Modulation of early cortical processing during divided attention to non-contiguous locations

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Abstract
We often face the challenge of simultaneously attending to multiple non-contiguous regions of space. There is ongoing debate as to how spatial attention is divided under these situations. Whereas, for several years, the predominant view was that humans could divide the attentional spotlight, several recent studies argue in favor of a unitary spotlight that rhythmically samples relevant locations. Here, this issue was addressed by the use of high-density electrophysiology in concert with the multifocal m-sequence technique to examine visual evoked responses to multiple simultaneous streams of stimulation. Concurrently, we assayed the topographic distribution of alpha-band oscillatory mechanisms, a measure of attentional suppression. Participants performed a difficult detection task that required simultaneous attention to two stimuli in contiguous (undivided) or non-contiguous parts of space. In the undivided condition, the classic pattern of attentional modulation was observed, with increased amplitude of the early visual evoked response and increased alpha amplitude ipsilateral to the attended hemifield. For the divided condition, early visual responses to attended stimuli were also enhanced, and the observed multifocal topographic distribution of alpha suppression was in line with the divided attention hypothesis. These results support the existence of divided attentional spotlights, providing evidence that the corresponding modulation occurs during initial sensory processing time-frames in hierarchically early visual regions, and that suppressive mechanisms of visual attention selectively target distracter locations during divided spatial attention.

Introduction
Attentional processes constantly filter sensory inputs, and only a subset of our environment receives fully elaborated perceptual processing. For example, each time that we make an eye movement, the eyes bring another part of our environment into the center of gaze for detailed processing. In addition to these overt shifts of attention, humans can deploy spatial attention without moving the eyes or the head, known as covert shifts of attention (von Helmholtz, 1867). One longstanding metaphor for covert spatial attention is the ‘attentional spotlight’, the notion that attention can only be allocated to one region of space at a time (e.g. Posner, 1980). These models postulate that the attentional spotlight cannot be divided, but that the size of the spotlight can be adapted to task requirements [i.e. the ‘zoom-lens’ model (Eriksen & St James, 1986)]. In the attended region of visual space, reaction times are lower and/or detection accuracy is higher than in unattended regions. This notion of a unitary, indivisible spotlight was supported by earlier visual evoked potential (VEP) studies (e.g. Heinze et al., 1994).

However, a growing number of studies have challenged the idea of a single, non-divisible attentional spotlight. Behavioral experiments provide evidence that humans can divide attention among multiple non-contiguous spatial locations (e.g. Castiello & Umilta, 1992; Awh & Pashler, 2000; Gobell et al., 2004), reporting that reaction time and accuracy are modulated in divided attention designs in the same way as in undivided cued attention paradigms.

Another line of evidence for a division of spatial attention has been put forward in steady-state VEP (SSVEP) and functional magnetic resonance imaging studies (e.g. Muller et al., 2003a; McMains & Somers, 2004, 2005). These studies reveal brain activation patterns that clearly fit with a divided spotlight account. In recent years,
studies providing evidence for a divided spotlight of attention were called into question, on the basis that their results can be explained by a unitary attentional spotlight that simply switches very rapidly between to-be-attended locations (e.g. Jans et al., 2010; VanRullen & Dubois, 2011). Correlates of such a periodic sampling of attention have been observed in electrophysiological experiments in non-human primates (Buschman & Miller, 2009) and in psychophysical experiments in humans (VanRullen et al., 2007). The dynamics of how attentional resources are redirected in the visual field are strongly debated, with estimates of latencies for attentional shifts of between approximately 70 ms (Nakayama & Mackeben, 1989) and 300 ms (Duncan et al., 1994). Given these widely deviating estimates for the dynamics of spatial attention, even the use of very short stimulus presentation times (below 200 ms) might not be enough to clearly discriminate between the divided attention hypothesis and the ‘blinking spotlight’ model (VanRullen et al., 2007). However, a distinction between the blinking spotlight and divided attention hypothesis might be observed for attentional suppression of distracter locations. The divided spotlight theory predicts that the number of suppressed spatial locations increases from the undivided to the divided attention condition, because the number of distracters increases from one (contiguous) to two or more in the divided case, and the attentional system will need to adjust to these changes in order to divide resources appropriately. This should be reflected in topographically specific increases in the amplitude of alpha oscillations, which have been shown to be tightly linked to suppression of visual space (e.g. Worden et al., 2000; Kelly et al., 2006; Thut et al., 2006; Green & McDonald, 2010; Romei et al., 2010; Gould et al., 2011). Given the behavioral findings for the blinking spotlight hypothesis (VanRullen et al., 2007), there are three different possible scenarios for attentional suppression under this model (see Predictions section in Materials and methods). The current study therefore examined the topographic distribution of suppressive alpha oscillations to examine whether they fit with the predictions of either model.

