



Using frequency tagging to quantify attentional deployment in a visual divided attention task

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ABSTRACT

Frequency tagging is an EEG method based on the quantification of the steady state visual evoked potential (SSVEP) elicited from stimuli which flicker with a distinctive frequency. Because the amplitude of the SSVEP is modulated by attention such that attended stimuli elicit higher SSVEP amplitudes than do ignored stimuli, the method has been used to investigate the neural mechanisms of spatial attention. However, up to now it has not been shown whether the amplitude of the SSVEP is sensitive to gradations of attention and there has been debate about whether attention effects on the SSVEP are dependent on the tagging frequency used. We thus compared attention effects on SSVEP across three attention conditions—focused, divided, and ignored—with six different tagging frequencies. Participants performed a visual detection task (respond to the digit 5 embedded in a stream of characters). Two stimulus streams, one to the left and one to the right of fixation, were displayed simultaneously, each with a background grey square whose hue was sine-modulated with one of the six tagging frequencies. At the beginning of each trial a cue indicated whether targets on the left, right, or both sides should be responded to. Accuracy was higher in the focused- than in the divided-attention condition. SSVEP amplitudes were greatest in the focused-attention condition, intermediate in the divided-attention condition, and smallest in the ignored-attention condition. The effect of attention on SSVEP amplitude did not depend on the tagging frequency used. Frequency tagging appears to be a flexible technique for studying attention.

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1. Introduction

Attention allows the selection of relevant objects from a cluttered scene, enhancing the perception or processing of a stimulus or a particular location. The neural mechanisms underlying it have been broadly investigated, with questions ranging from the locus of the control mechanisms for deciding what must be attended (see, e.g., Mehta et al., 2000; O'Connor et al., 2002; Vanduffel et al., 2000; Yingling & Skinner, 1976), to how the cognitive system trades off resources between different events (see, e.g., Desimone & Duncan, 1995; Kastner et al., 1998; Kok, 1997). A number of different techniques have been used to address how and when selectivity is expressed in the brain. For example, electroencephalography (EEG) has been used to show that the amplitude of the visual evoked potential associated with a stimulus is enhanced when the stimulus is presented in an attended rather than in an unattended location (for a review, see, Hillyard & Anillo-Vento, 1998). Similarly, intracellular recordings in monkeys have shown that attended stimuli evoke increased neural synchronization in the gamma frequency range (35–90 Hz, see, e.g., Fries et al., 2001) relative to unattended stimuli, and functional

magnetic resonance imaging (fMRI) in humans has shown enhanced stimulus-evoked activity when participants were attending to a stimulus or spatial location (for a review, see, Yantis & Serences, 2003).

A promising and increasingly popular technique to investigate the neural correlates of selective attention is *frequency tagging*. Frequency tagging is a method based on the steady state visual evoked potential (SSVEP; Regan, 1989) measured using EEG¹. The SSVEP is made up of the physiological responses evoked by series of sensorial stimulations. For example, the sudden appearance of a bright object (e.g., a white square) on a black computer screen evokes a response whose amplitude is highest in the primary visual cortex. If the stimulation is repeated with a fast enough frequency, the EEG trace will display a steady-state response, with the same frequency as the presentation rate of the oscillating objects. While the SSVEP (and its auditory analog, the auditory steady-state response) was originally thought to result from periodic superimposition of early-latency evoked responses (Galambos et al., 1981; Regan, 1989), recent evidence tends to support the hypothesis that the oscillatory response, at least for sufficiently high frequencies (>6 Hz) reflects a separate neural oscillation that is driven by the periodic stimulus (Ross et al., 2005).

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¹ The same technique can be used with magnetoencephalography (MEG).

Besides having frequency characteristics similar to the visual stimulation, the amplitude of the SSVEP is enhanced when attention is directed to the stimulus as compared to when that stimulus is ignored (Muller et al., 1998). This last property constitutes the strength of the frequency tagging technique: Because it is possible to use specific, different tagging frequencies for a number of different spatial locations in a visual display, it is possible to see in the EEG response which locations participants have attended and which they have ignored.

Morgan et al. (1996) and Hillyard et al. (1998) were among the first to demonstrate that SSVEPs could be used to study attention. They induced SSVEPs by presenting two squares that oscillated between black and white with two different frequencies at two different target locations (left and right on a computer screen). Two streams of alphanumeric characters were simultaneously displayed superimposed on the oscillating squares and participants, after having been instructed to attend to either the left or the right stream, emitted a speeded response any time the digit “5” was displayed in the stream that was to be attended. Consistent with the suggestion that the SSVEP is sensitive to the degree of attention deployed, analysis of the electrophysiological data showed that the SSVEP evoked from the attended side had a higher amplitude than the SSVEP evoked from the ignored stream.

In the experiments of Hillyard et al. (1998), attention was “all-or-none”, leaving open the question of whether the SSVEP is sensitive to gradations of attention across spatial locations. It has been shown that SSVEP amplitude is increased at attended versus unattended locations when two locations are to be attended (Muller et al., 2003; see also Malinowski et al., 2007). Muller et al. used four streams of symbols displayed horizontally with two locations to the left and two to the right of fixation, and asked their participants to attend to two of the locations simultaneously. Participants had to attend either the two locations in the left hemifield, the two locations in the right hemifield, or to either the left-most location and the third location from the left or the second location from the left and the right-most location. Participants were to respond whenever the digit 8 appeared simultaneously in both of the to-be-attended locations.

Muller et al. (2003) contrasted the conditions in which two locations in the same hemifield were to be attended with the conditions in which a to-be-ignored location was between the to-be-attended locations to test whether attention could be independently allocated to two locations. They reasoned that when a to-be-ignored location was situated between two to-be-attended locations, the amplitude of the SSVEP to that location would be enhanced if it were not possible to divide attention across two non-contiguous locations. Consistent with a multiple-spotlight hypothesis, no differences in SSVEP amplitude to the unattended locations as a function of location were found. The study of Muller et al. (see also Malinowski et al., 2007) shows that attention can act as multiple spotlights at multiple locations, and that SSVEP reflects this attentional deployment. However, because no comparison was made with a single focus of attention, it is not possible to say whether the amplitude of the SSVEP can be used as an index of the amount of attentional resources allocated to one versus two locations.

Amplitudes of early event-related brain potentials (ERPs, i.e., N1 and P1) have been shown to be linearly related to the amount of attention allocated to two competing items (Mangun & Hillyard, 1990), and that attention effects on early ERP components (in particular the N1 and N2) and those on the SSVEP are positively correlated (Muller & Hillyard, 2000). Here, we test whether the amplitude of the SSVEP is sensitive to attentional allocation by extending the paradigm used by Hillyard et al. – in which participants had to focus on one stream of items presented on an oscillating square while ignoring a second stream – by adding a divided-attention condition in which both streams were to be attended.

In addition to determining whether the SSVEP is sensitive to division of attention, we investigated the influence of different tagging frequencies on the SSVEP. Regan (1989) suggested that the complex pattern of activity related to an unpatterned flickering light may be related to the contributions of different functional subsystems which preferably respond to stimulation frequencies in the low (5–12 Hz), medium (12–25 Hz), or high (30–50 Hz) frequency ranges. The subsystems are sensitive to the physical properties of the stimulation, such as the luminance or color of the flickering. In addition, these subsystems are distinguished by other factors, such as the time between the onset of the flickering and the electrophysiological response associated to it, the topographical distribution of the EEG response to the flicker, and the properties of the fundamental and second harmonic (or frequency-doubled) EEG responses to the flicker suggest that different neural populations contribute to the response to flicker stimulation. Therefore different flicker frequencies may generate different, or affect in a different manner, the SSVEP (see also, Herrmann, 2001).

