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Top-Down Modulation of Early Visual Processing in V1: Dissociable Neurophysiological Effects of Spatial Attention, Attentional Load and Task-Relevance

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Abstract

Until today, there is an ongoing discussion if attention processes interact with the information processing stream already at the level of the C1, the earliest visual electrophysiological response of the cortex. We used two highly powered experiments (each N = 52) and examined the effects of task relevance, spatial attention, and attentional load on individual C1 amplitudes for the upper or lower visual hemifield. Bayesian models revealed evidence for the absence of load effects but substantial modulations by task-relevance and spatial attention. When the C1-eliciting stimulus was a task-irrelevant, interfering distracter, we observed increased C1 amplitudes for spatially unattended stimuli. For spatially attended stimuli, different effects of task-relevance for the two experiments were found. Follow-up exploratory single-trial analyses revealed that subtle but systematic deviations from the eye-gaze position at stimulus onset between conditions substantially influenced the effects of attention and task relevance on C1 amplitudes, especially for the upper visual field. For the subsequent P1 component, attentional modulations were clearly expressed and remained unaffected by these deviations. Collectively, these results suggest that spatial attention, unlike load or task relevance, can exert dissociable top-down modulatory effects at the C1 and P1 levels.

Key words: attentional load, C1, P1, spatial attention, task-relevance

Introduction

Visual sensory processing is shaped by attention, including early stages following stimulus onset in lower tier visual cortex (Schwartz et al. 2005; Kelly et al. 2008; Rauss et al. 2009). Since information processing is inherently capacity limited, attention allows selecting stimuli or features that are goal-relevant and can thereby be prioritized while suppressing or downplaying irrelevant information. This selectivity of attention enables a parsimonious and efficient allocation of cognitive resources (Broadbent 1958; Posner 1980; Treisman and Gelade 1980; Desimone and Duncan 1995). At the EEG level, the C1 component is the earliest electrophysiological response (~60–90 ms after stimulus onset), firstly described by Jeffreys and Axford (1972). The C1 mainly reflects neural activity from the primary visual cortex, Brodmann area 17 (Di Russo et al. 2002, 2003). This assumption is not only corroborated by its early time-course following stimulus onset and compatible with a feedforward effect taking place in the striate cortex but also by its compelling

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retinotopic properties. C1's amplitude and topography vary as a function of the stimulus position in the visual field, and these variations obey the cruciform model of V1, as convincingly demonstrated by Jeffreys and Axford (1972). Stimuli presented in the upper visual field (UVF) elicit a negative-going potential at posterior parietal sensors along the midline, whereas the exact same stimuli presented in the lower visual field (LVF) elicit a positive potential at the same electrode location instead (Jeffreys and Axford 1972; Clark et al. 1994). Hence, the polarity of the C1 changes depending on the spatial position along the vertical meridian. Of note, there are also functional differences between the upper and lower hemifields reported, showing a higher spatial resolution in the LVF (Skrandies 1987; Carrasco et al. 2001), even though their effects on the C1 ERP component remain unclear. The distinctive electrophysiological properties of the C1 can be related to the anatomical structure and location of V1. Hidden in the calcarine sulcus lying orthogonal to the interhemispheric fissure, the inversion between the external visual field and its representation in V1 leads to the polarity reversal as experienced (Holmes 1945). Recent studies using source-localization modeling methods, including multimodal imaging, reported that extrastriate visual areas could contribute to the generation of the C1 (Ales et al. 2010), but as far as the early phase of the C1 is considered (~50 to 60 ms post-stimulus onset), its main cortical generator is thought to be the primary visual cortex (Foxe and Simpson 2002; Vanni et al. 2004; Hagler et al. 2009; Plomp et al. 2010).

Until today, there is an ongoing debate in the cognitive neuroscience literature about whether top-down attention processes can interact with the information processing stream already at the C1 level or not, and thus, correspondingly, whether this early visual ERP component can be modulated by selective attention or not (see Slotnick 2018a for a recent overview of this debate). A majority of reported studies found no or weak effects of load or spatial attention (e.g., see Gonzalez et al. 1994; Heinze et al. 1994; Clark and Hillyard 1996; Martínez et al. 1999; Noesselt et al. 2002; Di Russo et al. 2003; Fu et al. 2010b; Baumgartner et al. 2018; Alilović et al. 2019), leading to the notion that the C1 response is determined mostly by the physical characteristics of the stimulus (its position, size, and contrast) and remains impermeable to top-down cognitive factors, including attention. In contrast to the initial null findings on C1 modulations by top-down attention, other and more recent studies reported significant C1 modulations by spatial attention (Kelly et al. 2008; Dassanayake et al. 2016), attentional load (Rauss et al. 2009, 2012b; Rossi and Pourtois 2012), or showed C1 attentional modulations only under conditions of high perceptual load (Fu et al. 2009, 2010a). When attention was directed to a task at fixation and peripherally presented C1 stimuli were distracters, increasing attentional load of the task at fixation decreased C1 amplitudes, corresponding to a filtering-out of irrelevant information. In contrast, attentional load increased C1 amplitudes when task-relevant stimuli at fixation and C1 stimuli were presented simultaneously, pointing toward a spill-over effect of load (see Rauss et al. 2011, for a review). More specifically, enhanced neural processing of taskrelevant stimuli under increasing attentional load spilled over to the processing of task-irrelevant distracters presented at the same time, thereby leading to larger C1 responses. This spill-over effect could suggest that task-relevant stimuli are processed in an enhanced manner at the C1 level under conditions of high versus low attentional load. Taken together, whether attention affects the C1 or not, and moreover, if true, in which direction then, are still open questions. The discrepancy between existing studies could partly stem from methodological factors, including study power, substantial variability in the experimental paradigms, and analytical differences such as the specific scoring method adopted for this early visual ERP component (see also Slotnick 2018b).

Furthermore, it appears crucial to disentangle the effects of different attentional factors, such as task relevance, spatial attention, and (attentional) load, even though there is no ERP study to date to the best of our knowledge which has attempted to do so. For example, in several studies on effects of spatial attention on C1 amplitudes, spatial attention effects could not easily be separated from task-relevance, as attended C1 stimuli were always also task-relevant (e.g., Fu et al. 2010b; Baumgartner et al. 2018). However, task relevance of stimuli has been shown to be an important factor in order to observe load by attention interactions with more complex stimuli (e.g., see Acunzo et al. 2019). Further, and as mentioned here above, attentional load effects for task-irrelevant C1 stimuli seem to differ depending on the temporal synchronization with the presentation of taskrelevant stimuli (Rauss et al. 2011). Moreover, it has not been investigated whether load effects interact with task relevance and spatial attention effects devoid of task relevance.

The current study aimed to systematically investigate the contribution of different top-down factors to the C1. We examined the effects of task relevance, spatial attention, and attentional load that were previously reasoned to affect C1 amplitudes. We opted to test for effects of attentional rather than perceptual load to control for perceptual differences between load conditions. Lavie's theory of load (Lavie, 2005) was initially limited to perceptual load and referred to the number of items being processed at the same time. However, perceptual differences between low and high load cause severe problems for ERP research. Attentional load controlled for such perceptual differences and manipulated processing demands, such as the number of operations required to solve a task, while keeping the visual display constant (see also Rauss et al. 2012a; Fu et al. 2012). Increasing attentional or perceptual load leads to a heightened allocation of attentional resources to relevant stimuli and reduced resources for the processing of distracters. In particular, we devised a new within-subject design allowing to separate the contribution of these three attention components and used Bayes Factors to provide evidence in favor of, or against, C1 modulations by them. Across conditions, we thus systematically manipulated attention allocated to the C1 eliciting stimulus, being either task-relevant and spatially attended, task-irrelevant but spatially attended, and lastly, neither task-relevant nor spatially attended. We had either a perceptually easy or difficult task to perform for all three levels, corresponding to low and high attentional load, respectively. Based on recent recommendations (Slotnick 2018b), we individualized C1 measurements. In the preregistered (https://osf.io/mwq8s) Experiment 1, we used a large sample size (N = 52) and examined C1 modulations by top-down attention when the C1-eliciting stimulus was shown in the upper visual field throughout. In Experiment 2, we collected EEG data from an equally large, independent sample (N = 52) in a different laboratory, but used LVF presentations of the C1-eliciting stimulus instead. This, in turn, enabled us to assess whether possible differences between the upper and LVF could be found for attentional effects at the C1 level. Given that some advantages have been reported for the lower compared to upper visual field regarding contrast sensitivity and spatial resolution (see Karim and Kojima 2010), we could assess whether effects of spatial attention, attentional load and task-relevance on the C1 could differ between these two hemifields.