Another question about the ability to split the attentional spotlight relates to the timing of the attentional modulation. SSVEP and functional magnetic resonance imaging studies have provided evidence that modulation occurs in early visual cortical areas. However, owing to the low temporal resolution of the methods employed, these studies are not suitable for investigating whether or not any cost involved in splitting the spotlight might impact on the precise temporal locus of attention, i.e. whether the modulation might occur during initial feedforward processing, or whether it reflects later feedback from higher cortical areas. The timing of visual cortical activity in humans is generally assessed by the use of VEPs. However, this method is hampered by the need to present sudden-onset probe stimuli, which tend to exogenously grab attention and alter evoked responses. This problem can be overcome using the multilateral m-sequence technique (Sutter, 2000; Schmid et al., 2009; Ales et al., 2010a). This method allows for simultaneous recording of independent cortical evoked responses from multiple locations, and for the assessment of oscillatory alpha rhythms. In this way, we can examine the timing of attentional modulation and whether these modulations are consistent with a divided spotlight account or one of the single spotlight hypotheses.

Materials and methods

Subjects

Nineteen healthy subjects (seven females) aged between 20 and 35 years participated in the study. In the final dataset, 14 participants were included, as five did not have enough usable data after correction for electroencephalography (EEG) artefacts and eye movements. All had normal or corrected-to-normal vision. The experimental procedures were approved by the Institutional Review Board at Albert Einstein College of Medicine, and conformed to the tenets of the Declaration of Helsinki. All participants provided written informed consent and received a modest fee.

Experimental stimuli and paradigm

The stimulus configuration is shown in Fig. 1. It consisted of two checkerboard stimuli located 2° above and on either side of a fixation spot at horizontal eccentricities of 2.5° and 7.9°, respectively. The size of the inner checkerboards was 3.5° × 3.5°, with a spatial frequency of 0.7 cycles per degree; the size of the outer checkerboards was 4.7° × 4.7°, with a spatial frequency of 0.5 cycles per degree (Fig. 1). The larger size of the outer stimuli was chosen to adjust visual stimuli for the reduction in visual cortical area devoted to peripheral space (Adams & Horton, 2003; Frey et al., 2013). Dark checks had a luminance of 0.1 cd/m², and white checks had a luminance of 118.2 cd/m². The refresh rate of the monitor (model VP265; ViewSonic, Walnut, CA, USA) was set to 60 Hz, and on every refresh the checkerboard pattern of each stimulus either remained constant or was inverted as determined by a binary m-sequence of order 7 (e.g. Sutter, 2000; Schmid et al., 2009). The binary m-sequence technique controls the inversion of the checkerboards displayed in each stimulus location by using a pseudo-random sequence, which ensures that inversions in one location are statistically independent from the inversions in all other stimulus locations. Cortical evoked responses are then obtained by cross-correlation of the continuous EEG data around stimulus reversals with the checkerboard reversal sequence. An order of 7 indicates that each sequence was 2^7 = 128 monitor refresh cycles (i.e. 2.1 s) long. This duration is sufficient to fit four evoked responses of duration 500 ms. In half of the trials, we used this sequence, and in the other half we used it inverse. Each trial was 2.95 s in length; however, the m-sequence used for estimating the evoked cortical response was only 2.1 s in length. In order to minimise stimulus onset artefacts, we used another random sequence for the first 850 ms of each trial, and this time-frame was excluded from further analysis.

