reactions consisting of 1 μl DNA, 1 μl Qiagen 10 × PCR buffer, 1 μl 2 μM dNTPs, 0.8 μl 25 mM $MgCl_2$, 1 μl 10 μM fluorescently tagged forward and reverse primers, 0.05 μl Qiagen *Taq* polymerase and 4.15 μl sterile water. All loci were amplified with the following programme: 94 °C for 4 min, 39 cycles of 94 °C for 30 s, 54 °C or 57 °C for 30 s and 72 °C for 1.5 min, then 72 °C for 6 min and pausing at 4 °C. Loci were detected on an ABI 377 automatic sequencer.

A single winged queen was used from each colony at Hidalgo and Junction to determine allele frequencies. For most colonies (73 of 76), the multilocus genotype of the queen could be classified into one of four distinct classes or lineages (see the text). The exceptions all possessed genotypes consistent with an F_1 hybrid between two lineages (heterozygous at all diagnostic loci); such queens were noted but excluded when calculating the allele frequencies of each lineage. Workers were used to calculate allele frequencies in the *P. barbatus* and *P. rugosus* populations.

MtDNA sequencing

We analysed a 433-base-pair portion of the mitochondrial gene *cox1*, encoding cytochrome oxidase *c* subunit I. *Pogonomyrmex californicus* was used as the outgroup for the analysis; this species has been placed in a different complex within the genus[17,18]. DNA was sequenced from a single winged queen or worker for five colonies of each lineage (determined from nuclear genotype) and the two parental populations. Universal insect *cox1* primers (forward, C1-J-1751; reverse, C1-N-2191) were used[19], except for the substitution of A for C at position 3 of C1-N-2191. DNA was amplified in 50-μl reactions (5 μl DNA, 5 μl Qiagen 10 × buffer, 4 μl 25 mM $MgCl_2$, 5 μl 10 μM forward and reverse primers, 20.75 μl water, 0.25 μl Qiagen *Taq* polymerase) and amplified with the following PCR conditions: 94 °C for 4 min, 35 cycles of 94 °C for 30 s, 48 °C for 30 s and 72 °C for 1.5 min, then 72 °C for 6 min and pausing at 4 °C. PCR products were purified with Qiaquick purification columns. Sequencing reactions and detection were performed by Microsynth GmbH, Switzerland. Both forward and reverse strands were sequenced.

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Correspondence and requests for materials should be addressed to S.H.C. (sara.helmscahan@ie-zea.unil.ch).

Sustained division of the attentional spotlight

M. M. Müller*, P. Malinowski†, T. Gruber* & S. A. Hillyard‡

** Institut für Allgemeine Psychologie, Universität Leipzig, Seeburgstrasse 14–20, 04103 Leipzig, Germany*
† School of Psychology, Liverpool John Moores University, 15–21 Webster Street, Liverpool L3 2ET, UK
‡ Department of Neurosciences, University of California at San Diego, 9500 Gilman Drive, La Jolla, California 92093-0608, USA

By voluntarily directing attention to a specific region of a visual scene, we can improve our perception of stimuli at that location[1]. This ability to focus attention upon specific zones of the visual field has been described metaphorically as a moveable spotlight or zoom lens that facilitates the processing of stimuli within its 'beam'[2,3]. A long-standing controversy has centred on the question of whether the spotlight of spatial attention has a unitary beam or whether it can be divided flexibly to disparate locations[2,4–6]. Evidence supporting the unitary spotlight view has come from numerous behavioural[3,7–10] and electrophysiological[11,12] studies. Recent experiments, however, indicate that the spotlight of spatial attention may be divided between non-contiguous zones of the visual field for very brief stimulus exposures (<100 ms)[13,14]. Here we use an electrophysiological measure of attentional allocation (the steady-state visual evoked potential) to show that the spotlight may be divided between spatially separated locations (excluding interposed locations) over more extended time periods. This spotlight division appears to be accomplished at an early stage of visual-cortical processing.

