Sustained division of spatial attention to multiple locations within one hemifield

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Abstract

Attending to a location in space significantly improves stimulus perception at that location. Everyday experience requires the deployment of attention to multiple objects at different locations. Recent empirical evidence suggests that the “beam” of attention can be divided between non-contiguous areas of the visual field. Whether this is only possible when stimuli are presented in different hemifields and harder, if not impossible, when stimuli are in the same hemifield is an ongoing debate. Here we use an electrophysiological measure of sustained attentional resource allocation (the steady-state visual evoked potential, SSVEP) to address this question. In combination with behavioural data we demonstrate that splitting the attentional “beam” is in principle possible within one hemifield. However, results showed that task performance was in general lower for same-hemifield presentation as opposed to our previous study with different-hemifield presentation [M.M. Müller, P. Malinowski, T. Gruber, S.A. Hillyard, Sustained division of the attentional spotlight, Nature 424 (2003) 309–312]. SSVEP amplitude showed a mixed pattern of results for stimuli presented in the upper versus lower quadrant of the left visual hemifield under conditions of attending to two separated locations. Results are discussed in the light of the bilateral distribution advantage hypothesis and differences in stimulus salience between the upper and lower visual field.

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Natural visual scenes are cluttered with different objects and attention helps to select a particular object for preferred stimulus processing. In recent years empirical evidence was provided that the deployment of attention over space is quite flexible and allows attending to separate locations or objects with irrelevant or to-be-ignored positions or objects in between them [1,4,7,9,15]. In one study we presented four stimuli aligned along the horizontal meridian that flickered with different frequencies for several seconds to elicit the frequency-coded steady-state visual evoked potential (SSVEP) [15]. The SSVEP is the electrophysiological response of the visual cortex to a rapidly repeating (flickering) stimulus and generally has a sinusoidal waveform with the same temporal frequency as the driving stimulus [21]. Previous studies have shown that its amplitude is substantially increased when attention is focused upon the location of the flickering stimulus [14,17] and, thus, serves as a direct neural index of the sustained deployment of attention across space.

In our recent study we found significantly decreased SSVEP amplitudes when the intermittent stimulus was ignored compared to when this stimulus was attended, supporting the view that the attentional spotlight can be split in spatially non-contiguous locations over periods of several seconds [15]. However, given that the stimuli were located in the left and right visual hemifield, the question arises whether splitting the attentional focus was only possible because each hemisphere was able to independently maintain one attentional spotlight or uses independent attentional processing resources. The bilateral distribution advantage hypothesis predicts that splitting is much harder or even impossible if stimuli are presented within one hemifield, due to the limited amount of processing resources of only one cortical hemisphere [12,19,23]. In this framework, a bilateral distribution advantage is always present when the
benefits of the cooperation between the two hemispheres outweigh possible costs [3,24].

Several behavioural studies provide evidence for this assumption. Performance was often found to be superior when stimulus processing required by a certain task could be distributed over the two hemispheres, especially for computationally complex or perceptually demanding tasks [2,10]. Furthermore, in a visual search task neuropsychological patients with surgically transected corpus callosum, resulting in disconnection of the two cerebral hemispheres, were able to scan bilaterally presented stimulus arrays faster than normal control subjects, suggesting that each hemisphere is able to maintain an independent focus of attention [11].

The present study intends to determine whether the ability to maintain two separate foci of attention necessarily requires that the attended locations fall into different hemifields. With other words, are participants still able to split the attentional focus when the separated and to-be attended locations fall into the same visual field? To answer that question we used a similar design as in our previous study [15], but stimuli were presented in the left visual hemifield only. Each stimulus flickered with a different frequency. By mathematically decomposing the electrophysiological brain response into the different stimulation frequencies we studied the deployment of attention to the presented stimuli by testing the amplitude of the respective SSVEP statistically.

All thirteen participants (eight females; mean age 24.3 ± 3.0 years) gave informed consent according to the Declaration of Helsinki. Excessive EEG artefacts resulted in the exclusion of three participants. Thus analysis is based on 10 remaining participants.

The design of the present study was almost identical to the one in our previous study [15], except that stimuli were arranged vertically within the left visual hemifield extending the upper and lower quadrant (see Fig. 1).