Moreover, although our focus was on the C1 component, we also analyzed attentional modulations of the subsequent P1 component, given that several previous ERP studies have reported significant effects of attention for this extrastriate visual component in the past (see Rauss et al. 2011 for a review). Finally, we also carried out several control analyses for both experiments to assess if the effects of attention on the C1 could be influenced by small but systematic deviations of the eye position across conditions.

Experiment 1—Muenster Sample (N = 52)

Methods

Participants

We examined a preregistered sample of 52 participants. In total, 57 participants were recruited through the weekly newsletter of the General Students' Committee of the University of Muenster. They gave written informed consent and received 10 Euros per hour for participation. Five participants were excluded due to preregistered exclusion criteria (three due to excessive artifacts, one due to an incorrect sampling rate, and one did not show a clear C1 response), leading to a final sample size of N = 52 (42 female, 10 male; M _{age} = 22.37, SD _{age} = 2.58). All participants had normal or corrected-to-normal vision, were right-handed, and had no reported history of neurological or psychiatric disorders. The study was granted ethics approval by the local ethics committee at University of Münster (2019-049-f-S).

Stimuli

The display always consisted of three elements: C1 stimuli in the upper visual field, one motion random dot kinematogram (RDK; e.g., Kelly and O'Connell 2013) in the upper visual field and another RDK in the LVF (see details below). There were three conditions, each of which required target detection in one of these elements, having two load levels each. C1 stimuli consisted of oriented white line elements (RGB: 1, 1, 1) with a length of about 2 degree of visual angle (deg) and a width of 0.08 deg on a black background, arranged in a regular grid (4 rows, 12 columns) subtending 24 \times 8 deg. All line elements were either oriented at 45° or 135° (alternating between successive grid presentations). The center of the grid was positioned 5 deg above the display center. The RDK stimuli each had a rectangular aperture with a width of 24 deg and a height of 8 deg and consisted of about 500 green dots (radius = 0.04 deg). The centers of the RDKs were 5 deg above and below the display center, respectively. Each dot moved for a lifetime of 0.5 s in a straight line at a speed of about 70 pixels per second in a randomized direction before fading out within 0.1 s. Whenever a dot disappeared, a new dot faded in at a random location within the aperture and moved in a newly randomized direction. The first dots' lifetime in an RDK was a random duration (max=0.5 s). Target stimuli for the motion stimuli consisted of a subset of these 500 dots changing their color from green (RGB: 0, 0.5, 0) to pink (RGB low load: 1, 0, 0.7; RGB high load: 0.4, 0.2, 0.2) within a circular region (radius of 2 deg) at a random location within the rectangular aperture. All regions were equally likely to be selected as a target region. After four participants, the difficulty of the high load condition was reduced by changing the color to a lighter pink (RGB: 0.6, 0.3, 0.5). For the C1 stimulus, target stimuli were the same line stimuli with one randomly selected line slightly or severely tilted

clockwise (low load: 45 deg; high load: 10 deg). All lines were equally likely to be selected as target line.

Procedure

Participants responded to a demographic questionnaire and were prepared for the EEG experiment. Before this, they were instructed to avoid eye movements and blinks during the stimulus presentation. Participants could take breaks between blocks and were told that they could pause the stimulus presentation within blocks by closing their eyes or looking away from fixation. Participants were required to focus on a fixation circle that was presented constantly in the display center. In all blocks, RDK stimuli were positioned in the upper and lower visual display field. C1 stimuli were always presented in the upper visual field (see a schematic example display in Fig. 1).

We implemented three attention tasks with two load levels each. Participants had to attend covertly to the C1 stimulus in one attention task, requiring them to detect whenever one bar orientation was tilted, being low in attentional load difficulty in one condition or high in the other condition (see Fig. 1b). In the second attention task, participants needed to attend to RDK stimuli in the upper visual field, either with low or high difficulty. Here, participants had to detect a color change, being low in difficulty in one condition but high in the other condition (see Fig. 1b). Finally, in the third attention task, participants had to attend to the RDK stimuli LVF and respond to a color change, being low in difficulty in one condition but high in the other condition (see Fig. 1b). Participants were instructed to press the space bar on a keyboard whenever they detected a target. Hits were defined as a button press occurring within 1000 ms after target onset. Prior to every block, participants were informed about the task to perform and the actual difficulty level they would encounter during it throughout. They were told that targets would only appear in the attended feature, i.e., a tilted bar in C1 stimuli, color change in upper RDK, or color change in lower RDK. During the task, they were continuously informed about misses, as well hits and false alarms.

Each of the six conditions (attention to the C1 stimulus, upper RDK or lower RDK with either high or low attentional load) was divided into three blocks of 200 C1 stimuli each. Participants were familiarized with the three attention tasks subsequently, starting with either high or low attentional load for each task, before starting with their first task. Task and difficulty order were counterbalanced across participants, resulting in 12 different versions. In each block, 200 C1 stimuli were presented. Each C1 stimulus was presented for 50 ms, followed by an interstimulus interval with a randomized duration between 500 and 700 ms. Thus, for each of the six conditions, 600 stimuli were presented, leading to a total of 3600 trials. Trial numbers were chosen based on piloting the signal-to-noise ratio for measuring the C1 amplitude (see Section 1 of the Supplementary Materials). Since we focused on genuine attentional effects (attentional load, spatial attention, and task-relevance), all trials followed by a response or a target were excluded from ERP analyses. A pseudorandomized number of between three and five targets appeared at pseudorandomized points in time within each block. We pseudorandomized the target occurrence by repeating the random distribution of between three and five targets across 200 trials per block until the average number of targets per condition was identical, the minimal distance between each pair of targets was more than five trials, and no target was presented within the first 10 or last 10 trials of the block. The



Figure 1. Example of the visual display. a) During this block, covert attention had to be directed to the RDK in the lower visual field. A C1 stimulus appeared for 50 ms there, followed by an ITI of 500–700 ms. After the ITI, at the moment of a new C1 stimulus onset, at a random location, a subset of the dots turned from green to pink (low load condition). Central fixation was required throughout and had to be anchored on the white circle shown below the peripheral C1 stimulus. b) All three attention tasks and respective easy and difficult targets are displayed. Please note that stimulus proportions were increased and adapted to enhance visibility.

onset of the target stimulus always coincided with the onset of a C1 stimulus. Gaze position was examined online with an eye tracker (EyeLink 1000, SR Research Ltd, Mississauga, Canada), stopping the presentation instantly whenever the center was not fixated (tolerance radius: 3 deg in any direction). After 5 s of missing fixation, the block was automatically interrupted and a recalibration was initiated.