In spite of documented differences in flicker sensitivity (Herrmann, 2001; Regan, 1989), it appears that the visual system can be entrained by a wide range of frequency tags (Stephen et al., 2006), with the effect of attention generally being an increase in amplitude of the SSVEP. Increases in amplitude of the SSVEP as a function of attention have been reported for a broad range of frequencies and for a broad range of attention tasks (e.g., Hillyard et al., 1997; Morgan et al., 1996, who used 8.6 and 12 Hz; Muller et al., 1998; Muller & Hillyard, 2000, who used 20.8 and 27.8 Hz, Belmonte, 1998, who used 8.9 Hz; Kim et al., 2007, who used 12.50 and 16.67 Hz; Kelly et al., 2006, who used 9.45, 10.63, 14.17, and 17.01 Hz). However, up to now only one study of which we know has studied systematically the dependency of the effects of attention on the tagging frequency used. In this study Ding et al. (2006) induced SSVEPs by simultaneously presenting two circular arrays of disks, one at fovea the other at periphery. The onset and offset of one of the two arrays served as the frequency tag (i.e., the oscillation intended to evoke the SSVEP). On each trial participants were instructed to direct their attention toward the array that was frequency tagged or away from it. Each trial was tagged with one of 15 different frequencies in the range between 2.5 and 20 Hz. The participant's task was to emit a response any time that a triangle appeared within the to-be-attended search array. For nearly all of the tagging frequencies used, Ding et al. found the usual enhancement in SSVEP amplitude in the focused relative to the ignored condition. However, for tagging frequencies within the lower alpha band (8–10 Hz), an increase in SSVEP amplitude to the peripheral array when attention was focused on the foveal array was found. On the basis of this finding Ding et al. concluded that the attention effect on the SSVEP response may depend on the tagging frequency used (Ding et al., 2006), and suggested that different frequencies recruit specific cortical networks. Because the result of Ding et al. of a lack of enhancement of attention on SSVEP amplitude when an attended object was flickering within the lower alpha rhythm range conflicts with the usual findings reported in the literature (i.e., an increase in SSVEP amplitude associated with attended stimuli, see e.g., Morgan et al., 1996; Muller & Hillyard, 2000), we included frequencies in the lower alpha range in our investigation of the effects of frequency on the attention effect on the SSVEP. In total we used six different tagging frequencies (8, 9.5, 10.5, 13, 17, and 23 Hz).

2. Experiment

Participants performed a speeded target-detection task in which a variable number of targets (the digit 5) were embedded among each of two streams of letters presented on sine-modulated monochrome background squares. The two streams were presented simultaneously to the left and right hemifields, with targets appearing asynchronously and equiprobably in either the left or right streams. Attention was cued on a trial-to-trial basis to the left, right, or both streams. Each

background square was “tagged” with one of six different frequencies. In addition to measuring the SSVEP evoked by each of the frequencies, ERPs elicited by targets were measured and the amplitudes of the components associated with effects of attention (P2, N2, and P3) were correlated with the attention effect on the SSVEPs. Response accuracy and reaction time (RT) were also measured.

2.1. Method

2.1.1. Participants

Fourteen healthy individuals (7 males) between the age of 20 and 30 ($mean = 24.3$, $s.d. = 4.9$) volunteered for the experiment and received €18 for their participation. All had normal or corrected-to-normal vision. The study adhered to the Declaration of Helsinki and was approved by the local ethics committee. Informed consent was obtained from all participants.

2.1.2. Stimuli and apparatus

Stimuli were generated with the Matlab Psychtoolbox (Brainard, 1997) and displayed on a monitor with conventional raster graphics (800 × 600 pixels with a 144-Hz refresh rate) and a 17-inch screen. Stimuli were the distractor letters “A” through “K” and “P” and the target number “5”. Two sequences of 60 distractors and targets (presented for 166 ms each for a total stream length of 10 s) were displayed on each trial, one in the left and one in the right visual field, 5.7 degrees lateral to a central fixation point. The stimulus sequences were randomized, with the constraint that repetitions and simultaneous presentation of a given character in the left and right display were not allowed. Characters were drawn in a blue (RGB: 0, 0, 255) Tahoma font, with a font size of 48 (corresponding to a width of 1.4° and a height of 1.9° of visual angle), and were presented serially in the same spatial location at a rate of 6 characters per s, with no interstimulus interval. In each sequence, the distractor letters A through K were each presented 5 times. Targets were not displayed in the first or last 500 ms of the stream presentation and were displayed with a minimum inter-target interval of 1 s in order to minimize the chances of overlap between target-related ERP components. Note that the inter-target interval applied across streams such that targets were never present in both streams at the same time. In the *focused-attention conditions* (attend left or attend right) 2, 3, or 4 targets were displayed on each side (for a total of 4, 6, or 8 targets). In the *divided-attention condition* (attend to both sides and respond to targets on both sides) 2, 3, 4, 6, or 8 targets were displayed on each trial. For the purposes of analysis, the unattended stream of the focused-attention condition is referred to as the *ignored-attention condition*. In order to equate stream length across trials, the letter “P:” was added to the stream in place of a target as necessary. With the exception of the three-target condition (in which two targets appeared on one side), potential targets were equally divided between the two sides of presentation.

An SSVEP for frequency tagging was induced by presenting a oscillating square (9.46° of visual field) centered at the location of each alphanumeric stream. The hue of each square oscillated sinusoidally from black (RGB: 0, 0, 0) to white (RGB: 255, 255, 255) with tagging frequencies of 8 and 9.5, 10.5 and 13, or 17 and 23 Hz for the left and right squares, respectively. Tagging frequencies were always presented in the abovementioned pairs²; side of presentation of the frequencies was factorially combined with attention condition and number of targets displayed. Three tagging frequencies (8, 9.5, and 10.5) were chosen in the alpha range and the other frequencies were

chosen so as not to include harmonics of these three frequencies while covering a relatively broad range of frequencies. The blue hue of the target-distractor streams was sine-modulated (from RGB: 0, 0, 0; to 0, 0, 255) with the same oscillation frequency (and phase) of the background square. In contrast with previous studies (e.g., Morgan et al., 1996; Muller et al., 2003; Malinowski et al., 2007) we chose to modulate the contrast of the stimulus stream in keeping with the modulation of the background square. This was done primarily to minimize the impact of the 6-Hz stimulus presentation rate on the perception of the background square.

2.1.3. Procedure

Participants were first instructed how to direct their attention to the left or to the right side without moving their eyes. Participants accommodated their chin on a chin rest at a distance of 60 cm from the display monitor. To minimize saccades or eye movements toward the attended side, participants were familiarized with the influence of eye movements and eye blinks on an on-line EEG recording. During this familiarization session, participants systematically moved their eyes from 1 to 10 degrees from center in 10 increasing steps, and from 10 to 1 degrees in 10 decreasing steps. After each movement the experimenter pointed out the changes in the electrooculogram (EOG) trace to the participants. Eye movements were monitored for the duration of the experiment using the EOG channels. Before the experimental trials commenced, each participant practiced the task in the focused-attention condition until a response accuracy criterion of 80% was reached (on average, 15 trials were sufficient to reach the criterion). During the practice session participants received feedback on their performance. A trial started with the presentation for 1 s of one or two red (RGB: 127, 0, 0) “arrows” (“<”, “>”, or “<>”) which indicated how attention should be directed (to the left, right, or both sides, respectively). After a 250-ms blank interval, and 750 ms before the presentation of the letter streams, a red fixation cross appeared in the center of the screen and remained on display for the duration of the trial (10 s). Participants were to direct their attention as indicated by the cue and to press any key on the computer keyboard whenever they detected the number “5” on an attended side. Participants were not informed as to the number of targets that would be displayed on each trial. After the presentation of the two sequences of alphanumeric characters, the red fixation cross remained in view for 1 s, after which the trial ended. No feedback regarding performance was given. Each trial was self paced. For each combination of number of targets in each attentional condition (2, 3, or 4 in the focus left condition, 2, 3, or 4 focus right condition, 2, 3, 4, 6 or 8 in the divided-attention condition) and tagging frequency (8, 9.5, 10.5, 13, 17 or 23), 3 trials were presented, resulting in 54 trials each for the focused-left- and focused-right- (and ignored-left- and ignore-right-) attention conditions and 90 trials for the divided-attention condition (198 trials in total). The entire experiment lasted approximately 1.5 h.