To study whether the beam of spatial attention may be divided over sustained periods of several seconds, we recorded frequency-coded steady-state visual evoked potentials (SSVEPs) to concurrently presented stimuli at attended and interposed unattended locations. 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[15]. Previous studies have shown that the SSVEP amplitude is substantially increased when attention is focused upon the location of the flickering stimulus[16,17]. The present study recorded SSVEPs to stimuli at four locations, each flickering at a different rate, so that measures of attentional allocation to spatially separated attended locations and interposed unattended locations could be obtained concurrently over periods of several seconds.

Informed consent was obtained from 15 subjects, who viewed the stimuli on a computer monitor while brain activity was recorded non-invasively from 30 scalp electrodes mounted in an elastic cap. During testing, the subject maintained fixation on a central white cross. The stimuli consisted of repetitively flashed white rectangles with superimposed red symbols that were presented at four positions along the horizontal meridian (Fig. 1). On each trial the rectangles were flashed continuously for 3.06 seconds at 15.2 Hz (position 1), 8.7 Hz (position 2), 20.3 Hz (position 3) and 12.2 Hz (position 4). Randomized sequences of five different symbols were presented at each location. Symbol presentations occurred in synchrony at the four locations with fixed durations of 181 ms.

The subject's task was to pay attention to the symbol sequences at two of the four positions, and to push a button upon detecting the simultaneous occurrence of a particular target symbol at those two positions. On separate blocks of trials, subjects were instructed verbally to attend to either the two left field positions (1 + 2), the two right field positions (3 + 4), or to two separated positions (1 + 3) or (2 + 4). Simultaneous target symbols occurred unpre-

Table 1 **Summary of behavioural results**

	TDR (%)	RT (ms)	FA (%)
Attend 1 + 2	79.8 ± 3.0	472.1 ± 10.1	4.8 ± 1.0
Attend 3 + 4	77.5 ± 3.2	467.1 ± 11.7	5.3 ± 1.2
Attend 1 + 3	84.0 ± 1.7	450.7 ± 8.6	4.4 ± 0.8
Attend 2 + 4	83.8 ± 2.1	462.4 ± 8.9	5.1 ± 0.9

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

dictably at the two attended locations (0–3 times per trial), as well as at the other locations.

The SSVEPs elicited by the flickering stimuli at the four positions were recorded concurrently, and as in previous studies[16,18] the maximum amplitudes at each frequency were observed at occipito-temporal scalp sites contralateral to the visual field of stimulation (Fig. 1). SSVEP waveforms were generally sinusoidal, with fundamental frequencies at the driving flicker rate. The SSVEP amplitudes for each attention condition and stimulus position were quantified by complex demodulation over the three-second trial epochs[15,16,19]. As in previous reports[16,18] SSVEP amplitudes were generally smaller for the higher flicker rates, but for all stimuli the amplitudes were enlarged when attention was directed to their position (Fig. 2a). These amplitude increases were significant over posterior, contralateral scalp sites for position 1 ($P < 0.04$), position 2 ($P < 0.005$), position 3 ($P < 0.04$) and position 4 ($P < 0.01$), under conditions where the two positions in one visual hemifield were attended.

For investigating the division of the attentional spotlight, the critical stimulus locations were the intermediate positions 2 and 3. The SSVEP to flicker at position 2 was significantly reduced during the attend 1 + 3 condition compared to the attend 2 + 4 condition ($P < 0.007$ at electrode sites showing the largest overall attention effects); similarly, the SSVEP to flicker at position 3 was smaller during attend 2 + 4 than during attend 1 + 3 ($P < 0.0005$). These results indicate that the SSVEP to an intermediate ignored position was reduced in relation to when that same position was attended, under comparable conditions of dividing attention between separated locations. These comparisons remained significant (both $P < 0.05$) when SSVEP amplitudes were tested across three standard posterior electrode locations (PO3/4, PO7/8, O1/2).