EEG Recording and Preprocessing

EEG signals were recorded from 64 BioSemi active electrodes using BioSemi Actiview software (www.biosemi.com). Four additional electrodes measured horizontal and vertical eyemovement. These were used only for the eye-movement correction control analyses (see paragraph Control Analyses below) and not for the correction of eye-related artifacts. Recording sampling rate was 1024 Hz. Offline data were rereferenced to average reference, high-pass filtered at 0.01 Hz (6 dB/oct) and low-pass filtered at 40 Hz (24 dB/oct). Eyemovement artifacts were corrected using the automatic eyeartifact correction method implemented in BESA (Ille et al. 2002). Here, a predefined source model was applied to the data, combining three topographies accounting for EOG activities, consisting of horizontal and vertical eye-movement and blinks (HEOG, VEOG, blink) with 12 regional sources modeling the different brain regions. The adaptive artifact correction method then performed a principal component analysis (PCA) for segments in which the correlation between data and artifact topography exceeded the HEOG (150 μ V) or VEOG (250 μ V) thresholds. All PCA components explaining more than the minimum variance were maintained and then recorded data were decomposed using all topographies into a linear combination of brain and artifact activities (Ille et al. 2002). The remaining artifacts were rejected based on an absolute threshold (<120 μ V), signal gradient (<75 μ V/ ∂ T), and low signal (i.e., the SD of the gradient, $> 0.01 \,\mu$ V/ ∂ T). Noisy EEG sensors were interpolated using a spline interpolation procedure. Filtered data were segmented from 200 ms before stimulus onset until 400 ms after stimulus presentation. Baseline-correction used the 200 ms interval before stimulus onset. On average, 2.19 electrodes were interpolated (Min = 0, Max = 6; SD = 1.69) and 537.96 trials (SD = 48.32) per condition (C1 task easy: Min = 384, Max = 589; C1 task hard: Min = 388, Max = 590; upper RDK task easy: Min = 194, Max = 600; upper RDK task hard: Min = 383, Max = 589; lower RDK task easy: Min = 328, Max = 591; lower RDK task hard: Min = 191, Max = 585) were kept after the trial rejection procedure. For mean trial numbers, a 3 \times 2 repeated measures analysis of variance (ANOVA) showed no differences in the amount of kept trials between the three tasks $(F_{(1.47,74.98)}=2.03,\,P=0.151,$ ηp^2 = 0.038), two load levels (F_(1,51) = 2.39, P = 0.128, ηp^2 = 0.045), and no interaction ($F_{(2,102)} = 0.93$, P = 0.397, $\eta p^2 = 0.018$).

Data Analyses

Behavioral data and EEG data were analyzed with JASP (www.ja sp.org/). For all Bayesian analyses, we specified the null hypothesis as a point-null prior (i.e., standardized effect size $\delta = 0$) and defined the alternative hypothesis as a Jeffreys–Zellner–Siow (JZS) prior, i.e., a folded Cauchy distribution centered around $\delta = 0$ with the scaling factor r = 0.707. This scaling factor assumes a rough normal distribution. To assign verbal labels to the strength of evidence, we followed the taxonomy suggested by Jeffreys (1961), labeling Bayes Factors with a BF₁₀ of below 1 as no evidence, BF₁₀ between 1 and 3 as anecdotal evidence, 3–10 as moderate evidence, and larger BFs as extreme evidence in favor of the alternative hypothesis. Please note, for completeness, we also included Frequentist analyses for all data in Section 2 of the Supplementary Material.

Based on Slotnick's (2018b) suggestions to maximize sensitivity to C1 attention effects, we implemented an individualized



Figure 2. Behavioral results for Experiment 1. For hit rates, data from 49 participants were used. For reaction times, the number of participants differed between conditions (C1 task: easy n = 47, hard n = 22; upper RDK: easy n = 35, hard n = 18; lower RDK: easy n = 47, hard n = 44). White dots represent the median, horizontal lines show the mean. The vertical gray lines reach from upper to lower quartile. Each dot shows the mean reaction time or hit rate from one participant in the specified condition, respectively.

approach to measure C1 amplitudes. More specifically, we semiautomatically identified the single best electrode and individual peak time point for each participant by collapsing across all conditions and detecting the parieto-occipital electrode (CP1, CP2, CP2, P1, P2, P2, PO3, PO2, or PO4) with the maximal negative deflection (amplitude in microvolt) between 40 and 70 ms post-stimulus. We then averaged over a window of ± 10 ms around the peak. Please note that by inspecting the electrode and time point depicting the maximal C1 amplitude for every participant, this approach did not inform about any differential C1 effects. Exploratory analyses also included the subsequent P1 component (see section Control Analyses), which was identified over lateral sensors (PO7, P7, P9, P5, PO8, P8, P10, P6) between 100 and 120 ms for Experiment 1 (see also Section 3 of the Supplementary Material).

All behavioral and ERP data were submitted to a three (attention task: C1 stimuli spatially attended and task-relevant, C1 stimuli spatially attended and task-irrelevant, C1 stimuli spatially unattended and task-irrelevant) by two (attentional load: high vs. low) Bayesian repeated-measures ANOVA. Following the pre-registration (see https://osf.io/mwq8s), we then performed two separate Bayesian repeated measures ANOVAs, testing specifically 1) for spatially attended C1 stimuli, if task relevance increased C1 amplitudes (C1 task-relevant vs. taskirrelevant; spatial attention always to the upper visual field), and if attentional load modulated C1 amplitudes differently across tasks. Secondly, we tested 2) for task-irrelevant C1 stimuli, if spatial attention increased C1 amplitudes (spatial attention to the upper or LVF, C1 stimuli always task-irrelevant), and if attentional load modulated C1 amplitudes differently across spatially attended or unattended C1 stimuli.

Results

Behavior

Mean reaction times for the different conditions were not compared at the statistical level as most participants did not have hits in all conditions (see Fig. 2). For accuracy, Bayesian repeatedmeasures ANOVA models showed that the interaction between task and attentional load difficulty explained the data best (see Table 1, Fig. 2). Post hoc Bayesian paired t-tests showed that high load conditions (M = 0.20, SD = 0.13) led to lower hit rates than low load conditions (M = 0.53, SD = 0.21, BF₁₀ = 1.278e+12). The upper RDK task (M = 0.18, SD = 0.17) led to lower hit rates than the C1 task (M = 0.34, SD = 0.17, BF₁₀ = 3169), which in turn elicited lower hit rates than the lower RDK task (M = 0.58, SD = 0.27, BF₁₀ = 12906). Load differences were larger in the C1 task (M diff = 0.26) compared to both the upper RDK (M diff = 0.28, SD = 0.29, BF₁₀ = 312.732) and the lower RDK task (M diff = 0.20, SD = 0.27, BF₁₀ = 2.472e+6).

C1 Amplitudes

The omnibus 3*2 Bayesian repeated-measures ANOVA showed that the winning model contained only the factor attention task (see Table 2). Notably, when we turned to the preregistered effects of task relevance and spatial attention (tested using two Bayesian repeated-measures ANOVAs; see Table 2), the winning models included only task relevance and only spatial attention as a factor, respectively, while load did not further explain C1 amplitude variations (see Table 2, Fig. 3c). For task relevance, Bayesian paired t-tests showed moderate evidence for more negative C1 amplitudes when the stimuli were task-relevant (M = -1.44μ V, SD = 0.90 μ V) compared to taskirrelevant (M = -1.26μ V, SD = 0.73μ V, BF₋₀ = 3.476, see Fig. 3a). For spatial attention, paired t-tests showed strong evidence against increased C1 amplitudes when spatially attended (M = -1.26μ V, SD = 0.73μ V) compared to spatially unattended (M = $-1.41 \ \mu\text{V}$, SD = $0.73 \ \mu\text{V}$, BF $_{-0}$ = 0.044, BF $_{0-}$ = 22.592, see Fig. 3b). Unexpectedly, C1 amplitudes were larger when spatially unattended (see Fig. 3b).