2.1.4. EEG recording

The EEG was recorded using an electro-cap with 64 tin electrodes (Electro-cap International Inc., Eaton, Ohio, USA). All scalp positions in the International 10–20 System were used, with additional sites located midway between the 10 and 20 locations (Sharbrough et al., 1991) and six electrode positions 10% inferior to the standard parieto-occipital electrodes (FT9, PO9, O9, FT10, PO10, O10). The amplifier was a REFA 8–72 (Twente Medical Systems, Enschede, The Netherlands). Brain electrical activity was amplified 20,000 times with a digital low-pass filter with a cutoff frequency of 135 Hz. Data were digitized to 22-bit accuracy at a rate of 500 Hz and stored on a hard disk for subsequent off-line analysis. Electrophysiological inputs were configured as a reference amplifier: all channels were amplified against the average of all connected inputs. Two electrodes were connected to the mastoids, the average of which served as an off-line reference for the EEG signal. An electrode on the sternum was used

² A pilot study ($N = 6$) showed that SSVEP amplitudes to higher frequency tags were smaller when a low frequency tag was present than when paired with a higher frequency tag. We therefore avoided pairing low with high frequency tags. This procedure also ensured that the difference between frequency tags was not salient to the subject.

for the subject ground. To monitor the electrooculogram (EOG), activity was recorded as bipolar input from the left and right horizontal eye channels (HEOGL and HEOGR) and from the vertical channels positioned above and below the left eye (VEOGL+, VEOGL-). Electrode impedances were kept below 5 k Ω for all the electrodes during the experiment. Data acquisition was controlled through Brain Vision Recorder (version 1.03, BrainProducts GmbH, Munich, Germany).

2.1.5. ERPs data processing

Epochs of 1.2 s were segmented starting 200 ms before and until 1 s after target onset. Epochs in which artifacts or vertical eye movements and blinks exceeded ± 80 μ V of electrode activity, and epochs in which horizontal eye movement exceeded ± 30 μ V of electrode activity, were excluded from further analysis (an average of 17.5% of segments was removed which left 182, 237, and 220 epochs for the analysis of the focused-, divided-, and ignored-attention condition respectively). Because horizontal eye movements toward target locations after target onset could bias the interpretation of the ERPs, visual inspection on the averaged horizontal eye channel was performed. According to Lins et al. (1993), a horizontal eye movement of more than 3 μ V propagates at posterior sites for less than 0.1 μ V. To exclude epochs contaminated from eye movements after target onset, visual inspection of the averaged horizontal eye movement channel for activity above 3 μ V was performed separately for each participant for each side of presentation and attention condition. None of the participants included in this dataset performed eye movements above the 3 μ V threshold.

The 200-ms interval before target onset served as baseline. Only segments corresponding to a correct response (i.e., to a “hit” if the target was to be attended and was responded to or a “correct rejection” if the target was to be ignored and was not responded to) were considered. Segments were averaged and filtered (cut-off = 26 Hz at 12 dB/Oct Butterworth zero-phase low-pass filter) before computing the mean voltage of the ERPs within a specified time window centered on the peak of interest. Grand-average waveforms (see Fig. 2) served as a reference to set the time windows from which each ERP deflection was estimated. Because the target onset was not phase-locked to the frequency tag, the possible effect of the different frequency tags on the target-locked ERPs should average out; for this reason tagging frequency was not included as a factor in the analysis of the ERPs (Di Russo & Spinelli, 1999a). The time window for the P2 component was set between 240 and 280 ms, for the N2 component between 325 and 355 ms, and for the P3 component between 440 and 600 ms.

2.1.6. Steady-state visual evoked potential (SSVEP) data processing

For computation of the SSVEP data were re-referenced to the average of the two mastoids. To exclude the possibility that eye movements toward the cued location could contribute to the enhancement of the amplitude of the SSVEP response, activity exceeding 3 μ V in the averaged horizontal eye channel was checked for (Fig. A1 in the on-line Appendix representing the Grand-average EOG for the three instructional conditions shows that none of the participants showed such activity). Epochs, 10 s long from the onset to the offset of the oscillating square, were classified according to the presentation side (left vs. right), the attention condition (focused, divided, or ignored), and frequency (8, 9.5, 10.5, 13, 17, or 23 Hz). Epochs were then visually inspected for the presence of artifacts, and eye blinks were corrected using the algorithm of Gratton, Coles and Donchin (1983). All trials of each frequency were concatenated, yielding 90-s epochs (10 s \times 9 trials, with 3 trials for each of the three target combinations (2, 3, or 4 targets)) in the focused-left- and in the focused-right-attention conditions, and a 150-s epoch (10 s \times 15 trials, with 3 trials for each of the five target combinations (2, 3, 4, 6 or 8 targets)) in the divided-attention condition. In order to minimize

contamination due to the stabilization time period of the band-pass filter, these epochs were copied twice and concatenated yielding a sequence of sufficient length to permit the distinction of frequencies with a resolution of 0.0037 Hz in the focused-attention condition and of 0.0022 Hz in the divided attention condition. The data thus obtained were filtered using a Gaussian filter centered on the tagging frequencies with a standard deviation of 0.01 Hz applied to the fast Fourier transform. After filtering, the second epoch of the concatenated sequence was kept and the first and third were discarded. To increase the reliability of the averaging process data were segmented in 1-s epochs and averaged together. Amplitudes of the SSVEPs were estimated by computing the square root of the variance of the averaged epochs.

To obtain a more robust estimate of the SSVEP, the amplitudes of a spatially contiguous group of electrodes having the highest amplitudes were averaged. These were the occipito-temporal electrodes contralateral to the side of presentation of the frequency tag. Before the averaging procedure, electrodes at posterior sites (using the central line, i.e., posterior to Cz), which is where the response to the tagging frequency is highest (Regan, 1989), were selected and sorted according to amplitude. Starting with the highest amplitude electrode, each next electrode was added to the current cluster or was used as the seed of a new cluster if it was not spatially contiguous to the previous electrode. The first (in order of amplitude) cluster of size 2 or greater (with a maximum of 8) was used for averaging, yielding the SSVEP amplitude for the specific condition.

For each subject, the SSVEP response was computed separately for each frequency, attention condition, and side. Given that the amplitude of an SSVEP depends on the tagging frequency (Regan, 1989), SSVEP amplitudes were normalized by dividing each amplitude by the average value obtained in the three attention conditions. This normalization procedure was performed separately for each subject, frequency, and side.

3. Results

3.1. Behavioral data

Responses in the target-detection task were classified as hits, false alarms, or misses. Hits were defined as the first responses in the time window from 200 to 800³ ms following the occurrence of a target at a to-be-attended location. Subsequent responses in this time window, as well as responses outside this window, were designated false alarms (less than 0.01% on average). Errors of selective attention, indicated by responses to targets displayed on the to-be-ignored side, were also considered false alarms (less than 0.04% on average). The failure to respond to a displayed target within the 200–800-ms time window was considered a miss. In the behavioral analysis, only the percentage of hits and the RTs were considered. The behavioral data are shown in Fig. 1.

The upper panels of Fig. 1 display the percentage of hits. Data were subjected to a repeated measures ANOVA with attention condition (focused vs. divided), side (left vs. right), and tagging frequency (8, 9.5, 10.5, 13, 17, or 23 Hz) as factors. Targets were detected more accurately in the focused- than in the divided-attention condition ($F(1,13) = 7.89$, $p = 0.015$, $MSE = 938.47$, $\eta_p^2 = 0.38$). Targets displayed on the left side were detected more accurately than those displayed on the right ($F(1,13) = 5.46$, $p = 0.036$, $MSE = 2337.83$, $\eta_p^2 = 0.29$). The Attention Condition \times Side interaction was significant ($F(1,13) = 14.15$, $p = 0.002$, $MSE = 934.06$, $\eta_p^2 = 0.52$). The effect of side was more pronounced in the divided-attention condition, as shown in the upper left panel of Fig. 1. The tagging frequency affected the accuracy of target detection

³ The same analysis was performed excluding latencies greater than 2 SD above or below the mean for a given participant to avoid extreme values. The results of the two analyses yielded congruent outcomes.