To illustrate these effects more clearly, the SSVEP amplitudes to stimuli at positions 2 and 3 were combined following normalization with respect to each subject's maximum amplitude (Fig. 2b). The normalized amplitude at these intermediate locations was significantly reduced when attention was directed to the surrounding flanking positions (unattended intermediate) in comparison to when those same locations were attended (attended separated) ($P < 0.0001$). Importantly, the reduced amplitude at the unattended interposed positions was not significantly different from that obtained when attention was directed to the two adjacent locations in the opposite visual field ($P =$ n.s.). There was also a small but significant tendency ($P < 0.05$) for the SSVEP amplitudes at attended positions 2 and 3 to be lower when attention was directed to two adjacent positions compared with two separated positions. This was paralleled in the behavioural data (Table 1) by a slightly reduced target detection rate during attention to adjacent relative to separated positions ($P < 0.02$). No significant differences were found in reaction time or false alarm rates among the different attention conditions.

To gain information about the cortical regions that mediate the divided allocation of attention, the scalp topographies of the SSVEP amplitude modulations with attention were mapped for stimulus positions 2 and 3 (Fig. 3). In both cases, the amplitude decrement for the interposed unattended location in relation to when the same stimulus was attended had a tightly focused voltage maximum over the occipital scalp contralateral to the visual field of the stimulus.

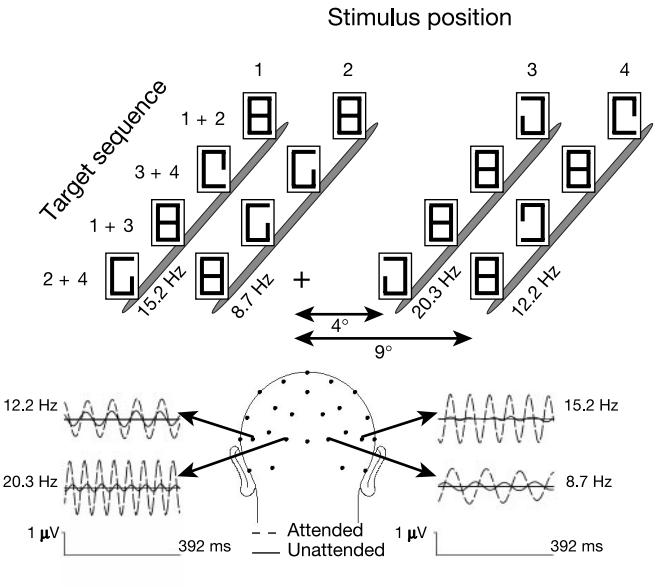

Figure 1 Schematic diagram of stimulus sequences, electrode positions and typical SSVEPs for attended (dashed lines) and unattended (solid line) conditions. Subjects reported simultaneous occurrences of the target symbol "8" at the two attended positions (either 2 + 4, 1 + 3, 3 + 4, or 1 + 2 on different blocks of trials). Stimulus sequences show examples of targets at the attended positions under the four conditions. SSVEP waveforms were obtained by a sliding average technique in the time domain[16,25]. SSVEPs shown were obtained under conditions of attention to positions 1 + 2 and to positions 3 + 4.

These SSVEP recordings provide evidence that the spotlight of spatial attention can be divided to facilitate processing of stimuli in spatially non-contiguous locations over periods of several seconds, which extends previous findings of split attentional foci for brief exposures[13,14]. A sustained division of attention could be inferred from the finding that SSVEP amplitudes were reduced at interposed unattended locations to the same degree as when attention was directed to adjacent stimuli in the opposite visual field. If attention had been divided only for brief, intermittent periods during task performance, one would expect less amplitude reduction at the interposed location than when attention was fully dedicated to the opposite field. The high level of accuracy at detecting the simultaneous targets in the separated positions (83–84% detection rate) with relatively few false alarms (4–5%) provides further evidence for a sustained rather than intermittent division of the attentional spotlight.

The use of brief (181 ms) target durations rules out the possibility that subjects were rapidly switching attention between the separated locations to achieve accurate performance rather than dividing attention between the locations. Although different studies have obtained varying estimates of the minimal time for switching attention, there is general agreement that the minimum time needed to identify a target at one location and then switch attention to identify a target at a second location is in the range of 200–500 ms (refs 20–24). Accordingly, the 181 ms durations used in the present study would make it impossible to achieve a high rate of target-pair detections using such a strategy.