Experiment 2—Ghent sample (N = 52) Methods

Participants

In total, 54 participants were recruited via Facebook and a database of volunteers for scientific studies provided by Ghent University. For their participation, they were reimbursed with a fixed amount of $30\in$. Two participants were excluded

3.872e-43

error %

3.220

3.599 1.994

1 714

Table 1 Results of Dayesian Repeated Measures Accounts Fredering Accuracy for Experiment 1								
Models	P(M)	P(M data)	BF _M	BF ₁₀				
AT + Load + AT * Load	0.200	1.000	9101.040	1.000				
Attention Task + Load	0.200	4.393e-4	0.002	4.395e-4				
Load	0.200	8.044e-27	3.218e-26	8.048e-27				
Attention Task	0.200	1 1386-27	4 550e-27	1 138e - 27				

3 870e-43

Table 1 Results of Bayesian Repeated Measures ANOVAs Predicting Accuracy for Experiment 1

0.200

Null model (incl. subject)

Note. All models include subject as factor. All models are compared against the best-fitting model listed in the first row, with BF_{10} quantifying evidence against the best model. How much of the data a model explains is listed in P(M|data). The change from prior to posterior odds is indicated in BF_M . Models with at least moderate evidence are highlighted in bold font. AT = Attention Task.

1 548e-42

Table 2 Results of Bayesian Repeated Measures ANOVAs Predicting C1 Amplitudes by Spatial Attention, Task relevance, and Load for Experiment 1

Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
3×2 (All Attention Tasks and Load	1)				
Attention task	0.200	0.831	19.707	1.000	
AT + Load	0.200	0.103	0.460	0.124	1.979
Null model (incl. subject)	0.200	0.051	0.213	0.061	0.622
AT + Load + AT * Load	0.200	0.009	0.036	0.011	1.726
Load	0.200	0.006	0.025	0.007	1.372
2 $ imes$ 2 (Task Relevance and Load)					
Task relevance	0.200	0.809	16.982	1.000	
TR + Load	0.200	0.130	0.599	0.161	1.869
TR + Load + TR * Load	0.200	0.031	0.127	0.038	2.723
Null model (incl. subject)	0.200	0.026	0.105	0.032	1.050
Load	0.200	0.004	0.017	0.005	2.132
2×2 (Spatial Attention and Load)					
Spatial Attention	0.200	0.802	16.194	1.000	
SA + Load	0.200	0.147	0.691	0.184	5.590
SA + Load + SA * Load	0.200	0.030	0.125	0.038	4.413
Null model (incl. subject)	0.200	0.017	0.071	0.022	3.369
Load	0.200	0.003	0.012	0.004	3.638

Note. All models include subject as factor. All models are compared against the best-fitting model listed in the first row, with BF_{10} quantifying evidence against the best model. How much of the data a model explains is listed in P(M|data). The change from prior to posterior odds is indicated in BF_M . Models with at least moderate evidence are highlighted in bold font. AT = Attention task, SA = Spatial Attention, TR = Task relevance.

because they did not show a clear C1 response, leaving a final sample of N =52 (42 female, 10 male; M $_{age}$ =22.08, SD $_{age}$ =4.18). All participants gave written informed consent, had normal or corrected-to-normal vision, were right-handed, and reported no history of neurological or psychiatric disorders.

Stimuli

In comparison to Experiment 1, only the position of the C1 stimuli was changed. RDKs were still presented in the upper and lower VF, but C1 stimuli were presented in the lower instead of the upper visual field. The center of the line grid was positioned 5 deg below the display center. All other aspects were kept the same.

Procedure

We maintained all procedures described in Experiment 1, except for the following changes. Participants read an English translation of the instructions on the screen and, if necessary, verbally received additional information in English or Flemish. Participants were seated in a dimly lit, and, in contrast to recordings in Experiment 1, electrically shielded chamber. Participants positioned their heads on a chin rest with a viewing distance of 63 cm from a 19" CRT monitor (resolution: 1600 \times 1200 pixels). During all tasks, one RDK was presented in each upper and LVF, C1 stimuli appeared in the LVF, and a fixation point was presented in the middle of the screen. Again, there were three attention tasks (attention to C1 stimuli, upper RDK, or lower RDK) with two difficulty levels, similarly to Experiment 1. Due to technical issues, we included six blocks of 100 stimuli for each of the six task and load conditions in counterbalanced order across participants instead of three blocks of 200 stimuli, resulting again in 600 stimuli per condition. In each of these shorter blocks, there was a pseudorandomized number of between one and three targets appearing at pseudorandomized points in time so that the average number of targets per condition stayed the same. Gaze position was monitored online with an eye-tracking system (Eyelink 1000; SR Research Ltd). Three subjects participated without eye-tracker.

EEG Recording and Preprocessing

Procedures were the same used in Experiment 1. On average, 0.79 electrodes were interpolated (SD = 1.14), and 554.95 trials



Figure 3. C1 results in Experiment 1 for (a) task relevance, (b) spatial attention, and (c) attentional load. Scalp topographies depict the differences between task relevance, spatial attention, and attentional load conditions. Please note, C1 time windows were quantified per participant, and time windows for scalp differences represent an approximation. ERP waveforms below show the time course for individualized C1 sensors. Bar plots, error bars show 95% confidence intervals, and lines connect individual data points. Respective difference plots contain 95% bootstrap confidence intervals of intra-individual differences.

(SD = 56.74) per condition (C1 task easy: Min = 348, Max = 600; C1 task hard Min = 309, Max = 600; upper RDK task easy: Min = 380, Max = 600; upper RDK task hard: Min = 372, Max = 600; lower RDK task easy: Min = 374, Max = 600; lower RDK task hard: Min = 373, Max = 600) were kept after the trial rejection procedure. A 3 × 2 repeated measures ANOVA showed no differences in the quantity of kept trials between the three tasks ($F_{(2,102)} = 2.64$, P = 0.076, $\eta p^2 = 0.050$), two load levels ($F_{(1,51)} < 0.01$, P = 0.988, $\eta p^2 < 0.01$), and no interaction effect ($F_{(2,102)} = 0.213$, P = 0.809, $\eta p^2 < 0.01$).

Data Analyses

Data analyses were similar to Experiment 1, with the only difference in the C1 identification approach that we identified the most positive deflection in the C1 time range since stimuli presented in the LVF exhibit a positive C1 amplitude deflection at parieto-occipital electrodes. Exploratory analyses on the subsequent P1 used the same sensors as in Experiment 1 (see section Control Analyses below), but the P1 was identified between 110 and 130 ms (for details, see Section 3 of the Supplementary Material).

Results

Behavior

Mean reaction times were not statistically compared across conditions (see Fig. 4). For accuracy, a Bayesian repeated-measures ANOVA showed that the best model included task, load, and the interaction term (see Table 3, Fig. 4). High load conditions (M = 0.10, SD = 0.08) led to lower hit rates than low load conditions (M = 0.47, SD = 0.15, $BF_{10} = 3.115e+22$). Moreover, the lower RDK task (M = 0.12, SD = 0.11) led to lower hit rates than the C1 task (M = 0.32, SD = 0.14, $BF_{10} = 1.181e+8$), which in turn led to lower hit rates than the upper RDK task (M = 0.41, SD = 0.21, $BF_{10} = 3.62$). Load differences were smaller in the lower RDK task ($M_{diff} = 0.47$, SD = 0.22, $BF_{10} = 2.861e+7$) and C1 task ($M_{diff} = 0.46$, SD = 0.24, $BF_{10} = 33 306$). There was moderate evidence against varying load differences in the upper RDK and C1 tasks ($BF_{01} = 6.25$).