For the experimental task, we overlaid each checkerboard with a central red ‘X’ (task stimulus). At the beginning of each block of 20 trials, participants were instructed to simultaneously attend to two of the checkerboards, and count how many times their task stimuli disappeared at the same time. This ensured that participants did not have to switch attention on each trial. Before each experimental trial, the two attended checkerboards were cued again, and, after a random interstimulus interval of 800–1200 ms, the experimental trial

![Fig. 1. Stimulus configuration and description of attentional conditions.](image-url)
was started. Participants were instructed to ignore the uncued checkerboards, as task stimuli could also disappear in the uncued locations. To ensure that participants attended to both cued checkerboards simultaneously, we also added ‘fake targets’, in which the task stimulus disappeared in only one of the two cued checkerboards. The task instructions were held constant throughout each block of 20 trials. There were up to two targets and ‘fake targets’ in each trial.

In order to analyse all possible aspects of spatial attention modulation, we asked participants to attend to contiguous and non-contiguous parts of visual space. For the undivided attention conditions, participants were instructed to attend to both stimuli in either the contiguous right hemifield (‘attend right’) or the left hemifield (‘attend left’). In order to obtain cortical responses during divided attention, participants had to attend to the inner right and outer left stimuli (‘split left’) or the inner left and outer right stimuli (‘split right’). For each of the divided attention conditions, 160 trials were run; for the conditions in which participants had to attend within a visual hemifield, 140 trials were run. Target presentation was limited to durations of up to 19 frames, i.e. for a maximum duration of approximately 317 ms. Given the flickering nature of the checkerboards (see Video S1 for an example of the task with target durations set to 350 ms) and the large distance between the stimuli in the divided condition (approximately 10.5°), it is highly unlikely that a high rate of target–pair detections would be achieved with a strategy of attending to one of the stimuli and shifting attention to the second stimulus as soon as a possible target is detected.

Data acquisition

One hundred and sixty-eight-channel scalp EEG recordings were amplified and digitised at 512 Hz by the use of ActiveTwo systems (Biosemi, Amsterdam, Netherlands) with an analog low-pass filter at 103 Hz. The acquisition of the data occurs relative to an active two-electrode reference, which drives the average potential of the participant as close as possible to the reference voltage of the analog-to-digital converter box (for a description of the Biosemi active electrode system referencing and grounding conventions, see www.biosemi.com/faq/cms&drl.htm).

Eye movements were recorded with an EyeLink 1000 system (SR Research, Mississauga, Ontario, Canada). Even though participants rested the head on a comfortable chinrest, the eye-tracker was set to head-free mode. In this setting, the eye-tracker corrects for head movements and remains very accurate even with changing head position. Eye position was recorded at 500 Hz and synchronised with the EEG recording by the use of triggers at the onset of each trial. Every eight blocks, the eye-tracker was re-calibrated by the use of a nine-point grid.

Eye-tracking analysis

The raw eye-tracking data were filtered by use of a fourth-order Butterworth low-pass filter with a 15-Hz cut-off to eliminate rarely occurring high-frequency errors. Owing to calibration error, the eye-tracker may represent the participant’s horizontal gaze position up to 1° to the left or right of the intended position. This ‘misrepresentation’ will be consistent for all blocks during a calibration period. We therefore used the following method to determine the coordinate for fixation. If, within one set of eight blocks with the same calibration, the difference between median eye position in the different blocks was < 1°, we used the median x-values and y-values across all blocks as the fixation point coordinates. Otherwise, the eye-tracking data were analysed without this correction. On this filtered data, we removed all trials in which the subjects’ eyes moved by more than 1.75° from the fixation point. Two participants were excluded because of excessive eye movements.