The observed SSVEP amplitude modulations cannot be explained as a consequence of a single focus of attention being expanded to encompass the separated locations (that is, in the manner of a zoom lens). Such an expansion would necessarily include the intermediate position, and hence would result in an enhanced SSVEP for that position relative to positions outside the attended region, a pattern that was not observed. Moreover, the critical comparisons here were matched for the spatial separation of

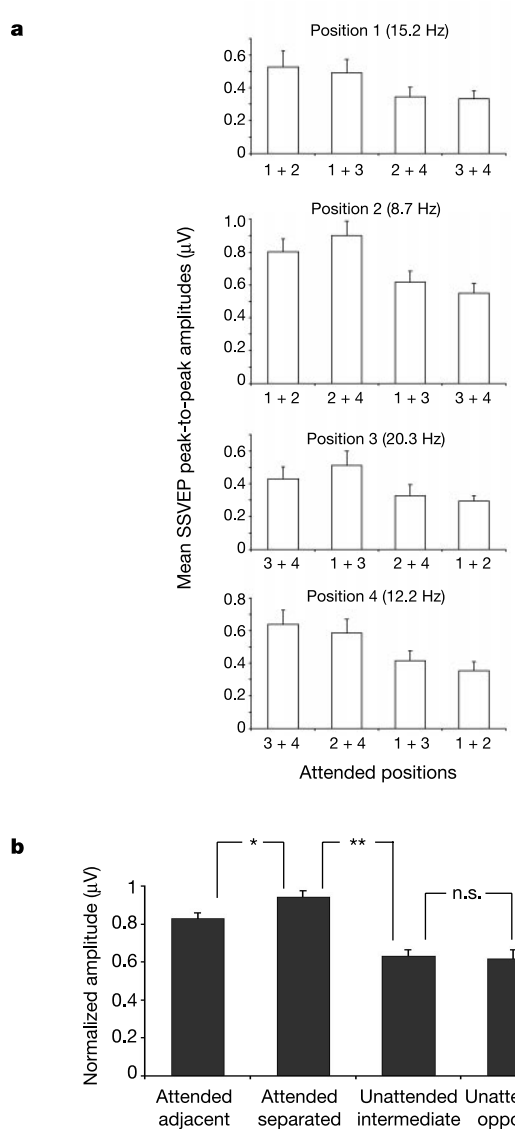

Figure 2 Mean SSVEP amplitudes at each position under the four experimental conditions and normalized amplitudes averaged across the 8.7 Hz and 20.3 Hz SSVEPs. **a**, Mean SSVEP peak-to-peak amplitudes (+ standard errors) at each position under the four experimental conditions averaged across 14 subjects. SSVEP amplitudes were obtained from electrode locations showing the largest overall attention effect. **b**, Normalized amplitude values averaged across the 8.7 Hz and 20.3 Hz SSVEPs (at positions 2 and 3, respectively) under different attention conditions. **Indicates the highly significant difference ($P < 0.0001$) between the conditions when the 8.7 Hz and 20.3 Hz stimulus sequences were attended (that is, attend 2 + 4 for 8.7 Hz and attend 1 + 3 for 20.3 Hz) as compared to conditions when these positions were intermediate and ignored (that is, attend 1 + 3 for 8.7 Hz and attend 2 + 4 for 20.3 Hz). *Indicates the significant difference ($P < 0.05$) between conditions when adjacent positions were attended (that is, attend 1 + 2 for 8.7 Hz and attend 3 + 4 for 20.3 Hz) as compared to conditions when separated positions were attended (that is, attend 2 + 4 for 8.7 Hz and attend 1 + 3 for 20.3 Hz). No significant differences were found when comparing unattended intermediate positions versus unattended positions in the hemifield opposite to the attended adjacent positions.

the attended locations, and both the behavioural and SSVEP results suggest that there was no cost for attending to two separated positions in comparison with attending to two adjacent positions (indeed, a slight advantage for the separated positions was obtained). This contrasts with findings of reduced performance during attention to larger areas as predicted by the zoom lens model[3], and raises questions about the applicability of this model to