Figure 4. Behavioral results for Experiment 2. For hit rates, data from all 52 participants were used. For reaction times, the number of participants differed between conditions (C1 task: easy n = 52, hard n = 29; lower RDK: easy n = 39, hard n = 9; upper RDK: easy n = 50, hard n = 36). White dots represent the median, horizontal lines show the mean. The vertical gray lines reach from upper to lower quartile. Each dot shows the mean reaction time or hit rate from one participant in the specified condition, respectively.

Table 3 Results of Bayesian Repeated Measures ANOVAs for Accuracy for Experiment 2

Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
AT + Load + AT * Load	0.200	1.000	1.909e+7	1.000	
Attention Task + Load	0.200	2.095e-7	8.382e-7	2.095e-7	2.538
Load	0.200	3.902e-28	1.561e-27	3.902e-28	2.458
Attention Task	0.200	4.525e-50	1.810e-49	4.525e-50	2.547
Null model (incl. subject)	0.200	1.029e-60	4.116e-60	1.029e-60	2.303

Note. All models include subject as factor. All models are compared against the best-fitting model listed in the first row, with BF₁₀ quantifying evidence against the best model. How much of the data a model explains is listed in P(M|data). The change from prior to posterior odds is indicated in BF_M. Models with at least moderate evidence are highlighted in bold font. AT = Attention Task.

C1 Amplitudes

The omnibus 3*2 Bayesian repeated-measures ANOVA showed that the winning model contained only the factor attention task (see Table 4), closely following the result found for Experiment 1. When evaluating the preregistered effects, the winning ANOVA models showed strong evidence for the model including only task relevance or only including spatial attention, respectively, but not attentional load (see Table 4, Fig. 5c), again very much in line with the results found for Experiment 1. Bayesian paired t-tests resulted in strong evidence against larger amplitudes in reaction to task-relevant (M = 1.73 μ V, SD = 1.08 μ V) compared to task-irrelevant stimuli (M = 1.86 μ V, SD = 1.08 μ V, BF₊₀ = 0.043, $BF_{0+} = 23.319$; see Fig. 5a) and very strong evidence against larger amplitudes for spatially attended (M = 1.86 μ V, SD = 1.08 μ V) compared to when they were spatially unattended C1 stimuli $(M = 2.35 \ \mu V, SD = 1.28 \ \mu V, BF_{+0} = 0.016, BF_{0+} = 63.168)$. C1 amplitudes were larger when C1 stimuli were spatially unattended and task-irrelevant (see Fig. 5).

Interim Discussion

Our aim was to disentangle the effects of different attentional factors on the C1, especially task relevance and spatial attention, as their possible differential effects were not separated in previous research (e.g., Clark and Hillyard 1996; Kelly et al. 2008; Baumgartner et al. 2018). Concerning the effect of task relevance, in Experiment 1, we found enhanced C1 amplitudes for

task-relevant stimuli, while in Experiment 2, we found decreased C1 amplitudes for task-relevant stimuli. Tentatively, this increase in negativity for task-relevant C1 stimuli observed in both hemifields might be explained by the presence of an overlapping selection negativity (SN) ERP component. Although it is usually observed in later time windows than the C1, the SN can sometimes influence early stages of sensory processing as well, including the C1 (Proverbio et al. 2010). Moreover, functional differences between the two hemifields might account for these conflicting effects of task relevance (Skrandies 1987; Carrasco et al. 2001). The C1 and RDK stimuli overlap increased the general task difficulty when comparing the two RDK tasks (see Figs 2 and 4). Differences in spatial resolution between the hemifields might account for differences in the segregation of C1 and RDK stimuli between hemifields. Alternatively, these might reflect small but systematic eye-gaze shifts (see more details below).

Concerning the effect of spatial attention, in both experiments, larger amplitudes for spatially unattended stimuli were found, which was in contrast to our preregistered prediction. Although discrepant results have been reported in the past, several previous ERP studies consistently found either no effect of spatial attention ("majority view"; e.g., Clark and Hillyard 1996; Di Russo et al. 2003; Baumgartner et al. 2018; Alilović et al. 2019) or enhanced C1 amplitudes for spatially attended stimuli (Proverbio et al. 2007; Kelly et al. 2008; Zani and Proverbio 2009, 2012; but see Mohr et al. 2020). In these previous studies, spatial

Models P(M)		P(M data)	BF _M	BF ₁₀	error %					
3 × 2 (All Attention Tasks and Load)										
Attention task	0.200	0.887	31.470	1.000						
AT + Load	0.200	0.105	0.469	0.118	2.314					
AT + Load + AT * Load	0.200	0.008	0.031	0.009	8.126					
Null model (incl. subject)	0.200	7.666e – 22	3.066e – 21	8.641e – 22	1.873					
Load	0.200	9.450e – 23	3.780e – 22	1.065e – 22	2.244					
2 $ imes$ 2 (Task Relevance and Load)										
Task relevance	0.200	0.824	18.664	1.000						
TR+Load	0.200	0.120	0.544	0.145	7.550					
TR + Load + TR * Load	0.200	0.028	0.116	0.034	6.986					
Null model (incl. subject)	0.200	0.024	0.100	0.030	7.400					
Load	0.200	0.004	0.017	0.005	7.056					
2×2 (Spatial Attention and Load)										
Spatial Attention	0.200	0.849	22.451	1.000						
SA+Load	0.200	0.125	0.569	0.147	1.708					
SA + Load + SA * Load	0.200	0.027	0.109	0.031	5.251					
Null model (incl. subject)	0.200	2.449e – 13	9.798e – 13	2.886e – 13	0.966					
Load	0.200	3.602e - 14	1.441e – 13	4.244e - 14	1.281					

Table 4 Results of Bayesian Repeated Measures ANOVAs Predicting C1 Amplitudes by Spatial Attention, Task Relevance, and Load for Experiment 2

Note. All models include subject as a factor. All models are compared against the best-fitting model listed in the first row, with BF₁₀ quantifying evidence against the best model. How much of the data a model explains is listed in P(M|data). The change from prior to posterior odds is indicated in BF_M. Models with at least moderate evidence are highlighted in bold font. SA = Spatial Attention, TR = Task relevance.

attention effects were examined for stimuli that were always task-relevant, in contrast to our paradigm in which we tested for effects of spatial attention for stimuli that were always taskirrelevant. Reduced C1 amplitudes for spatially attended stimuli in our study could potentially be explained by the suppression of these stimuli, as they were task-irrelevant distracters that spatially overlapped with the task-related ones, and were hence highly interfering distracters (van Moorselaar and Slagter 2020). However, during attention to the task-relevant C1 stimuli, no inhibition of the C1 but rather the suppression of the RDK stimuli was necessary, but also here, C1 amplitudes were decreased, specifically in Experiment 2. Tentatively, predictive coding might explain this unpredicted effect in both experiments, showing larger C1 amplitudes for unattended than attended stimuli (see Kok et al. 2012; see also Yon et al. 2019). According to this framework, spatially attended stimuli could reduce the C1, while when there were unattended, the predicted repetition of stimuli might not decrease to a similar amount (Kok et al. 2012). Alternatively, we could suspect that although eyefixation was enforced, participants slightly but systematically moved their eyes along the vertical meridian when attending either to the upper or LVF. Hence, we could surmise that a slight but systematic shift of the eye position at stimulus onset across conditions could influence the amplitude of the C1, which is highly sensitive to the position and eccentricity of the stimulus in the visual field (Jeffreys and Axford 1972; Clark et al. 1994; Capilla et al. 2016). While participants had to fixate within a margin of 3 deg to enable stimulus presentation, this probably could not prevent small but systematic drifts of the eye position around the fixation between conditions.