EEG analysis

All EEG data analyses were performed in MATLAB with the fieldtrip toolbox (Oostenveld et al., 2011) as well as custom scripts. The EEG recording was high-pass-filtered with a low cut-off of 0.5 Hz, by the use of fourth-order Chebyshev filters with zero phase-shift. This filter has the advantage of very high attenuation in the stop band with minimal attenuation in the pass-band (< 0.1 dB). After filtering, bad channels were determined from the statistics of neighboring channels, and interpolated by the use of linear, distance-weighted interpolation. The EEG data were then referenced to the average. In addition to the deletion of trials on the basis of eye movements, there was also an EEG threshold of ±125 μV. If more than six channels or any of the occipital electrodes of interest exceeded this threshold, the trial was discarded. Otherwise, high-amplitude channels were interpolated by the use of linear, distance-weighted interpolation. Three participants were excluded because of large numbers of trials with EEG artefacts, bringing the total number of participants used in further analysis to 14. After removal of artefact trials, an average of 117 trials per condition and participant remained.

Temporal second-order kernels (e.g. Sutter, 2000) representing evoked cortical responses were extracted for each electrode and each of the four stimulus locations, by reverse-correlating the EEG response with the known sequence of pattern reversals. The second-order response takes into account the history of visual stimulation, i.e. whether the current pattern is the same as the one presented one monitor refresh before.

Statistical analysis

Given the findings of previous studies on spatial attention (e.g. Lalor et al., 2007; Kelly et al., 2008; Frey et al., 2010), we expect attentional modulation of the evoked responses during early cortical processing, as represented by responses in the C1 and P1 time-frame. As evoked response kernels represent activity in the early retinotopic cortex, which is very variable across participants (Ales et al., 2010a), the topographical distribution of peak activity was inconsistent across participants. For each stimulus location, we therefore selected two electrodes for each participant by determining mean activity across all four experimental conditions and selecting the two electrodes on the peak of the C1 and P1 topography, respectively. Therefore, for each participant and stimulus location, the two electrodes of interest were constant across experimental conditions. There is considerable variability in early visual cortical geometry between individuals, and locations for which reliable C1 components can be elicited are participant-specific (Kelly et al., 2008). However, we did have to present stimuli in the same stimulus locations for all participants to be able to examine the topographic distribution of attentional modulation. Therefore, not all stimulus locations were optimal for observing C1 modulations.

The amplitude in the time-frame of the early components was extracted for each participant by use of the mean of a 20-ms window (C1) and a 30-ms window (P1) centered on the peak of the grand average. For C1, the time range was 65–85 ms, and for P1 it was 110–140 ms. These amplitudes were analysed with repeated measures ANOVA (SPSS v.21.0), with attention (attended/unattended)
and spotlight (split/non-split) as factors, and location (inner/outer) as a covariate.

**Alpha oscillation analysis**

An important aspect of providing evidence for a divided spotlight of attention is to examine the ‘landscape’ of attentional modulation during the task (Jans et al., 2010). In the current study, we examined the topographic distribution of attentional suppression for the different experimental conditions, because enhancing and suppressive effects of attention are tightly linked (Pinsk et al., 2004; Frey et al., 2010). Brain oscillations in the alpha (8–14 Hz) range are known to index attentional suppression of regions of visual space (Foxe et al., 1998; Worden et al., 2000; Romei et al., 2010; Foxe & Snyder, 2011), and the topography of alpha power reflects which part of visual space needs to be ignored (Rihs et al., 2007). As experimental trials were > 2 s in length, we were able to analyse alpha amplitude and its topography concurrently with evoked activity. Alpha oscillations are not expected to be differentially affected by the m-sequence, as the flickering was present in all conditions, and only task demands were varied.

For determination of alpha amplitude, EEG trial data were filtered between 8 and 13 Hz by use of a fourth-order Butterworth filter. These band-pass-filtered data were Hilbert-transformed, and the absolute value was taken. We removed the first and last 100 ms of data of each trial, because these contained edge artefacts of the filter. For each time-point, the average of all different conditions was used as the baseline. For the display of alpha topographies, the remaining 1.9 s was averaged in order to yield one amplitude value per channel and trial. Alpha topographies were normalised (z-score) for every participant, and the grand average of z-scores across participants was displayed.