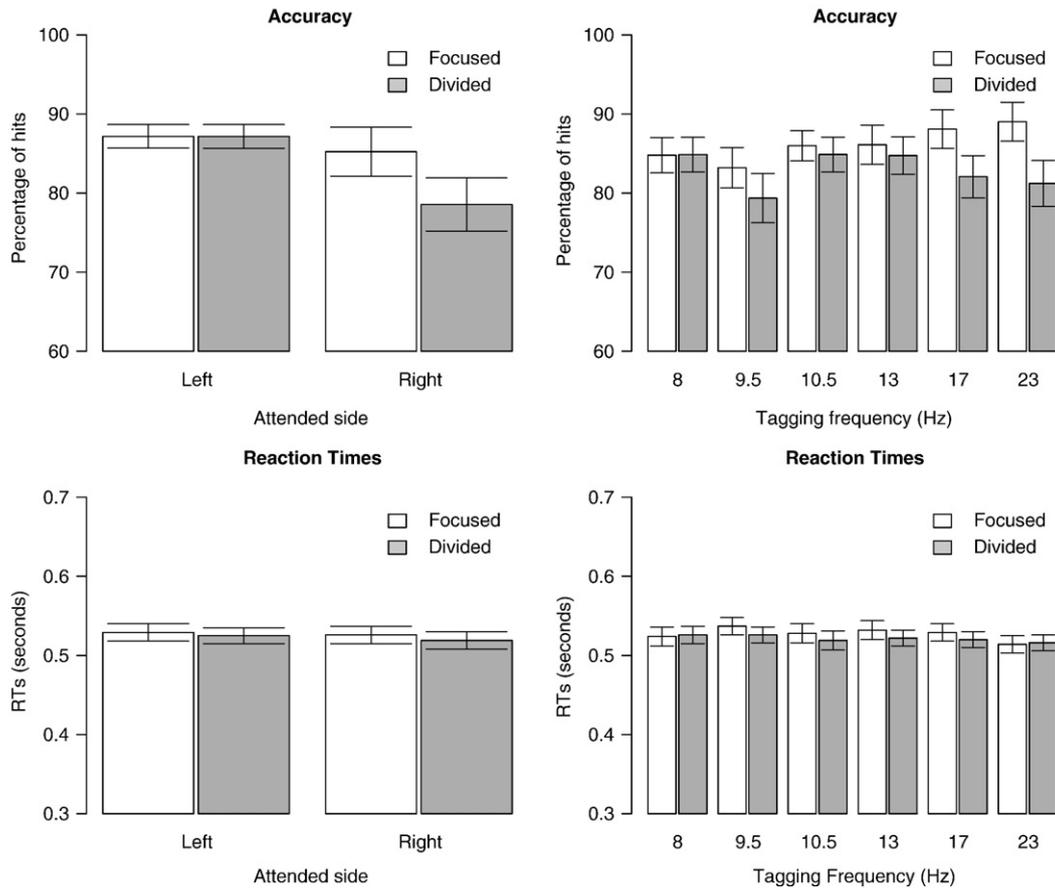


Fig. 1. Percentage of hits (upper panels) and reaction times (lower panels) in the target detection task. Panels on the left show performance as a function of attended side (left vs. right) and attention condition (focused vs. divided), and panels on the right show performance as a function of frequency tag (8, 9.5, 10.5, 13, 17, and 23) and attention condition (focused vs. divided). Error bars show the standard error of the mean.

($F(5,65) = 3.63, p = 0.018, MSE = 223.65, \eta_p^2 = 0.21$); accuracy was 84.82, 81.28, 85.43, 85.42, 85.08, and 85.12% for the tagging frequencies 8, 9.5, 10.5, 13, 17, and 23 Hz, respectively. Pairwise comparisons (Bonferroni corrected) revealed a significant difference between accuracy for the 9.5 Hz and 8 Hz ($p = 0.044$) tagging frequencies and for 9.5 Hz and 13 Hz ($p = 0.007$). The difference between the 9.5 Hz and 23 Hz frequencies was not significant ($p = 0.07$). The Attention \times Frequency interaction was not significant ($F(5, 65) = 3.09, p = 0.055, MSE = 296.58, \eta_p^2 = 0.19$). From Fig. 1, the focused-divided difference seems to increase steadily with increasing tagging frequency (with a possible exception of the 9.5 Hz). Contrasts performed on the Attention \times Frequency interaction confirmed such a significant linear relationship ($F(1, 13) = 8.17, p = 0.013, MSE = 427.3, \eta_p^2 = 0.39$). No other effect reached significance (all $ps > 0.2$).

Reaction times (RTs) are displayed in the lower panels of Fig. 1. Reaction times were submitted to a repeated measures ANOVA with attention condition (focused vs. divided), side (left vs. right), and tagging frequency (8, 9.5, 10.5, 13, 17, or 23 Hz) as factors. Tagging frequency had an effect on RT ($F(1, 5) = 3.17, p = 0.022, MSE = 0.002, \eta_p^2 = 0.19$); RT was 525, 531, 524, 527, 525, and 515 ms for the tagging frequencies 8, 9.5, 10.5, 13, 17, and 23 Hz, respectively. Pairwise comparisons revealed significantly faster RTs with the 23-Hz than the 9.5-Hz tagging frequency ($p = 0.036$; Bonferroni corrected). No other effect on RT approached significance.

3.2. ERP amplitudes

The grand-averaged target-elicited ERPs at Pz and Cz for the three attention condition (focused, divided, and ignored) are shown in Fig. 2. Note that the P1 and N1 components are largely missing, probably due to the interference caused by the rapidly flickering

backgrounds. The panels show the modulation of the amplitude of the P2 and P3 components as a function of attention, however ERPs amplitudes did not differ between focused and divided attention.

Statistical tests were based on the electrodes for which the responses were largest. For the P2 and N2 components this was at

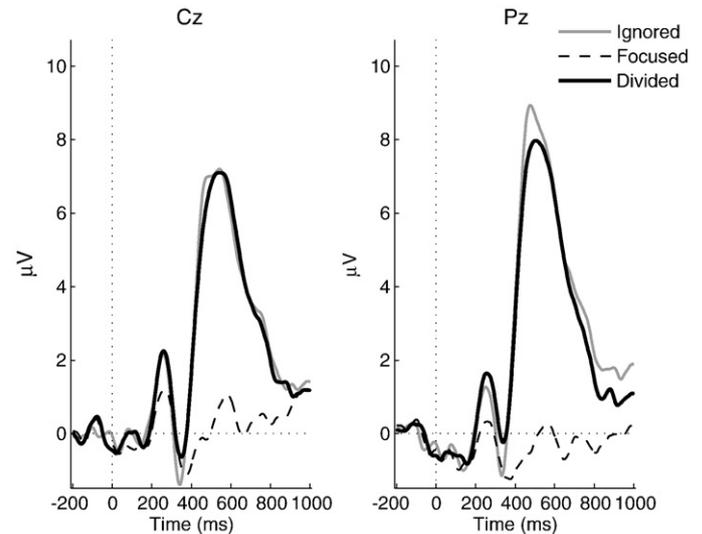


Fig. 2. Event-related potentials at Cz and Pz, in the focused-, divided-, and ignored-attention conditions time-locked to target onset. Amplitudes were computed at Cz for P2 and N2 components, Pz for the P3 component. Positive ERP values are plotted upwards.

Cz, and for the P3 component this was at Pz. The amplitudes of each of these ERP components as a function of attention were tested with separate repeated measure ANOVAs with attention condition (focus, ignore, divide) and side (left vs. right) as within subjects factors. P2 component amplitude (240–280 ms after target onset) was affected by the attention condition ($F(2, 26) = 4.37, p = 0.04, MSE = 13.6, \eta_p^2 = 0.25$). Pairwise comparisons (Bonferroni corrected) were performed to compare the three attention conditions, but did not yield significant differences. Polynomial contrasts showed a linear trend between attention condition and P2 component amplitude ($F(1, 13) = 6, p = 0.029, MSE = 13.6, \eta_p^2 = 0.32$). The nature of this linear contrast between P2 component amplitude and attention was further tested with a t -test, but where P2 component amplitudes in the focused- and divided-attention conditions were averaged together and compared to the ignored-attention condition. P2 component amplitude was significantly higher in the focused-divided- than in the ignored-attention condition ($t(1, 13) = 2.47, p = 0.028$). No other factors influenced the amplitude of the P2 component (all $ps > 0.4$). The N2 component (325–355 ms after target onset) was not significantly affected by any of the factors (all $ps > 0.1$). The P3 component (440–600 ms after target onset) amplitude was affected by the attentional condition ($F(2, 26) = 103.5, p < 0.001, MSE = 968.1, \eta_p^2 = 0.89$). Pairwise comparisons (Bonferroni corrected) of the attention conditions showed that P3 component amplitude was significantly higher in the focused- than in the ignored-attention condition ($p < 0.001$) and in the divided- than in the ignored-attention condition ($p < 0.001$), but did not differ between the focused- and the divided-attention condition ($p > 0.2$). No other factor influenced the amplitude of the P3 component (all $ps > 0.1$).