Analysis of the eye-tracking data substantiated this reasoning: In Experiment 1, Participants fixated slightly below the fixation point when doing the lower RDK task (M $_y = -0.59$ deg, SD $_y = 0.61$) and fixated slightly above the fixation point when doing the upper RDK task (M $_y = 0.56$ deg, SD $_y = 0.69$, BF₁₀ = 1.449e+8). Similar effects were found in Experiment 2 between the RDK tasks in the LVF (M $_y = -0.33$ deg, SD $_y = 0.74$) compared to the UVF (M $_y = 0.79$ deg, SD $_y = 0.70$, BF₁₀ = 1.222e+9). The correlation of

the individual gaze deviation between the upper and lower RDK task with the corresponding C1 spatial attention effect was positive for both experiments (see Section 4 of the Supplementary Material). To follow up, we performed a control analysis for both experiments. We extracted the eye position at stimulus onset at the single-trial level and corrected the amplitude of the C1 accordingly through a linear regression analysis (see Section 4 and Section 5 of the Supplementary Material). This enabled us to estimate the effects of spatial attention and task relevance on the C1 when we carefully controlled for this shift in the eye position between conditions. For the P1 alike, we assessed whether this factor influenced the effects of spatial attention and task relevance.

Control Analyses

We used a linear regression approach on the single-trial data to correct EEG amplitudes for gaze position effects. To estimate the possible association between C1/P1 ERP amplitudes and gaze positions at the single-trial level, we initially opted for a linear relationship as it is the most simple statistical model. Visual inspection of individual scatterplots (see Supplementary Material) confirmed that this model was mostly valid. First, for each participant, each sample, and each channel, but across all trials, we regressed the vertical position of the gaze at stimulus onset onto the EEG amplitudes. The residuals were then split by conditions, and the average amplitude per condition was added. The resulting ERP was again baseline-corrected using the interval-200 to 0 ms as the baseline. For the single-trial correction of the EEG data with the eye-gaze position, the two data sets needed to be aligned correctly (i.e., EEG and eye-tracking). Missing trials or lack of eye-tracking data led to the exclusion of participants, eventually resulting in 28 (Experiment 1) and 38 participants (Experiment 2).

For Experiment 1, results showed no evidence for the effect of task relevance on C1 amplitudes ($BF_{+0} = 0.135$, $BF_{0+} = 0.336$,



Figure 5. C1 results in Experiment 2 for (a) task relevance, (b) spatial attention, and (c) attentional load. Scalp topographies depict the differences between task relevance, spatial attention, and attentional load conditions. ERP waveforms below show the time course for individualized sensors. Bar plots, error bars show 95% confidence intervals, and lines connect individual data points. Respective difference plots contain 95% bootstrap confidence intervals of intra-individual differences.

see Fig. 6a), with task-irrelevant C1 stimuli (M = -1.29μ V, SD = 0.60 μ V) and task-relevant C1 stimuli (M = -1.35 μ V, SD = 0.75 μ V) eliciting comparable C1 amplitudes. Likewise, when controlling for the eye-gaze, differences between spatially attended and unattended task-irrelevant C1 stimuli disappeared (BF $_{+0}$ =0.684, BF $_{0+}$ =0.099, see Fig. 6a), with no differences between spatially unattended stimuli (M = -1.38μ V, SD =0.66 μ V) and spatially attended stimuli (M = -1.29 μ V, SD = 0.60 μ V). For Experiment 2, the effect of task relevance on C1 amplitudes decreased but remained (BF $_{+0}$ = 0.071, BF $_{0+}$ = 14.168, see Fig. 6b), with task-irrelevant C1 stimuli (M = 2.13 μ V, SD = 1.02 μ V) eliciting larger amplitudes that task-relevant C1 stimuli (M = 2.03 μ V, SD = 0.96 μ V). Differences between spatially attended and unattended task-irrelevant C1 stimuli likewise decreased but remained ($BF_{+0} = 0.039$, $BF_{0+} = 25.909$, see Fig. 6b) with spatially unattended stimuli (M =2.36 μ V, SD =1.16 μ V) leading to larger amplitudes than spatially attended stimuli (M = 2.13 μ V, SD = 1.02 μ V).

For the P1, the Bayesian-repeated measures ANOVAs showed that the winning model only contained the factor attention task (see Table 5). In Experiment 1, differences between spatially attended and unattended stimuli were found

 $(BF_{10} = 13377.152$, see Fig. 7a) with spatially attended stimuli (M = 0.81 μ V, SD = 0.54 μ V) leading to larger amplitudes than spatially unattended stimuli (M = 0.52 μ V, SD = 0.44 μ V). When controlling for the actual eye-gaze position, the effect of attention remained (BF10 = 666.858, see Fig. 7b) with spatially attended stimuli (M = 0.71 μ V, SD = 0.53 μ V), leading to larger P1 amplitudes than spatially unattended stimuli (M = 0.52 μ V, SD = 0.47 μ V). There was no evidence for a difference regarding task relevance regarding uncorrected ($BF_{10} = 0.170$) or corrected data (BF₁₀ = 0.205, see Fig. 7a,b). In Experiment 2, for uncorrected data, differences between spatially attended and unattended stimuli were found (BF10 =928.116, see Fig. 7c) with spatially attended stimuli (M = 0.97 μ V, SD = 0.72 μ V) leading to larger amplitudes than spatially unattended stimuli (M = 0.70 μ V, SD = 0.63 μ V). When controlling for the actual gaze position, the effect of spatial attention remained (BF₁₀ = 2695.767, see Fig. 7d), with spatially attended stimuli (M = 1.03 μ V, SD = 0.76 μ V) leading to larger P1 amplitudes than spatially unattended stimuli (M = 0.82 μ V, SD = 0.71 μ V). Concerning task relevance, there was no evidence for a difference, neither for the uncorrected (BF $_{10}$ =0.233), nor for the corrected data (BF $_{10}$ =0.300, see Fig. 7c,d).



Figure 6. Effects of single-trial eye-gaze correction on C1 effects in (a) Experiment 1, and (b) Experiment 2. ERP waveforms below show the time course for individualized C1 sensors. Bar plots, error bars show 95% confidence intervals, and lines connect individual data points. Respective difference plots contain 95% bootstrap confidence intervals of intra-individual differences.

General Discussion

With this study consisting of two separate experiments, we aimed to disentangle the effects of three top-down attentional factors on the C1 and P1 ERP components, namely spatial attention, task relevance, and attentional load, and test whether the C1 component is, in contrast to the majority view (e.g., see Baumgartner et al. 2018), influenced by specific attention factors or not. At the methodological level, we closely followed the guidelines proposed by Slotnick (2018b) to maximize the likelihood to disclose modulatory effects of selective attention on the