A common finding for undivided spatial attention tasks is a lateralised increase in alpha amplitude when participants attend to one hemifield, with higher amplitude over the right hemisphere for the ‘attend right’ condition and higher alpha amplitude over the left hemisphere for the ‘attend left’ condition. Twelve participants had clean alpha oscillatory data that allowed us to quantify the number of topographic peaks, and were included in the analysis of the number of peaks.

In order to determine peaks of alpha amplitude, channels with alpha amplitudes larger than the median amplitude plus 1.5 times the median absolute deviation (a robust measure of variability in a sample) across all channels were selected in an occipito-parietal region of interest, which covered the back of the head. A peak was defined as a group of at least two neighboring channels. As the number of peaks was in a very limited range and not normally distributed, we determined the mean number for the divided and undivided conditions for each participant, and used the Wilcoxon signed rank test to compare the means between conditions. In addition, we determined the center location of each alpha peak, and determined the great-circle distance (the shortest distance between two points on a sphere) with the haversine formula (Sinnott, 1984). Assuming that the occipito-parietal part of the skull approximates a sphere, we used the width of a template head model as the diameter. If there were more than two alpha peaks (one participant with four detectable peaks in the ‘split right’ condition, and two participants with three peaks in the ‘split left’ condition), we chose the peaks with the largest distance.

**Predictions**

Different attentional theories predict different patterns of excitatory and suppressive modulation of cortical activity when attention is allocated to non-contiguous parts of the visual field (Fig. 2A).

For the evoked responses, we expect excitatory attentional modulation of the evoked responses for the inner stimuli in different conditions during early cortical processing. Examining the inner left stimulus, the single spotlight theory predicts that the evoked cortical response will be similar/identical for the ‘split left’ and ‘split right’ conditions (Fig. 2B), as the attentional spotlight will encompass this stimulus for both of these conditions. The same holds for the right inner stimulus. In contrast, the blinking and divided spotlight theories predict that, for the inner left stimulus, the evoked responses in the ‘split left’ and ‘split right’ conditions will differ, with the ‘split right’ response being modulated by attention.

For suppression of distracter locations (Fig. 2C), the single spotlight theory predicts no change in the number of alpha peaks, as there is only one stimulus that receives suppression. However, the topographic map of alpha suppression should change in order to adjust for the increase in attended space. Although the divided and blinking spotlight hypotheses predict the same pattern of attentional modulation for evoked responses, the two theories do not provide identical predictions for suppression of distracter locations. The divided spotlight theory predicts that the number of suppressed spatial locations will increase from the undivided to the divided attention condition, because the number of distracters increases from one in the contiguous condition to two in the divided condition, and the attentional system will need to adjust to these changes in order to divide resources appropriately. This should be reflected in an increase in the number of peaks in the alpha topography from the undivided condition to the divided condition. For the blinking spotlight model of attention (VanRullen et al., 2007), we derived three possible predictions for suppression of the to-be-ignored stimuli. In this theory, the attentional spotlight is thought to constantly move between all available stimuli. Therefore, the first prediction is that all unattended stimuli will be suppressed individually. That is, we assume that a similar mechanism exists for both suppression and excitation. For the current experimental paradigm, such a
mechanism would result in two peaks of suppression for both the divided attention condition and the undivided attention condition. The second prediction is that there will be no suppression of to-be-ignored stimuli, as the blinking spotlight of attention might only selectively enhance target locations. This should obviously result in alpha topographies that do not possess distinctive occipito-parietal peaks. The third prediction is that, while the attentional focus switches rhythmically between all possible target locations, suppression will be allocated to distracter locations in a static fashion. This would result in the same topographic distribution and increase in the number of peaks in the divided attention condition as for the divided spotlight account, and indicate a static split of suppression.