Stimuli were presented against a dark background on a 17-inch computer monitor (800 × 600 pixels, vertical refresh rate 59.25 frames/s). Each white rectangle comprised a visual angle

Fig. 1. Schematic diagram of stimulus sequences for all four experimental conditions. Subjects reported a match of the target symbol “8” at the two attended positions (either 1 + 2, 3 + 4, 1 + 3 or 2 + 4) on different blocks of trials.
of $2.4^\circ \times 3.0^\circ$ with an eccentricity of $4^\circ$ from the inner edges of the stimuli to the vertical meridian. The vertical distance between each stimulus was $1.6^\circ$. The stimuli flickered at position 1 to 4 at rates of 19.75 Hz, 8.46 Hz, 14.80 Hz and 11.84 Hz, corresponding to cycle durations of 3, 7, 4, and 5 frames, respectively. All rectangles were displayed for one 'on' frame (16.88 ms), followed by the corresponding number of 'off' frames to achieve the respective stimulation frequency (e.g. one ‘on’ frame followed by 4 ‘off’ frames for 11.84 Hz). Five different geometrical red symbols (see Fig. 1) were placed on top of the flickering rectangles and one of them served as target symbol. Randomised sequences of these symbols were presented at all four positions simultaneously for 11 frames (185.68 ms) followed directly by the next symbol array. Thus, the symbol onsets and offsets did not occur in synchrony with the background flickering rectangles that drove the SSVEP. Individual target symbols occurred equally often at all four stimulus positions.

Subjects placed their head on a chin rest while fixating the central fixation cross and paid attention to the symbol sequences at two of the four positions. They were asked to push a button upon detecting the simultaneous occurrence of the target symbol at those two positions (subsequently referred to as target). On separate trial blocks subjects had to attend to either the two upper quadrant positions (1 + 2), the two lower quadrant positions (3 + 4), or to two separated positions (1 + 3 or 2 + 4). 75% of the trials contained one or three targets, to which subjects had to respond. These targets were randomly presented within a given trial (see Fig. 1) with additional single target symbols presented occasionally at any of the four positions. Single target symbols also occurred in trials without target. Targets were separated by a minimum interval of 928.4 ms. Each trial lasted for 3440 ms, with the fixation point appearing on the screen 300 ms before flicker onset. Perfect synchronisation of the four flicker frequencies occurred at 540 ms after flicker onset and served as reference point for extracting the epochs for EEG analysis. The inter-trial interval varied randomly between 900 and 1300 ms. The experiment consisted of 12 blocks of 40 trials each, resulting in 120 trials for each of the four experimental conditions. The block order was randomised, the response hand usage was counterbalanced across subjects. The stimuli flickered at position 1 to 4 at the respective frequency (i.e. 0.54–2.94 s. after flicker onset). Complex demodulation resulted in the peak-to-peak amplitude for the attended position. As expected, due to our selection criterion, the attention effect for each individual position was significant when we compared the respective SSVEP amplitudes, when the adjacent positions were attended versus ignored (see Table 2, left columns).

<table>
<thead>
<tr>
<th>Table 1 Summary of behavioural data</th>
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<tbody>
<tr>
<td>TDR (%)</td>
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<tr>
<td>Attend 1 + 2</td>
</tr>
<tr>
<td>Attend 3 + 4</td>
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<tr>
<td>Attend 1 + 3</td>
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<tr>
<td>Attend 2 + 4</td>
</tr>
</tbody>
</table>

Mean target detection rates (TDR), reaction times (RT) and false alarms (FA) for the four conditions. Data are shown ± standard errors.

One factor repeated-measure ANOVAs yielded significant mean differences for target detection rates ($F(9,3) = 14.55$, $p < 0.0001$), response times ($F(9,3) = 7.74$, $p < 0.001$) and error rates ($F(9,3) = 12.61$, $p < 0.0001$). Bonferroni/Dunn corrected post-hoc t-tests revealed that the mean differences for detection rates and response times were based on lower performance (slower responses, fewer target detections) in the attend 1 + 2 condition compared to all other conditions ($p < 0.005$ for all comparisons), whereas false alarm rates were higher in both attend-adjacent conditions (attend 1 + 2, attend 3 + 4), than in both attend-separate conditions (attend 1 + 3, attend 2 + 4; all $p < 0.005$ for all comparisons).