Table 5	Bayesian Rep	peated Measures	ANOVAs for P1	Amplitu	des for I	Uncorrected	l and Eye-ga	aze Corrected	l Data From Bo	th Experiments
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Experiment 1	P(M)	P(M data)	BF _M	BF ₁₀	error %
3×2 (All Attention Tasks and Load	d) Uncorrected Eye-gaze	(N = 52)			
Attention task	0.200	0.866	25.927	1.000	
AT + Load	0.200	0.126	0.576	0.145	4.594
TR + Load + TR * Load	0.200	0.008	0.032	0.009	4.279
Null model (incl. subject)	0.200	4.982e-12	1.993e-11	5.751e-12	3.394
Load	0.200	7.368e-13	2.947e-12	8.504e-13	8.261
3×2 (All Attention Tasks and Load	d) Corrected Eye-gaze (N	I = 28)			
Attention task	0.200	0.843	21.452	1.000	
AT + Load	0.200	0.141	0.655	0.167	1.466
TR + Load + TR * Load	0.200	0.016	0.066	0.019	2.927
Null model (incl. subject)	0.200	1.363e-4	5.452e-4	1.617e-4	0.624
Load	0.200	2.285e-5	9.142e-5	2.712e-5	1.260
Experiment 2	P(M)	P(M data)	BF _M	BF ₁₀	error %
3×2 (All Attention Tasks and Load	d) Uncorrected Eye-gaze	(N = 52)			
Attention task	0.200	0.844	21.594	1.000	
AT + Load	0.200	0.144	0.674	0.171	2.410
TR + Load + TR * Load	0.200	0.012	0.049	0.014	4.059
Null model (incl. subject)	0.200	8.099e-9	3.240e-8	9.599e-9	1.050
Load	0.200	1.470e-9	5.880e-9	1.742e-9	1.491
3×2 (All Attention Tasks and Load	d) Corrected Eye-gaze (N	I = 38)			
Attention task	0.200	0.736	11.127	1.000	
AT + Load	0.200	0.229	1.188	0.311	3.179
TR + Load + TR * Load	0.200	0.035	0.147	0.048	2.180
Null model (incl. subject)	0.200	2.077e-6	8.309e-6	2.824e-6	1.016
Load	0.200	5.618e-7	2.247e-6	7.638e-7	1.504

Note. All models include subject as factor. All models are compared against the best-fitting model listed in the first row, with BF_{10} quantifying evidence against the best model. How much of the data a model explains is listed in P(M|data). The change from prior to posterior odds is indicated in BF_M . Models with at least moderate evidence are highlighted in bold font. AT = Attention task.

C1 ERP component. Our paradigm rendered a C1-eliciting stimulus either both spatially attended and task-relevant, spatially attended but task-irrelevant, or task-irrelevant and spatially unattended, with two levels of attentional load manipulated (low vs. high) for each of these three main conditions. Moreover, given some functional differences reported between the UVF and LVF (Skrandies 1987; Carrasco et al. 2001), we also assessed these three top-down attention effects on the C1 and P1 in each of these two hemifields separately. Lastly, we ran a control analysis to assess the impact of the actual eye-gaze position for effects of attention on the C1 and P1 ERP components. In both experiments (each N = 52), a similar pattern of results emerged, yet with some important differences found between them. Spatial attention substantially influenced both the C1 and P1 components, yet in opposite directions for these two successive ERP components: attended stimuli elicited a lower C1 compared to unattended ones, while the opposite was found for the P1. Concerning task relevance, it increased C1 amplitudes in the upper visual field (Experiment 1), while it decreased them in the LVF (Experiment 2). However, when we controlled for the actual eye-gaze position at the single-trial level, we found that these C1 effects disappeared in the upper visual field (Experiment 1) but not in the LVF (Experiment 2), whereas this correction did not affect the P1. Attentional load neither affected C1 nor P1 amplitudes, both when considering the main effect or interactions with the other factors.

Effects of Spatial Attention

In both experiments alike, we observed that the C1 was larger for unattended than attended stimuli, which was an unexpected result, opposite to the preregistered effect and contradicting earlier ERP studies. Many previous ERP studies reported no difference between spatially attended and unattended stimuli (Clark and Hillyard 1996; Di Russo et al. 2003; Baumgartner et al. 2018; Alilović et al. 2019), while some other studies reported larger amplitudes for spatially attended stimuli (Proverbio et al. 2007; Kelly et al. 2008; Zani and Proverbio 2009, 2012; Mohr et al. 2020), and some observed even reduced C1 amplitudes (Fu et al. 2008). We noted that participants fixated slightly closer to the C1 stimuli when they were spatially attended, reducing their eccentricity and, in turn, the amplitude of the C1. In line with this interpretation, the results of the control analysis showed that this upside-down spatial attention effect for the C1 wholly disappeared (and normalized) when we applied a mathematical correction to the ERP data, whereby the actual position of the eye-gaze along the vertical meridian at the single-trial level was modeled and taken into account to recompute the C1 and P1 amplitudes. The results of the control analysis clearly showed for the two experiments that systematic deviations in the eyegaze position strongly influenced spatial attention effects occurring at the C1 level.

While eye-gaze position strongly influenced spatial attention effects for the C1 in both Experiments, for the LVF stimulation (Experiment 2), evidence remained in favor of decreased C1 amplitudes after correcting for the systematic eye gaze shift between conditions. This result corroborates the assumption that there may be critical functional differences for spatial attention effects between the UVF and LVF (Skrandies 1987; Carrasco et al. 2001). Moreover, the observation that in this hemifield unattended C1-stimuli led to a larger C1 component than attended one might tentatively be explained using a predictive



Figure 7. Uncorrected and single-trial eye-gaze corrected P1 effects in Experiment 1 (a,b) and Experiment 2 (c,d). Scalp topographies depict the differences between task relevance and spatial attention conditions. ERP waveforms below show the time course for individualized P1 sensors. Bar plots, error bars show 95% confidence intervals, and lines connect individual data points. Respective difference plots contain 95% bootstrap confidence intervals of intra-individual differences.

coding framework (Kok et al. 2012; see also Yon et al. 2019) according to which prediction errors are lower or absent when the C1 stimuli were spatially attended. In comparison, the subsequent P1 component was consistently increased by spatial attention (e.g., see Luck and Hillyard 1994; Clark and Hillyard 1996; Luck et al. 2000), and eye-gaze corrections did not alter this effect in both experiments. Thus, our findings for the UVF are compatible with the "majority view" according to which spatial attention influences the P1 but not the preceding C1 component (Clark and Hillyard 1996; Di Russo et al. 2003; Baumgartner et al. 2018; Alilović et al. 2019). However, they also suggest indirectly that in the LVF, this striate component could be influenced by predictive coding, and this effect could precede the normal gain control effect driven by top-down attention at the P1 level. However, caution is needed to interpret this early effect of predictive coding in the LVF since it was not hypothesized a priori and appears to be confined to this hemifield only for currently unclear reasons (see also limitations and outlook below). Alternatively, to provide a more parsimonious interpretation of this intriguing finding, the reduced C1 component for the attended (yet task-irrelevant) stimuli could potentially result from a tight competition for attention selection with the task-relevant ones (i.e., the RDK task; see Desimone and Duncan 1995), which might be reduced artificially for the unattended ones. In this scenario, the shared spatial location (e.g., in the LVF in Experiment 2) between the C1 and RDK stimuli could bias the competition toward the RDK stimuli (which is task-relevant most of the time for the participants) and thereby reduce the C1 component. Instead, when attention was oriented to the UVF, and the C1 stimulus was therefore fully unattended (in the LVF) and not competing in space with the RDK stimulus, this competition decreased and the C1 component thereby increased. Future studies are needed to decide between the predictive coding and the biased competition account.