Results

Behavior

Participants were successful at performing the difficult attentional tasks. With chance level at 33.3%, the mean percentages of correct responses were approximately 50% for the attentional task conditions involving the outer right stimulus, and approximately 45% for those involving the left outer stimulus (Fig. 3). These performance values are somewhat lower than in other studies of attention, but the experimental task was more difficult, owing to the randomly flickering stimuli that were necessary to estimate the brain’s impulse response to all four stimuli.

Electrophysiology

For the C1 time-frame, the repeated measures ANOVA revealed no significant main effects ($F_{1,54} = 0.2; P = 0.657$). Only for the inner left stimulus was there significant modulation of activity with attention ($F_{1,13} = 4.78; P = 0.048$). This indicates that there was no influence of attention on cortical processing in this very early time-frame, or that the locations of the four different stimuli were not optimal for obtaining C1 responses.

However, for the P1 component, repeated measures ANOVA revealed a main effect of attention, with the mean amplitude during the P1 time-frame being significantly larger for the conditions in which the participant had to attend to a stimulus ($F_{1,54} = 4.58, P = 0.037$). For both conditions (divided and undivided), the amplitude was significantly larger for attended than for unattended stimuli (Fig. 4). This pattern of evoked responses is in line with the predictions of the divided spotlight hypothesis.

To examine the attentional modulations observed in more detail, we analysed the topographic distribution of alpha oscillatory amplitude for the different conditions. As alpha oscillatory amplitude is closely linked to attentional suppression, we would expect additional foci of alpha synchronisation in the divided as compared with the attend hemifield conditions if humans were able to divide the attentional spotlight.

We found additional foci of alpha synchronisation in the divided attention condition (Fig. 5). The median number of alpha peaks in the attend hemifield condition across participants was 1.25, whereas it was 2 for the divided attention conditions ($P < 0.05$, Wilcoxon signed rank test). The median distance of the peak centers on the scalp for the ‘attend right’ condition was 12.3 cm, whereas it was 10.8 cm for the ‘attend left’ condition (Fig. 5C). Only one peak was detected for four participants in the ‘split right’ condition and for two participants in the ‘split left’ condition. The topographic distribution of suppressive oscillatory activity is therefore in line with the predictions of the divided spotlight theory of attention.

Discussion

The present results support previous research providing evidence for the divided spotlight hypothesis. Topographic analyses showed that oscillatory suppressive mechanisms flexibly adjust to task demands, and that, whenever more than one spatial location has to be ignored, there is a corresponding increase in the number of alpha oscillatory foci over the occipito-parietal scalp. In addition, we provide evidence that attentional modulation for each attended stimulus, whether in contiguous or non-contiguous parts of space, occurs during early sensory-perceptual processing in extrastriate visual areas (Di Russo et al., 2002; Frey et al., 2010).

![Fig. 3. Percentage of correct responses (with standard error of the mean) in the four different experimental conditions.](image)

![Fig. 4. Evoked cortical responses for all stimuli and conditions. The upper panel represents responses obtained for the inner stimulus locations, and the lower panel those for the outer stimuli. The C1 time-frame is highlighted in orange and the P1 time-frame in green.](image)
Participants. The red area in the examination of attention account, it follows that the number of topographic foci of ipsilateral to the attended visual hemi.

Even modalities (Fu et al., 2013), visual features (Snyder & Foxe, 2010), and even modalities (Fu et al., 2001; Banerjee et al., 2011). Experiments examining attentional allocation to contiguous parts of visual space have revealed topographically specific increases in the visual cortex ipsilateral to the attended visual hemifield (e.g. Worden et al., 2000; Kelly et al., 2006; Thut et al., 2006).

Under the divided spotlight of attention account, it follows that the number of topographic foci of alpha should increase from the undivided to the divided attention condition, as an additional stimulus needs to be ignored. This is exactly what we found in the current study.