3.3. SSVEP amplitude

The amplitude of the SSVEP was tested with a repeated measures ANOVA with attention condition (focus, ignore, and divide), side (left vs. right), and frequency (8, 9.5, 10.5, 13, 17, or 23 Hz) as within-subject factors. The amplitude of the SSVEP was affected by attention condition ($F(2, 26) = 11.78, p = 0.001, MSE = 1.1, \eta_p^2 = 0.48$) such that amplitudes were higher in the focused-attention condition (1.086⁴) than in the divided-attention condition (0.986⁴) and in the ignored-attention condition (0.932⁴). This linear trend was confirmed in a trend analysis ($F(1, 13) = 14.81, p = 0.002, MSE = 1.54, \eta_p^2 = 0.53$). Additionally tests of attentional effects on SSVEP amplitudes using pairwise comparisons (Bonferroni corrected) showed that the amplitude of the SSVEP in the focused-attention condition was significantly higher than in both the divided- ($p = 0.013$) and ignored-attention conditions ($p = 0.006$). SSVEP amplitude differences between the ignored- and divided-attention conditions were not statistically significant ($p > 0.1$). As should be expected from the fact that SSVEP amplitudes were normalized across frequencies, tagging frequency did not have an effect on the amplitude of the SSVEP ($p > 0.7$), nor did it interact with attention condition ($p > 0.7$). No other effects on SSVEP amplitude approached significance (all $ps > 0.1$) (Fig. 3).

Although both performance data and SSVEP amplitude suggests graded attention allocation across conditions, it could be argued that subjects adopted an attention-switching strategy in the divided attention condition, either within or across trials (Miller & Bonnel, 1994, VanRullen et al., 2007). This attention-switching possibility was explicitly addressed using a mixture modeling approach based on the distributions of instantaneous amplitudes in the various conditions. The theoretical basis of this approach and the detailed results of the various tests are presented in the Appendix A. To summarize, the results seem to argue strongly against the idea that performance and SSVEP amplitude in the divided-attention condition can be accounted for in terms of within- or between-trial probabilistic switching

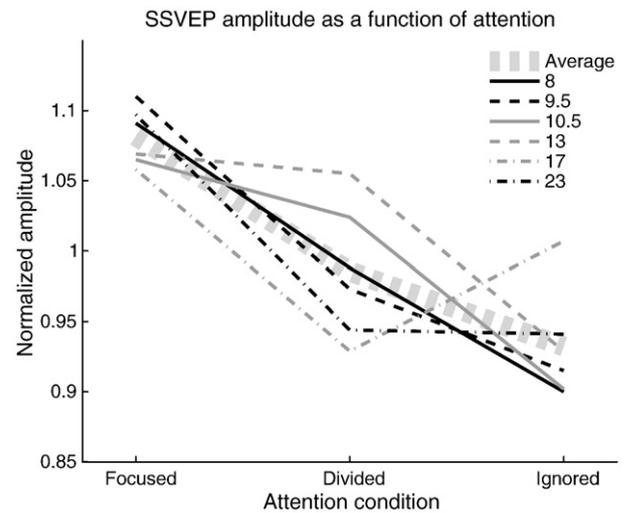


Fig. 3. Normalized SSVEP amplitude as a function of tagging frequency.

between the two streams. Thus, participants do seem to have distributed attention as instructed. It is important to point out, however, that we cannot exclude the possibility of people having switched attention between locations at higher frequencies than our analysis procedure was sensitive to (e.g., > 2 Hz). Though we feel that this possibility is unlikely, we note that the idea that attention might rely on a rapid, intrinsically periodic sampling process has recently been advocated (VanRullen et al., 2007).

3.4. Correlational analyses

Correlational analyses were performed to examine the attentional effects on the ERP components and SSVEP. Attentional effects were estimated by computing the difference in amplitude in the focused- and ignored-attention conditions of the raw⁵ P2, N2, and P3 components of the ERP and of the normalized SSVEP for each of the tagging frequencies. Differences were based on the electrodes showing the highest amplitude for each ERP component and tagging frequency. The results of the correlation analyses are shown in Table 1. Although not always significant, the attentional effects were positively correlated across tagging frequencies, with the exception of the 23 Hz (see Table 1). Attention effects on ERP components were also positively correlated. However, there were no significant correlations between the attention effects as measured by the SSVEP and ERP.

4. Discussion

An experiment in which participants were to detect target digits embedded in a stream of letter distractors presented on an oscillating background was conducted to investigate the effects of visuospatial attention on SSVEP amplitude. Focused- and divided-attention conditions were compared to determine whether the SSVEP is sensitive to gradation of attention. Six different tagging frequencies were used in order to investigate possible dependencies on tagging frequency of attentional effects on SSVEP amplitude.

Participants detected fewer targets in the divided- than in the focused-attention condition, but RTs were similar in the two conditions. An apparent bias to attend left, especially in the divided-attention condition, was revealed by higher hit rates for left- than for right-side targets (see Hollander, Corballis, Hamm, 2005, for similar results). The difference in hit rate in the divided- and focused-

⁴ The values reported for these amplitudes are scale-free because when data are normalized they lose their dimensions.

⁵ Normalized amplitudes of the ERPs components did not yield any difference to the outcome of this analysis.

Table 1

Correlation between ERP amplitude (for the P2, N2, and P3 components) and the normalized SSVEP amplitude for each of the tagging frequencies.

Pearson correlation	9.5 Hz	10.5 Hz	13 Hz	17 Hz	23 Hz	P2	N2	P3
8 Hz	0.444	0.481	0.483	0.030	0.029	-0.143	-0.259	-0.059
9.5 Hz		0.749**	0.563*	0.696**	-0.462	-0.156	-0.312	-0.224
10.5 Hz			0.359	0.568*	-0.215	-0.139	-0.094	0.006
13 Hz				0.063	-0.326	0.229	-0.362	0.061
17 Hz					-0.516	-0.139	0.023	-0.052
23 Hz						0.081	0.013	0.017
P2							0.510	0.774**
N2								0.632*

* Correlation is significant at the 0.05 level (2-tailed).

** Correlation is significant at the 0.01 level (2-tailed).

attention conditions tended to increase with increasing tagging frequency, reflecting a combination of higher accuracy in the focused condition and lower accuracy in the divided condition as a function of increasing tagging frequency. These differences may reflect subtle perceptual effects caused by interactions between the frequency of RSVP presentation (6 Hz) and the frequency of the intensity modulation of both the alphanumeric characters and the background. Importantly, such interactions may have critically depended on the fact that the characters were intensity modulated in phase with the background. However, the nature of such interactions and how these might result in opposite effects on target-detection performance in the focused-attention and divided-attention conditions, remains to be understood. As discussed in some detail below, differential involvement of parvocellular and magnocellular visual pathways for low and high tagging frequencies may be responsible, at least in part, for these effects of tagging frequency on overt performance (see also Kim et al., 2007).

Across attentional conditions, the pattern of results for the P2 and P3 components amplitude were the same. Both components showed a lower amplitude in the ignored condition than in the focused- and divided-attention conditions, which did not differ. The finding that P2- and P3-component amplitude was essentially the same for all correctly reported targets—whether in the divided- or in the focused-attention condition—suggests that the P2 and P3 components reflect the outcome of attentional selection rather than top-down biasing effects on visual processing that mediate or cause visuospatial attentional selectivity (see Mangun & Hillyard, 1990). In other words, the P2 and P3 components are associated with higher processing stages such as identification of specific properties of the target items which are unaffected by the amount of perceptual resources allocated to target selection.