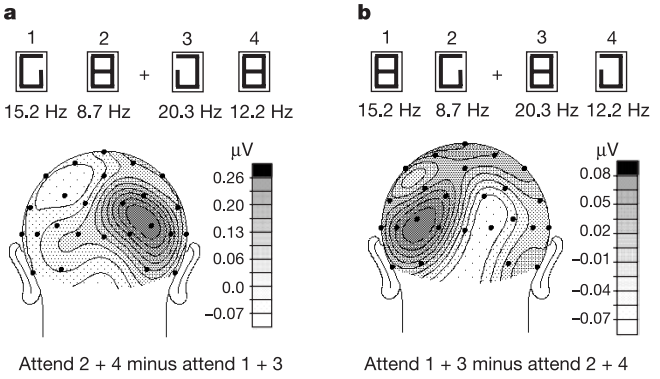

Figure 3 Spline-interpolated isocontour maps of the grand average attend minus unattend amplitude under conditions of attending to separated locations. Data are shown for the 8.7 Hz SSVEP amplitude at position 2 (**a**) and the 20.3 Hz SSVEP at position 3 (**b**). Note the different voltage scales for the two maps.

continuously presented stimuli as in the present design. Previous studies of SSVEPs have similarly found evidence for highly flexible allocations of attention to flickering stimulus patterns (for example, to stimuli in the form of a ring, excluding the centre[25]). This suggests that spatial allocation of attention may be governed by different principles for continuously presented (for example, flickering) stimuli than for briefly flashed stimuli, and it seems reasonable to propose that the former may more closely simulate the natural environment of relatively permanent objects.

The lateral occipital scalp topography of the SSVEP modulations during divided attention is consistent with neural activity localized to extrastriate visual cortical areas of the occipital lobe[16,26,27]. Previous studies using both steady-state and transient stimulation have found that stimuli falling within the spotlight of attention elicit enhanced neural responses in extrastriate visual cortex[16,28,29], and that this facilitation of attended signals occurs early in visual processing, with a latency or phase lag of 80–140 ms following stimulus onsets[17,29]. The present findings provide evidence that the spotlight may be divided for sustained periods, thereby facilitating inputs from separated locations at the level of the extrastriate occipital pathways. This would appear to be a highly efficient early selection mechanism for distributing attention optimally to dispersed stimuli in the visual surroundings. □

Methods

Stimuli

Stimuli were presented against a dark background at four different locations, lined up along the horizontal meridian of a 19-inch computer monitor set to a resolution of 800 × 600 pixels with a refresh rate of 60.8 frames s^{-1}. At a viewing distance of 70 cm, each individual white rectangle subtended a viewing angle of 2.5 × 3.2° with an eccentricity of 4° for the medial and 9° for the lateral rectangles, respectively (distance between the inner edges of the elements to the central fixation cross). As depicted in Fig. 1, the rectangles at positions 1 to 4 flickered at rates of 15.20 Hz, 8.69 Hz, 20.27 Hz and 12.16 Hz, respectively, corresponding to cycle durations of 4, 7, 3 and 5 frames. Each rectangle was 'on' for 1 frame (16.45 ms), followed by the appropriate number of 'off' frames to achieve the respective stimulation frequency (for example, one 'on' frame followed by 3 'off' frames for 15.20 Hz). Five different symbols were used, with one symbol serving as the target. The symbols were presented simultaneously at the 4 locations for 11 frames (180.95 ms) followed immediately 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. Target symbols occurred equally often at all stimulus positions, following randomized sequences.

Experimental procedure

Each trial lasted 3,060 ms, and perfect synchronization of all four flicker frequencies was set at 526 ms after flicker-onset, which served as reference point for extracting epochs for electroencephalogram (EEG) analysis. The fixation cross and four rectangles that outlined the stimulus positions remained visible during the inter-trial intervals. On about 75% of the trials, between one and three target pairs (simultaneous occurrences at the two attended locations) were randomly presented. Paired targets were separated by a

minimum interval of 905 ms (55 frames). The experiment consisted of 12 blocks of 40 trials each, resulting in 120 trials per experimental condition. Blocks were administered in random order. The responding hand was changed halfway through the experiment, and the sequence of hand usage was counterbalanced across subjects. One subject was excluded from further analysis because of difficulty in detecting the matching symbols.