On the basis of the description of the blinking spotlight model of attention (VanRullen et al., 2007), we derived three possible predictions for suppression of the to-be-ignored stimuli. As the spotlight is thought to constantly move between all possible target stimuli, the first prediction is that all unattended stimuli are suppressed individually. That is, we assume that a similar mechanism exists for both suppression and excitation. For the current experimental paradigm, such a mechanism would result in two peaks of suppression for both the divided attention condition and the undivided attention condition. The second prediction is that there will be no suppression of to-be-ignored stimuli, as the blinking spotlight of attention can be focused selectively on possible targets. Obviously, this should result in alpha topographies without peaks over occipito-parietal brain areas. The results of the current study are not in line with either of these possible predictions of the blinking spotlight model.

A third prediction refers to the possibility that, while the attentional focus switches rhythmically between all possible target locations, suppression is static, as for the divided spotlight account. Such a prediction fits with the current results, but would indicate that at least attentional suppression behaves according to the divided attention hypothesis. Taken together, the current results provide evidence that humans are able to divide spatial attention across two locations for a considerable amount of time, if the task requires them to do so.

**Suppressive mechanisms in divided attention**

A very interesting observation can be made for the alpha topographies in the divided attention conditions. For the undivided conditions, where participants try to suppress a whole visual hemifield, we find a large increase in alpha amplitude ipsilateral to the attended hemifield. However, in the divided attention conditions, alpha amplitudes show a large peak over the contralateral visual cortex. For example, in the ‘split right’ conditions, in which the inner left and outer right stimuli are attended to, we find a large alpha peak over the left occipito-parietal cortex. This peak has higher amplitude and a larger extent than the alpha peak over the right visual cortex. A very similar pattern holds for the ‘split left’ condition.

A likely explanation for this finding is that, under divided attention conditions, stimuli appearing in locations between target stimuli are especially distracting, as they are positioned between the targets and are close to the fixation location. It therefore seems especially important to suppress this intervening distractor location. In contrast, the unattended outer stimulus should interfere less with task demands, and therefore can receive less suppression. These results indicate that the brain can flexibly adjust suppression to changing task demands.

**Attentional demand**

Why do some studies find evidence for a divided attention model and others not? Reviewing the scientific literature, we find that a common difference between those studies in support of and against the divided spotlight concerns the number and nature of distracter stimuli. In most electrophysiological and neuroimaging studies providing evidence for a divided attentional spotlight (Muller et al., 2003a; McMains & Somers, 2004; Niebergall et al., 2011), as well as in the current study, the experimental task contained a small number of distracting stimuli that were continuously present and...
placed between to-be-attended stimuli at known locations. This experimental design allows participants to prepare for suppression of the distracters in order to deal more efficiently with the to-be-attended stimuli. Only one electrophysiological study using a comparable experimental design did not find any evidence for the divided spotlight (Heinze et al., 1994). However, this study employed a VEP paradigm with sudden-onset probe stimuli at distracter locations, which probably captured exogenous attention. Therefore, it is not clear whether attentional modulation of the distracter stimuli was attributable to a failure to divide the attentional spotlight or to exogenous grabbing of attention by the probe stimuli.

Most studies providing support for serial attentional deployment have not provided a priori-defined distracters located between attended stimuli. For example, in the electrophysiological studies of Woodman and Luck (Woodman & Luck, 1999, 2003), a visual search paradigm was used, providing evidence that possible target locations are examined in a serial fashion. In this visual search paradigm, participants do not know a priori where distracters or possible targets will occur. Therefore the optimal strategy is to enhance only possible target locations, which were defined by colors. Other studies have employed designs with a circular arrangement of stimuli, asking participants to detect targets in a number of possible locations (Barriopedro & Botella, 1998; Muller et al., 2003b; Thornton & Gilden, 2007; VanRullen et al., 2007; Dubois et al., 2009). Even though two of these studies found some evidence for a divided spotlight of attention (Thornton & Gilden, 2007; Dubois et al., 2009), they are often regarded as supporting a single spotlight model. The circular arrangement of stimuli works in such a way that the distracter stimuli are not directly between the attended stimuli. Having distracters in locations where they are not very distracting or in locations that are not defined a priori probably affects the demand of the attentional system to suppress them.