SSVEP amplitude in the focused-attention condition was substantially larger for the attended than for the ignored stimulus stream, in line with results from numerous recent SSVEP studies (see Belmonte, 1998; Cosmelli et al., 2004; Di Russo & Spinelli, 1999a,b; Hillyard et al., 1997; Kelly et al., 2006; Kim et al., 2007; Malinowski et al., 2007; Morgan et al., 1996; Muller et al., 1998; Muller et al., 2003; Muller & Hillyard, 2000; Pei et al., 2002; Srinivasan et al., 1999; Srinivasan et al., 2006; Wang et al., 2007; and others). An important, novel, finding in the present study is that SSVEP amplitude in the divided condition fell in between those in the focused and ignored conditions. It is important to point out that we explicitly addressed the possibility that this result might be explained in terms of within- or between-trial switching of attention in the divided attention condition, and found that the evidence argues against this possibility (see Appendix A). This suggests that, unlike P2 and P3 components, SSVEP amplitude may reflect gradations of visuospatial attention or, more precisely, the graded allocation of capacity-limited top-down modulation or biasing of visual processing across multiple locations or objects.

Evidence for graded effects of attention on SSVEP amplitude was also found in a recent study of Andersen et al. (2008). They showed that the amplitude of the SSVEP associated with an amplitude-modulated object increased linearly and additively with the number of target-defining features that it contained (i.e., two, one, or none). They interpreted this result as evidence for parallel additive amplification of physiological responses across two or more visual dimensions (e.g., orientation and color). Note that their results do not address the issue of whether distributing or biasing top-down attention across multiple dimensions comes with a divided-attention cost. Our results do address this latter issue, but for the case of spatial attention, and show that division of attention across multiple locations is reflected by a reduction in SSVEP amplitude. Thus, the two studies provide somewhat complimentary results regarding graded effects of attentional control and attentional effects on SSVEP amplitude.

Tagging frequency did not significantly modulate the attention effects on SSVEP amplitude. In the case of the difference in SSVEP amplitudes for the focused- and ignored-attention conditions, this lack of dependency is in line with a range of studies using different tagging frequencies but showing similar attention effects on SSVEP amplitude (e.g., Hillyard et al., 1997; Morgan et al., 1996, who used 8.6 and 12 Hz; Muller et al., 1998; Muller & Hillyard, 2000, who used 20.8 and 27.8 Hz; Belmonte, 1998, who used 8.9 Hz; Kim et al., 2007, who used 12.50 and 16.67 Hz; Kelly et al., 2006, who used 9.45, 10.63, 14.17, and 17.01 Hz). The present results do not support the suggestion of Ding et al. (2006) that attentional effects on SSVEP amplitude depend on the specific attentional network that is recruited by a particular tagging frequency. It should be noted that Ding et al.'s suggestion was based on only a subset of their overall results, limited to one of four experimental conditions and to 2 of the 15 tagging frequencies that were used.

Correlational analyses of the difference in amplitudes for the focused- and ignored-attention conditions between the late ERP components (P2, N2, P3) revealed that attentional effects for the various ERP components were positively correlated. The same was true for the SSVEP amplitudes associated with the different tagging frequencies, with the exception of 23 Hz.⁶ In contrast, the correlations between effects on ERP amplitudes on the one hand and SSVEP amplitudes on the other were all weak and nonsignificant, regardless of the precise way in which these amplitude differences were quantified or normalized.

Similar evidence that effects of visuospatial attention on the amplitudes of late ERP components are independent from those on the amplitudes of SSVEPs was reported by Muller and Hillyard (2000). These authors did, however, obtain significant positive correlations between attentional effects on the amplitude of early ERP components (N1, N2) and the amplitude of SSVEPs. In the present study, we were unable to reliably measure the amplitudes of early ERP components. The likely reason for this is that, unlike in the Muller and Hillyard (2000) study, target onset was not phase locked to the tagging frequency. This lack of phase locking probably resulted in a substantial amount of jitter in the latency of the early evoked components. For instance, target onset could occur at a time when the luminance of both the background and letter were near zero. Such jitter would result in early components in the ERPs being lost in the averaging process. The lack of correlations between attentional effects on late ERP-component amplitude and SSVEP amplitude is consistent with the idea that different EEG measures reflect different and dissociable aspects of visuospatial selectivity. SSVEP amplitude (as well as that of the N1 and P1 components; see Mangun & Hillyard, 1990) seems to reflect the graded top-down modulation or biasing of visual processing at different locations in the visual field. In contrast,

⁶ Correlations pattern was generally positive although not all the correlations were significant.

later ERP components reflect the effects or outcome of top-down processing, such as target categorization for the P3 component (e.g., Mangun & Hillyard, 1990; Kok, 1997), or enhancement of task-relevant information for the P2 component (e.g., Freunberger et al., 2007).

A seemingly anomalous aspect of the results was the lack of correlation of the attentional effects on SSVEP amplitude at 23 Hz with those at the lower tagging frequencies. A possible reason for this pattern of correlations may be that only the magnocellular processing system but not the parvocellular system is sensitive to flicker frequencies above 20 Hz (Derrington and Lennie, 1984, Levitt et al., 2001). Thus, whereas the attentional effects on SSVEP at the lower frequencies are likely to reflect a mixture of attentional modulations of parvocellular and magnocellular processing, those at 23 Hz are likely exclusively due to attentional modulation of magnocellular processing. That the relative contribution of the two systems is relevant to the outcomes of this experiment is suggested by Yeshurun and Levy's (2003) evidence that spatial attention may have different effects on processing in parvo- and magnocellular pathways. This conclusion is based on the finding that spatial attention enhances spatial resolution but reduces temporal resolution. Yeshurun and Levy argue that these opposite effects of attention on spatial and temporal resolution can be explained most parsimoniously in terms of spatial attention enhancing parvocellular processing and inhibiting, either directly or indirectly, by means of competitive interactions between parvo- and magnocellular pathways, magnocellular processing. The overall effects of attention on SSVEP amplitude at 23 Hz do not support the idea that spatial attention inhibits magnocellular processing (otherwise the attention effect would be smaller since only the relatively inhibited magnocellular system would contribute to performance). Instead, the present results seem to indicate generally facilitative effects of spatial attention on parvo- and magnocellular processing.

An enhanced parvocellular contribution at frequencies below 20 Hz may also help explain the finding that the difference in accuracy between the focused- and divided-attention conditions increased with increasing tagging frequency. As tagging frequency increases, the limited temporal sensitivity of the parvocellular pathway results in a gradual transition in perception from a stimulus (alphanumeric character and background) that clearly flickers at the lowest frequency (8 Hz) but that is perceptually stable at the highest frequency (23 Hz). This perceived stability may have increased the parvocellular pathway's contribution to target detection at the higher tagging frequency. If focused spatial attention results in relatively more parvocellular than magnocellular processing at attended locations, this beneficial effect of higher tagging frequencies on target detection in the parvocellular pathway should be expected to be considerably higher in the focused as compared to the divided-attention condition. While this perspective can account for larger differences in performance between focused- and divided-attention conditions at higher tagging frequencies, it fails to explain why, as our results suggest, target detection in the divided-attention condition seems to deteriorate as tagging frequency is increased.

In conclusion this study showed that the amplitudes of the SSVEP and ERP are functionally related to the deployment of attention to stimuli. Attention effects were such that amplitudes in the focused-attention condition were higher than the amplitudes in the ignored-attention condition both for SSVEPs and ERPs. However, although attention effects were consistent between amplitudes of ERP components and SSVEP at the different tagging frequencies, correlations between the two were not significant. More interestingly, this study showed that dividing attention between two locations is associated with a reduction in the amplitude of the SSVEP, showing that SSVEPs are sensitive to gradation of attention. For the ERPs, however, there were no differences between focused and divided

attention conditions, providing further support for the claim that SSVEPs and ERPs reflect physiological responses associated with distinct attentional mechanisms. The consistency of the effects of attention on the SSVEP across tagging frequencies suggests that the frequency tagging procedure can be applied flexibly in a range of paradigms.