Data acquisition

The electrode positions shown schematically in Fig. 1 are specified in a previous report[30]. The EEG was recorded with a sampling rate of 250 Hz and a bandpass of d.c. to 50 Hz. Individual trials were discarded on the basis of blink or electromyogram (EMG) artefacts in the scalp channels exceeding 75 μV, or when lateral eye movements monitored in the horizontal electro-oculogram (EOG) deviated more than 11 μV (1°) from fixation. These stringent criteria resulted in a mean rejection rate of 30% of the trials. In order to analyse the SSVEP, artefact-free EEG epochs were averaged separately for each experimental condition and algebraically re-referenced to averaged mastoids by subtracting one-half of the averaged signal recorded from the mastoid opposite the reference mastoid from the averaged signals at each scalp site. The averaging epochs extended from 500 ms before to 2,500 ms after the time point when all streams were synchronized (that is, from 26 to 3,026 ms after flicker onset). SSVEP amplitudes were extracted by means of complex demodulation of the averaged waveforms[15,19,25]. To avoid including the visual evoked response to flicker onset in the SSVEP measurements, the first 500 ms of each epoch were excluded from analysis. Thus, mean SSVEP amplitudes were calculated over the interval 526 to 3,026 ms after flicker onset.

Data analysis

For testing the significance of SSVEP amplitude changes, the posterior electrode site that exhibited the largest overall attention effect (comparing attended versus ignored positions) was selected for each subject. These amplitude values were subjected to paired *t*-tests between conditions, and corrected for multiple comparisons by the Bonferroni–Dunn criterion. As a reliability check, the averaged amplitudes across three standard electrode locations (PO3/4, PO7/8 and O1/2) were also subjected to paired *t*-tests for the attended versus ignored SSVEPs at 8.69 Hz and 20.27 Hz under conditions of attention to separated locations.

Only button-presses occurring between 250 and 1,000 ms after target-pair onset were accepted as correct detections. False alarms for the adjacent condition were defined as button presses occurring in response to a target presented at only one of the attended locations. For the separate conditions, false alarms were defined as button presses in response to a target presented in only one of the attended locations and/or in the intermediate to-be-ignored position. Target detection rates, reaction times and false alarms were tested by one factor repeated measures analysis of variance (experimental condition).

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Correspondence and requests for materials should be addressed to M.M.M. (m.mueller@rz.uni-leipzig.de).

Perceptual consequences of centre–surround antagonism in visual motion processing

Duje Tadin, Joseph S. Lappin, Lee A. Gilroy & Randolph Blake

Vanderbilt Vision Research Center, Vanderbilt University, 111 21st Avenue South, Nashville, Tennessee 37203, USA

Centre–surround receptive field organization is a ubiquitous property in mammalian visual systems, presumably tailored for extracting image features that are differentially distributed over space[1]. In visual motion, this is evident as antagonistic interactions between centre and surround regions of the receptive fields of many direction-selective neurons in visual cortex[2–6]. In a series of psychophysical experiments we make the counterintuitive observation that increasing the size of a high-contrast moving pattern renders its direction of motion more difficult to perceive and reduces its effectiveness as an adaptation stimulus. We propose that this is a perceptual correlate of centre–surround antagonism, possibly within a population of neurons in the middle temporal visual area. The spatial antagonism of motion signals observed at high contrast gives way to spatial summation as contrast decreases. Evidently, integration of motion signals over space depends crucially on the visibility of those signals, thereby allowing the visual system to register motion information efficiently and adaptively.

Centre–surround neurons, especially those in the middle temporal visual area (MT), are believed to be crucially involved in the perception of object motion[3,7], in figure–ground segmentation[7–9] and in the registration of three-dimensional shape from motion[9,10]. By analogy with other aspects of vision[11], if centre–surround antagonism is an integral part of motion processing, we should expect to see a perceptual signature of this antagonism in the form of impaired motion visibility with increasing stimulus size. However, existing evidence shows that increasing the size of a low-contrast moving stimulus enhances its visibility[12,13], presumably