Effects of Task Relevance

A strength of our study is that the effects of spatial attention could be disentangled from the effects driven by task relevance. Previous ERP studies typically requested participants to respond to C1 stimuli appearing at the spatially attended position and ignore stimuli appearing at another location, conflating the effects of spatial attention with those of task relevance (e.g., Clark and Hillyard 1996; Kelly et al. 2008; Baumgartner et al. 2018). Here, we also assessed whether making the C1-eliciting stimulus task-relevant could gate early sensory processing in V1, at the C1 level, compared to the condition in which attention was allocated to the RDK instead in the same hemifield, hence while controlling carefully for effects of spatial attention. In Experiment 1, we found larger C1 amplitudes in reaction to taskrelevant stimuli in the upper visual field. This result is compatible with earlier animal studies and human imaging studies showing enhanced neural activity for task-related stimuli in V1 (Haenny and Schiller 1988; Roelfsema et al. 1998; Watanabe et al. 1998; Ciaramitaro et al. 2011) as well as reports of modulations of the C1 component by involuntarily directed non-spatial attention or modality-selective task-dependent attention (Zani et al. 1999; Karns and Knight 2009; Zani and Proverbio 2009, 2012, 2018; Proverbio et al. 2010). In Experiment 2, in which the C1-eliciting stimulus was presented in the LVF, the effect for task relevance was opposite compared to Experiment 1, with lower amplitudes for task-relevant C1 stimuli. The presence of an overlapping selection negativity could potentially explain the increase of the C1 observed when the line bars were taskrelevant (Proverbio et al. 2010). Conversely, when we corrected the C1 data according to the actual eye-gaze position at stimulus onset, the effect of task relevance became inconclusive in Experiment 1 and decreased in Experiment 2. This strong influence of gaze-position might appear surprising at first sight, as both taskrelevant and task-irrelevant stimuli were presented in the same hemifield (i.e., UVF for Experiment 1 and LVF for Experiment 2). However, analyses of the eye data (Experiment 1) showed that participants fixated closer to the peripheral C1 stimulus when it was task-relevant, while participants (Experiment 2) fixated closer to the C1 stimulus when they did the RDK task. These opposing variations in the eye position between Experiment 1 and 2 could account for the observed asymmetric effect for the C1 regarding task relevance. Alternatively, the overlap of the C1 and RDK stimuli increased the general task difficulty when comparing the two RDK tasks (see Figs 2 and 4), which had different effects based on reported differences in spatial sensitivity (Skrandies 1987; Carrasco et al. 2001). Of note, given the lack of load effect on the C1 (and P1) in both the UVF and LVF (see below), task difficulty alone seems not sufficient to explain these conflicting effects of task relevance. Task-relevance did not affect the P1 either but affect subsequent components, starting with the N1 and influencing the N2 and P3 as well (e.g., see Fig. 7).

Effects of Attentional Load

According to the load theory of selective attention, the more demanding a task is (i.e., high perceptual or attentional load), the more attentional resources it draws, and the earlier distractor information can be suppressed during visual processing (Lavie and Tsal 1994; Lavie et al. 2004, 2014). However, there is no consensus about where exactly load can interfere with visual information processing (Lavie 2010). Some studies reported decreased C1 amplitudes, interpreted as a reduction of V1 activity, to distracting stimuli shown in the upper visual field under high attentional or perceptual load conditions (Rauss et al. 2009; Rossi and Pourtois 2012), while other ERP studies failed to do so (Fu et al. 2010b; Ding et al. 2014). To our knowledge, no study so far tested for effects of perceptual load on the C1 when the C1-eliciting stimulus was task-relevant. Despite the observation of clear behavioral effects of load in both experiments, we did not find any corresponding ERP effects of perceptual load, however. This result contrasts with Rauss et al. (2009) and Rossi and Pourtois (2012, 2014), where effects of attentional or perceptual load, respectively, on the C1 were reported. Both Rauss et al. (2009) and Rossi and Pourtois (2012) reported decreased C1 responses to peripheral distracters under high load at fixation, while Rauss et al. (2012b) found the opposite effect when presenting distracters and task-relevant stimuli simultaneously. These ERP findings were interpreted as reflecting an early gain control effect in V1 driven by load, in line with previous fMRI studies (Schwartz et al., 2005). However, other studies failed to report modulatory effects of load on the C1 component (Fu et al. 2010b; Ding et al. 2014). Further, perceptual load effects on the P1 appear to be inconsistent and mostly depend on the specific operationalization of load, as well as stimulus timing used (e.g., see Schindler, Bruchmann, et al. 2021; Schindler, Wolf, et al. 2021), whereas larger N1/N170 amplitudes under low load are found more systematically (e.g., see Schindler et al. 2020a; Schindler, Bruchmann, et al. 2021). Our new results are compatible with these latter studies and suggest that irrespective of the hemifield in which the stimulus is shown, attentional load does not influence the C1 and P1 components but affects later stages of stimulus processing, including the N1 (for reported interactions with attention, see Fu et al. 2008), the N2 and P3.

Limitations and Outlook for Future Research

Although load differences at the behavioral level were clearly expressed in both experiments, the tasks turned out to be highly challenging. Presumably, this could be suboptimal to reveal load effects on the C1 or P1. Accordingly, in future studies, it could be beneficial to opt for a more subtle calibration and parametric modulation of load, where different levels could be used and compared to each other (e.g., see Rossi and Pourtois 2014; Schindler et al. 2020; Schindler, Bruchmann, et al. 2021). Further, although we found an intriguing dissociation for effects of spatial attention on the C1 between the UVF and LVF, whether or not this difference can be related to predictive coding (in the LVF), as we suggest, remains currently largely speculative. Future studies are therefore needed to test this assumption more formally, preferably using within-subject experimental designs. Finally, accuracy turned out to be low in the high load condition, which might suggest that participants gave up or did not complete the task. However, this interpretation appears unlikely for several reasons. First, participants alternated between high and low load blocks to avoid fatigue or systematic habituation effects. Second, we warned participants that the high load blocks would be challenging yet doable, and based on their feedback at the end of the experiment, they were motivated and did not feel like it was impossible to do. Third, the reaction time data are not easily compatible with a mere disengagement account. Fourth, load had no effect on C1 or P1 ERP components in neither hemifield, suggesting that visual processing was similar between these two conditions and given that participants performed well above chance level in the low load conditions, it seems unlikely that vigilance substantially dropped in the high load conditions. Nevertheless, it might be beneficial in future studies to use staircase procedures to equate accuracy between low and high load conditions, and this way yields comparisons between them at the ERP level, which are not influenced by this variable.

Conclusions

In summary, we manipulated three factors of top-down attention, namely spatial attention, task relevance, and attentional load, and evaluated their possible modulatory effects on the C1 and P1 components separately for the upper (Experiment 1) and LVF (Experiment 2). Using a large sample size for each experiment, the pre-registration of our hypotheses (Experiment 1), an optimized paradigm suited to disentangle three different top-down attention control effects, continuous eye-tracking, and rigorous statistical testing based on Bayes factors altogether helped to shed new light on the modulation of the C1 and P1 ERP components by these effects. Spatial attention and task relevance effects were found at the C1 level but strongly driven by slight but systematic deviations of the eye position across conditions, providing evidence for the importance of eye movement controls. Our new results speak against an early modulation of the C1 by top-down attention control factors in the UVF, and as such, they contrast with some previous ERP studies that reported such effects (Pourtois 2004; Stolarova et al. 2006; Kelly et al. 2008; Rauss et al. 2009; Dassanayake et al. 2016), while being compatible with more recent ones (Baumgartner et al. 2018; Alilović et al. 2019). In the LVF, we found evidence for decreased C1 amplitudes when the stimuli were spatially attended, which tentatively could be interpreted using a predictive coding account. Spatial attention did influence the subsequent P1 component consistently in both hemifields, which was larger for attended than unattended stimuli, in line with many previous studies (Martínez et al. 1999; Di Russo et al. 2002), while there were no modulatory effects of load and task relevance, both influencing later stages of processing (N1, N2 & P3). Accordingly, one class of top-down control processes, namely spatial attention, consistently increases early sensory

processing in the extrastriate visual cortex (P1) irrespective of where the stimulus is shown in the visual field. In contrast, in the striate cortex (C1), predictive coding effects could take place and precede this P1 gain control effect, yet when stimuli are shown in the LVF selectively.

Supplementary Material

Supplementary material can be found at Cerebral Cortex online.

Data availability statement

All data are available at the Open Science Framework. Due to capacity limitations, data from Experiment 1 can be retrieved at https://doi.org/10.17605/OSF.IO/EU2B7 and data from Experiment 2 at https://doi.org/10.17605/OSF.IO/3GY6K.

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