Appendix A

Both the within-trial and the between-trial versions of the attention-switching hypothesis of divided attention imply that the distributions of SSVEP instantaneous amplitude for the left and right locations in the divided-attention condition, computed either within or between trials, should consist of a binary mixture of the corresponding distributions for the focused and ignored conditions. As explained below, this allows us to compute a predicted variance for the instantaneous amplitude in the divided-attention condition from those in the focused-attention condition and the ignored-attention condition. Comparing this predicted variance to the empirically obtained variance provides a test of whether a mixture is actually present, that is, whether people did not divide attention but switched between locations.

The variance of a binary-mixture distribution, σ_{Mix}^2 , is known to obey the following equation (Falmagne et al., 1975, p. 371):

$$\sigma_{\text{Mix}}^2 = x\sigma_1^2 + (1-x)\sigma_2^2 + x(1-x)(\bar{A}_1 - \bar{A}_2)^2, \quad (1)$$

where σ_1^2 and σ_2^2 are the variances of the two basis distributions, \bar{A}_1 and \bar{A}_2 the corresponding means, and x the mixing probability. The third term on the right side of the equation ($x(1-x)(\bar{A}_1 - \bar{A}_2)^2$) is generally referred to as the inflation factor. In the present application, the divided-attention condition provides the mixture distribution, the focused condition provides the first basis distribution (σ_1^2) and the ignored condition the second basis distribution (σ_2^2). It is important to note that the binary mixture distribution is a bimodal distribution. The inflation factor represents the impact of this bimodality on overall variance and this impact increases as a function of the difference in mean between the two basis distributions. Because the mean amplitudes in the focused and ignored condition differed substantially, the inflation factor should represent a sizable contribution to overall variance (σ_{Mix}^2). If, contrary to what the mixture model assumes, people did not switch attention between locations but truly divided attention between locations as instructed, the actual amplitude distribution would be unimodal and its variance should therefore be overestimated by the mixture model. Eq. (1) was used to predict the variance of instantaneous amplitudes in the divided-attention condition separately for each combination of location (left or right) and tagging frequency (8, 9.5, 10.5, 13, 17, or 23), separately for each participant. Following the definitions of the basis distributions, the mixing probability, x , represents the probability that attention happened to be focussed on that particular location and frequency when it was presented in the divided-attention condition. Because results were subsequently averaged across all possible combination of frequency and location, we assume x to be close to .5, that is, at chance level.

For these analyses, trials were 14-s epochs starting 2 s before the onset of the frequency tag and ending 2 s after the offset of the frequency tag. Epochs were then filtered with a Gaussian filter centered on the tagging frequency with a bandwidth of 0.1 Hz for the between-trial tests and 0.75 Hz for the within-trial tests. Instantaneous amplitude was estimated through Hilbert transformation of the filtered signal. A_1 and A_2 in Eq. (1) were estimated by computing mean instantaneous amplitudes for single trials in the focused and ignored conditions (excluding the first and last 3 s of the epoch (leaving epochs of 8 s) to compensate for the stabilization period of

the Gaussian filter), and then averaging across the single trials. Between-trial variances for all attention conditions were computed from estimates of single-trial mean amplitudes. Within-trial variances were computed across the same epochs (8 s) and then averaged across trials.

Eq. (1) was used to compute predicted variance for the divided-attention condition from the estimated mean amplitudes and variances in the focused and ignored conditions. In order to normalize these predicted values before further analysis, the ratio between the empirical and estimated variance was computed ($\sigma^2_{\text{Mix}} : \sigma^2_{\text{Empirical}}$), separately for each tagging frequency, location, and posterior electrode (i.e., posterior to Cz). To enhance robustness, ratio values were first averaged across the posterior electrodes, then, log-transformed ratio values were averaged across all combinations of tagging frequency and location (consistent with the assumption that the overall value of x in Eq. (1) must be close to .5). Note that if people attended or facilitated processing at both locations by switching between them, either on a within-trial or a between-trial basis, predicted and empirical variances would be expected to be very similar and the average ratio value should be close to 1. On the other hand, if people did not actually attend both locations by switching between them, the inflation factor in Eq. (1) would cause an overestimation of the true variance, given that we obtained consistent amplitude differences in the focused and ignored conditions (A1 and A2 in Eq. (1)). This overestimation would result in ratio values ($\sigma^2_{\text{Mix}} : \sigma^2_{\text{Empirical}}$) larger than 1. Therefore, if ratio values would be found to be substantially and significantly larger than 1, this would strongly argue against the attention-switching idea.

Fig. A1 shows the ratio $\sigma^2_{\text{Mix}} : \sigma^2_{\text{Empirical}}$ for SSVEP instantaneous amplitude for within-trial and between-trial switches for all individual participants and the average across all the participants. For the between-trial ratio values, a t -test revealed that the ratio values were significantly different from 1 ($t(13) = 6.53, p < .001$). For the within-trial ratio values, the same test also yielded a significant difference ($t(13) = 4.87, p < .001$ – the fact that the latter values tend to be much smaller than the ratio values in the between-trial case is due to the fact that $\sigma^2_{\text{Empirical}}$ is much greater in the within-trial case).

The results of this analysis establish a consistent and sizable overestimation of the actual variance of SSVEP amplitude in the divided-attention condition, and would thus seem to argue strongly against the idea that performance and SSVEP amplitude in this condition can be accounted for in terms of within- or between-trial probabilistic switching between the two streams. Thus, with the

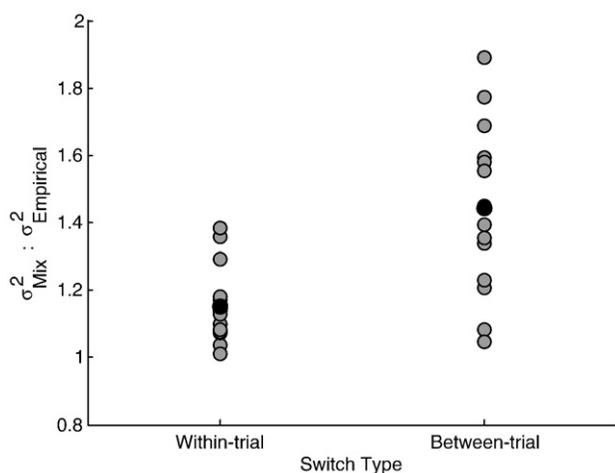


Fig. A1. Spread of the ratio between the empirical and estimated variance ($\sigma^2_{\text{Mix}} : \sigma^2_{\text{Empirical}}$) across participants for the within- and between-trial switches (grey dots). For both within- and between-trial switches the mean values (black dots) are larger than 1.

possible exception of a small subset of participants, people do seem to have distributed attention as instructed.⁷ It is important to point out, however, that we cannot exclude the possibility of people having switched attention between locations at higher frequencies than our analysis procedure was sensitive to (e.g., >2 Hz). Though we feel that this possibility is unlikely, we note that the idea that attention might rely on a rapid, intrinsically periodic sampling process has recently been advocated (VanRullen et al., 2007).

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ijpsycho.2009.01.006.