To analyse SSVEP amplitudes, artefact-free epochs were averaged separately for each experimental condition. SSVEP waveforms were generally sinusoidal, with fundamental frequencies at the driving flicker rate (see Supplementary data). The SSVEP amplitudes for each experimental condition and stimulus position were quantified by complex demodulation [16,21] over 2400 ms epochs starting with the time point of flicker-synchronisation (i.e. 0.54–2.94 s. after flicker onset). Complex demodulation resulted in the peak-to-peak amplitude for the respective frequency, which was calculated by averaging across the analysed epoch for each electrode and experimental condition. As in our previous studies [15,17], SSVEP amplitudes were generally smaller for higher flicker rates (see Fig. 2).

For testing SSVEP amplitude changes we selected one posterior electrode for each participant with the largest attention effect in the two adjacent attention conditions (see Supplementary data). As cross check, the averaged amplitudes of three neighbouring occipito-parietal standard electrodes, centred at electrode locations Oz and POz, were tested for the splitting conditions.

Fig. 2 depicts the grand mean SSVEP amplitudes for the individual best electrode across all subjects for each condition and position. As expected, due to our selection criterion, the attention effect for each individual position was significant when we compared the respective SSVEP amplitudes, when the adjacent positions were attended versus ignored (see Table 2, left columns).
Fig. 2. Mean SSVEP amplitudes for selected electrodes. Mean SSVEP peak-to-peak amplitudes (+ standard errors) at each position under the four experimental conditions averaged across 10 subjects. Shown are SSVEP amplitudes for individually best electrodes having had the greatest attention effect in conditions attend to adjacent positions.

Table 2

<table>
<thead>
<tr>
<th>Position</th>
<th>Selected electrode sites</th>
<th>Standard electrodes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n(9)</td>
<td>p</td>
</tr>
<tr>
<td>1 (19.8 Hz)</td>
<td>5.344</td>
<td>0.001</td>
</tr>
<tr>
<td>2 (8.5 Hz)</td>
<td>5.163</td>
<td>0.001</td>
</tr>
<tr>
<td>3 (14.8 Hz)</td>
<td>2.264</td>
<td>0.050</td>
</tr>
<tr>
<td>4 (11.8 Hz)</td>
<td>2.804</td>
<td>0.021</td>
</tr>
</tbody>
</table>

Group statistics (t- and p-values) for the SSVEP amplitude at positions 1 to 4 when the adjacent positions were attended or unattended for electrodes exhibiting the greatest attention effect across both adjacent conditions (selected electrode sites, columns 2 and 3) and averaged across three standard electrodes (columns 4 and 5).

For testing the division of the attentional spotlight, the critical stimulus locations were the intermediate positions 2 and 3. SSVEP amplitude driven by 8.5 Hz (position 2) was significantly reduced during the attend 1 + 3 condition compared to the attend 2 + 4 condition ($t(9) = 3.07, p = 0.013$). However, at position 3 no such effect was observed (see Fig. 2). SSVEP amplitude for attend 2 + 4 and attend 1 + 3 did not differ significantly ($t(9) = 1.01, p = 0.34$).

Statistics for the mean SSVEP amplitude across three standard electrodes yielded the same pattern of results, except that the SSVEP attention effect at position 3 was no longer significant when attending to positions 3 + 4 versus 1 + 2 (see Table 2, right columns). With regard to the separate spotlight conditions the attention effect for position 2 was significant ($t(9) = 2.42, p = 0.039$), when comparing conditions 1 + 3 with 2 + 4, with no significant difference in SSVEP amplitude for position 3 ($t(9) = 1.33, p = 0.22$), see Fig. 3.

The present study addressed the question whether the attentional focus can be divided into separate beams over sustained periods of time within one visual hemifield. Replicating previous findings [14,15], mean SSVEP amplitudes were significantly greater for each single frequency when stimulus locations were attended than when they were ignored. Together with behavioural data, it confirms that subjects were compliant and followed the instructions. As expected, the increase in SSVEP amplitude with attention is also present when all stimuli are presented in one visual hemifield. With regard to our central question, results were mixed. While behavioural performance clearly indicates that the attentional spotlight can be split even without costs as compared to attending to adjacent positions in one hemifield, electrophysiological data support that notion only when the to-be ignored intermittent stimulus was located in the upper quadrant (i.e. position 2). When subjects had to attend to positions 2 and 4 and to ignore the intermittent position 3, located in the lower quadrant, SSVEP amplitude...
did not differentiate as opposed to when they were attending to positions 1 and 3, although behavioural data indicated that subjects were able to split their beam successfully. How can this discrepancy be explained?

