133–152, <http://dx.doi.org/10.1016/j.brainres.2005.11.087>.
- Van der Lubbe, R.H.J., Utzerath, C., 2013. Lateralized power spectra of the EEG as an index of visuospatial attention. *Adv. Cognit. Psychol.* 9, 184–201, <http://dx.doi.org/10.5709/acp-0144-7>.
- Van der Lubbe, R.H.J., Woestenburg, J.C., 2000. Location selection in the visual domain. *Psychophysiology* 37, 662–676.
- Waldhauser, G., Johansson, M., Hanslmayr, S., 2012. Brain oscillations indicate inhibition of interfering visual memories. *J. Neurosci.* 32, 1953–1961, <http://dx.doi.org/10.1523/JNEUROSCI.4201-11.2012>.
- Ward, E.J., Chun, M.M., Kuhl, B.A., 2013. Repetition suppression and multi-voxel pattern similarity differentially track implicit and explicit visual memory. *J. Neurosci.* 33, 14749–14757, <http://dx.doi.org/10.1523/JNEUROSCI.4889-12.2013>.
- Wascher, E., Wauschkuhn, B., 1996. The interaction of stimulus- and response-related processes measured by event-related lateralizations of the EEG. *Electroencephalogr. Clin. Neurophysiol.* 99, 149–162.
- Wühr, P., Ansorge, U., 2007. A Simon effect in memory retrieval: evidence for the response-discrimination account. *Psychon. Bull. Rev.* 14, 984–988.