Attentional resources in humans are limited in terms of the number of objects or locations that can be processed simultaneously (e.g. Trick & Pylyshyn, 1993); for a review, see Cavanagh & Alvarez (2005). In the current study, there might be a neurophysiological correlate of this limitation. We find that the peak alpha amplitude in the divided attention condition is about half the amplitude in the undivided condition. The divided spotlight of attention account predicts that the number of to-be-ignored locations increases from one in the undivided condition to two in the divided attention condition. Our data therefore indicate that there is a relationship between an increase in the number of suppressed locations and reduction in the amplitude of the measure of attentional suppression. Such a relationship would logically result in a limit on the number of locations/objects that can be suppressed, because, at some point, the amplitude of suppressive alpha oscillations might become too small to be effective. Because, in many circumstances, the enhancing and suppressive effects of attention are closely related (Pinsk et al., 2004; Frey et al., 2010), this decrease in suppressive alpha amplitude might directly affect the number of objects that can be processed simultaneously. Given this reasoning, it seems reasonable that the brain is able to employ a divided spotlight of attention for only a limited number of stimuli/objects. Whenever the threshold is crossed, the attentional system might settle into a blinking mode (VanRullen et al., 2007) or settle into a serial search.

We therefore hypothesise that a divided spotlight of attention can only be achieved with a limited number of stimuli and distracters, which forces the attentional system to suppress them on the basis of their location and nature. It may even be that attentional suppression is a necessary prerequisite for having a divided spotlight of attention. This idea is somewhat at odds with the hypothesis of Cave et al. (2010), who proposed a model with four different modes of attention, with selection of non-contiguous regions of space and inhibition of distracter locations as separate modes. Examining the limits of divided attention and its relationship with suppression is therefore an interesting avenue for future research.

**Theoretical considerations**

In their review on attention to multiple stimulus locations, Jans et al. (2010) introduce several lines of evidence for their argument that divided attention is unlikely to be a standard feature of the attentional system. For example, they point out that the saliency map (Koch & Ullman, 1985), an influential model for visual attention, encodes relevance in a single spatial location. However, Jans et al. did not clearly mention that the original description of the saliency map model was based on psychophysical experiments in support of a serial model of visual search (Treisman & Gelade, 1980), and therefore implements a winner-take-all process in selecting a single location at a time. Put another way, the saliency map model was defined on the basis of the experimental results at the time when it was invented, and the predominant view of visual attention was that involving a serial process. Therefore, the saliency map is not a valid model with which to generate hypotheses regarding whether or not the attentional spotlight can be divided.

**Timing of attentional modulation**

The current study did not provide evidence that the earliest detectable evoked activity is modulated by attention for all stimuli across the visual field. In only one of the four locations did we find significant modulation of this C1 component. The evoked activity in this time range is thought to largely represent processing in V1 (Kelly et al., 2013), with possible contributions from extrastriate areas V2 and V3 (Ales et al., 2010b). Our results could therefore be interpreted as evidence for attention not modulating afferent activity in early visual areas. However, they could also indicate that only one stimulus was in a location for which we could observe attentional modulation. The difficulty in obtaining robust C1 responses has been described in detail by Kelly et al. (2008). For a large number of participants in their study, a stimulus in the upper left hemifield was optimal. This location is comparable to that for which we find clear modulations in the C1 time-frame. Therefore, we interpret our results as indicating that divided spatial attention probably modulates the earliest evoked cortical activity. However, a paradigm with stimulus locations mapped to individual participants is necessary to provide evidence that this modulation occurs across the visual field.

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Conflicts of interest

All authors of this paper declare no conflicts of interest, financial or otherwise, that could have biased their contributions to this work. The senior author, J. J. Foxe, attests that all authors had access to the full dataset and to all stages of the analyses.

Abbreviations

EEG, electroencephalography; VEP, visual evoked potential.

References