One obvious reason might be the different signal-to-noise ratio between the SSVEP amplitudes for the 8.5 Hz and 14.8 Hz stimuli. As depicted in Fig. 2, amplitudes for the 14.8 Hz stimuli are about half the magnitude as amplitudes for the 8.5 Hz stimuli. But this is not a sufficient explanation, given that the SSVEP amplitude was even somewhat greater when position 3 was the to-be-ignored intermittent stimulus. A second reason might be cross-talk between the 14.8 Hz and 11.8 Hz stimulus. We tested that possibility by re-analysing the data with other filter settings to exclude that possibility, and found no differences.

A third reason might lie in the finding that perceptual performance is usually better in the lower than in the upper visual field, since spatial resolution and thus stimulus saliency is higher in the lower visual field [3,20]. Behavioural data of the present study is in line with this, since performance was significantly better for TDR and RT when subjects attended to the adjacent positions in the lower, compared to when they attended to the adjacent positions in the upper quadrant. In several behavioural studies it has been shown that even under conditions of high perceptual load salient distractors will attract attention if they share task-relevant features with the target stimuli [6]. A possible explanation thus is, that due to the higher spatial resolution and resulting higher salience the ignored intermittent stimulus in the lower quadrant (position 3) attracted more attentional resources than the ignored intermittent stimulus in the upper quadrant (position 2). This could explain why we found the split attention effect at position 2 but not position 3. Although behavioural data did not indicate that the target symbol presented at position 3 influenced performance at positions 2 and 4 significantly (but see slight RT-differences in Table 1), SSVEP amplitude as a more sensitive electrophysiological marker for the allocation of attentional resources across space clearly points in that direction.

Previous studies localized the cortical sources of the SSVEP in early visual areas such as V1 and V2 [8,18], and, thus, related the signal to early perceptual processes. This was confirmed in a study that combined SSVEP recording and functional magnetic resonance imaging (fMRI), indicating that one major source of the SSVEP is located in V1 [5]. Recent fMRI studies confirmed selective, retinotopically specific enhanced activation in striate and extrastriate visual cortical areas for attended locations when splitting the beam within and across hemifields [13], providing additional evidence that spotlight division is accomplished at a low level, early stage of stimulus processing. In the present study the scalp topography of the split attention effect shows a maximum over occipital parietal area supporting this interpretation (see Supplementary data).

When we compared the behavioural results of the present study with the ones of our previous study, where the task and stimulus design were identical, but stimuli were aligned along the horizontal meridian [15], attending to multiple stimuli within one visual hemifield clearly introduced costs. These costs were obvious in all behavioural measures (average hit rate across conditions: 67.7% present versus 81.3% previous; average response time across conditions: 519 ms present versus 463 ms previous; and average false alarm rate across conditions: 10.8% present versus 4.9% previous). These costs support the idea of a different-hemifield advantage as suggested by Sereno and Kosslyn [23] and also are in line with results of previous studies, which reported better performance along the horizontal than along the vertical axis [3,22]. Further support for the bilateral distribution advantage hypothesis comes from a recent behavioural study, which demonstrated the influence of task difficulty on the ability to split the focus of attention [9]. Participants had to match two out of four simultaneously presented transient stimuli. Relative task performance decreased when task difficulty increased only when subjects had to split the attentional focus within one hemifield.

To summarize, the present study adds to the growing empirical evidence that attending to spatially separate locations is possible across as well as within visual hemifields. However, attending to stimuli in one hemifield introduces costs compared to attending to stimuli distributed across two hemifields. Differences in stimulus salience resulting from higher spatial resolution in the lower than the upper visual field may contribute to the mixed findings in this study. Whether the observed effects are due to a harder competition for limited processing resources allocated in one hemisphere as opposed to competition for processing resources in both hemispheres, or due to intrahemispheric inhibition given the spatial proximity of stimuli is subject to future studies.

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Appendix A. Supplementary data


References