References

- Andersen, S.K., Hillyard, S.A., Muller, M.M., 2008. Attention facilitates multiple stimulus features in parallel in human visual cortex. *Curr. Biol.* 18, 1006–1009.
- Belmonte, M., 1998. Shifts of visual spatial attention modulate a steady-state visual evoked potential. *Cognitive Brain Res.* 6, 295–307.
- Brainard, D.H., 1997. The psychophysics toolbox. *Spat. Vis.* 10, 433–436.
- Cosmelli, D., David, O., Lachaux, J.P., Martinerie, J., Garnero, L., Renault, B., Varela, F., 2004. Waves of consciousness: ongoing cortical patterns during binocular rivalry. *Neuroimage* 23, 128–140.
- Derrington, A.M., Lennie, P., 1984. Spatial and temporal contrast sensitivities of neurons in lateral geniculate nucleus of macaque. *J. Physiol.* 357, 219–240.
- Desimone, R., Duncan, J., 1995. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* 18, 193–222.
- Ding, J., Sperl, G., Srinivasan, R., 2006. Attentional modulation of SSVEP power depends on the network tagged by the flicker frequency. *Cereb. Cortex* 16 (7), 1016–1029.
- Di Russo, F.D., Spinelli, D., 1999a. Electrophysiological evidence for an early attentional mechanism in visual processing in humans. *Vis. Res.* 39, 2975–2985.
- Di Russo, F.D., Spinelli, D., Sep 1999b. Spatial attention has different effects on the magno- and parvocellular pathways. *Neuroreport* 10, 2755–2762.
- Falmagne, J.C., Cohen, S.E., Dwivedi, A., 1975. Two-choice reactions as an ordered memory scanning process. In: Rabbitt, E.M.A., Dornic, S. (Eds.), *Attention and performance V*. Academic Press, San Diego, CA, pp. 296–344.
- Freunberger, R., Klimesch, W., Doppelmayr, M., Holler, Y., 2007. Visual p2 component is related to theta phase-locking. *Neurosci. Lett.* 426, 181–186.
- Fries, P., Reynolds, J.H., Rorie, A.E., Desimone, R., 2001. Modulation of oscillatory neuronal synchronization by selective visual attention. *Science* 291, 1560–1563.
- Galambos, R., Makeig, S., Talmach, P.J., 1981. A 40-hz auditory potential recorded from the human scalp. *Proc. Natl. Acad. Sci. U. S. A.* 78, 2643–2647.
- Gratton, G., Coles, M.G., Donchin, E., Apr 1983. A new method for off-line removal of ocular artifact. *Electroencephalogr. Clin. Neurophysiol.* 55, 468–484.
- Herrmann, C.S., 2001. Human EEG responses to 1–100 Hz flicker: resonance phenomena in visual cortex and their potential correlation to cognitive phenomena. *Exp. Brain Res.* 137, 346–353.
- Hillyard, S.A., Anllo-Vento, L., 1998. Event-related brain potentials in the study of visual selective attention. *Proc. Natl. Acad. Sci. U. S. A.* 95, 781–787.
- Hillyard, S., Hinrichs, H., Tempelmann, C., Morgan, S., Hansen, J., Scheich, H., Heinze, H., 1997. Combining steady-state visual evoked potentials and fMRI to localize brain activity during selective attention. *Hum. Brain Mapp.* 5, 287–292.
- Hollander, A., Corballis, M.C., Hamm, J.P., 2005. Visual-field asymmetry in dual-stream RSVP. *Neuropsychologia* 43, 35–40.
- Kastner, S., Weerd, P.D., Desimone, R., Ungerleider, L.G., 1998. Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science* 282, 108–111.
- Kelly, S.P., Lalor, E.C., Reilly, R.B., Foxe, J.J., Jun 2006. Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. *J. Neurophysiol.* 95, 3844–3851.
- Kim, Y.J., Grabowecy, M., Paller, K.A., Muthu, K., Suzuki, S., 2007. Attention induces synchronization-based response gain in steady-state visual evoked potentials. *Nat. Neurosci.* 10, 117–125.
- Kok, A., 1997. Event-related potential (ERP) reflections of mental resources: a review and synthesis. *Biol. Psychol.* 45, 19–56.
- Levitt, J.B., Schumer, R.A., Sherman, S.M., Spear, P.D., Movshon, J.A., 2001. Visual response properties of neurons in the LGN of normally reared and visually deprived macaque monkeys. *J. Neurophysiol.* 85, 2111–2129.
- Lins, O.G., Picton, T.W., Berg, P., Scherg, M., 1993. Ocular artifacts in EEG and event-related potentials. I: Scalp topography. *Brain Topogr.* 6, 51–63.

⁷ We also found no evidence for attentional switching during the divided attention condition using a correlational approach based on a procedure developed by Andersen and coworkers (2008). The approach is based on the notion that attentional switching between the left and right locations should cause correlations in SSVEP amplitude for the left and right location in the divided-attention condition to be considerably more negative than those obtained in the focused condition. No such systematic and reliable differences were however obtained.

- Malinowski, P., Fuchs, S., Muller, M.M., 2007. Sustained division of spatial attention to multiple locations within one hemifield. *Neurosci. Lett.* 414, 65–70.
- Mangun, G.R., Hillyard, S.A., 1990. Allocation of visual attention to spatial locations: tradeoff functions for event-related brain potentials and detection performance. *Percept. Psychophys.* 47, 532–550.
- Mehta, A.D., Ulbert, I., Schroeder, C.E., 2000. Intermodal selective attention in monkeys. I: Distribution and timing of effects across visual areas. *Cereb. Cortex* 10, 343–358.
- Miller, J., Bonnel, A.M., 1994. Switching or sharing in dual-task line-length discrimination. *Percept. Psychophys.* 56, 431–446.
- Morgan, S.T., Hansen, J.C., Hillyard, S.A., 1996. Selective attention to stimulus location modulates the steady-state visual evoked potential. *Proc. Natl. Acad. Sci. U. S. A.* 93, 4770–4774.
- Muller, M.M., Hillyard, S., 2000. Concurrent recording of steady-state and transient event-related potentials as indices of visual-spatial selective attention. *Clin. Neurophysiol.* 111, 1544–1552.
- Muller, M.M., Picton, T.W., Valdes-Sosa, P., Riera, J., Teder-Slejrvi, W.A., Hillyard, S.A., 1998. Effects of spatial selective attention on the steady-state visual evoked potential in the 20–28 Hz range. *Brain Res. Cogn. Brain Res.* 6, 249–261.
- Muller, M.M., Malinowski, P., Gruber, T., Hillyard, S.A., 2003. Sustained division of the attentional spotlight. *Nature* 424, 309–312.
- O'Connor, D.H., Fukui, M.M., Pinsk, M.A., Kastner, S., 2002. Attention modulates responses in the human lateral geniculate nucleus. *Nat. Neurosci.* 5, 1203–1209.
- Pei, F., Pettet, M.W., Norcia, A.M., 2002. Neural correlates of object-based attention. *J. Vis.* 2, 588–596.
- Regan, D., 1989. *Human brain electrophysiology: evoked potentials and evoked magnetic fields in science and medicine*. Elsevier.
- Ross, B., Herdman, A.T., Pantev, C., 2005. Right hemispheric laterality of human 40 Hz auditory steady-state responses. *Cereb. Cortex* 15, 2029–2039.
- Sharbrough, F., Chatrian, G., Lesser, R., Luders, H., Nuwer, M., Picton, T., 1991. American electroencephalographic society guidelines for standard electrode position nomenclature. *J. Clin. Neurophysiol.* 8, 200–202.
- Srinivasan, R., Russell, D.P., Edelman, G.M., Tononi, G., 1999. Increased synchronization of neuromagnetic responses during conscious perception. *J. Neurosci.* 19, 5435–5448.
- Srinivasan, R., Bibi, F.A., Nunez, P.L., 2006. Steady-state visual evoked potentials: distributed local sources and wave-like dynamics are sensitive to flicker frequency. *Brain Topogr.* 18, 167–187.
- Stephen, J.M., Ranken, D.F., Aine, C.J., 2006. Frequency-following and connectivity of different visual areas in response to contrast-reversal stimulation. *Brain Topogr.* 18, 257–272.
- Vanduffel, W., Tootell, R.B., Orban, G.A., 2000. Attention-dependent suppression of metabolic activity in the early stages of the macaque visual system. *Cereb. Cortex* 10, 109–126.
- VanRullen, R., Carlson, T., Cavanagh, P., 2007. The blinking spotlight of attention. *Proc. Natl. Acad. Sci. U. S. A.* 104, 19204–19209.
- Wang, J., Clementz, B.A., Keil, A., 2007. The neural correlates of feature-based selective attention when viewing spatially and temporally overlapping images. *Neuropsychologia* 45, 1393–1399.
- Yantis, S., Serences, J.T., 2003. Cortical mechanisms of space-based and object-based attentional control. *Curr. Opin. Neurobiol.* 13, 187–193.
- Yeshurun, Y., Levy, L., 2003. Transient spatial attention degrades temporal resolution. *Psychol. Sci.* 14, 225–231.
- Yingling, C.D., Skinner, J.E., 1976. Selective regulation of thalamic sensory relay nuclei by nucleus reticularis thalami. *Electroencephalogr. Clin. Neurophysiol.* 41, 476–482.