



Watching where you look: modulation of visual processing of foveal stimuli by spatial attention

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Received 16 February 2001; received in revised form 15 May 2002; accepted 22 May 2002

Abstract

Two experiments investigated the effect of sustained selective spatial attention upon the perceptual analysis of stimuli within the center of gaze. Spatial attention has typically been studied in relation to peripheral stimuli, and its relevance to the processing of central stimuli has remained relatively ignored. Here, behavioral measures in normal human volunteer participants showed that focused spatial attention can also influence responses to central stimuli, over and beyond the advantage conferred by their foveation. Event-related potentials (ERPs) showed that the action of attention upon foveal stimuli included the modulation of perceptual processing in extrastriate visual areas. Surprisingly, the visual modulation revealed an intriguing and consistent pattern of hemispheric asymmetry, in both experiments. These findings show that in addition to the established right hemisphere dominance of the brain areas that direct attention, the consequences of directed attention may also be asymmetrical.

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Keywords: Visual processing; Foveal; Event-related potential; Selective attention

1. Background

The ability to focus resources selectively on specific peripheral locations covertly, without accompanying eye movements, is firmly established [32]. Mechanisms governing selective spatial attention to peripheral stimuli have been under intensive investigation, and have been shown to involve perceptual modulation of visual information [15,19,36]. Looking straight ahead at the relevant stimulus, however, is the most obvious mode of visual selective attention, where foveation inherently enhances the relevant image. Interestingly, whether and how selective spatial attention may affect foveal stimuli remain largely unexplored.

Brain imaging experiments have compared conditions in which attention is directed toward stimulation at the center of gaze or toward stimulation in a more peripheral, extrafoveal ring [34]. Comparison of foveal and extrafoveal attention conditions resulted in modulation in several visual areas in a retinotopic manner, including primary visual cortex. These results show that attention to foveal stimuli can

have physiological consequences in the visual system, but do not reveal the timing or the dynamic mechanisms involved. In addition, foveal and extrafoveal stimuli were presented concurrently, making it difficult to isolate the modulations that were specific to processing the foveal stimulus. For example, the overall modulation of visual areas mapping the center of gaze may have occurred late, reflecting modulation in top-down signals into visual areas [30,33]; or may have resulted from relative enhancement or inhibition of processing of the concurrent peripheral stimulus.

Event-related potentials (ERPs) provide on-line measures of stimulus processing that permit the analysis of transient modulations in early visual activity. Previous ERP experiments of visual selective attention have almost exclusively concentrated on peripheral stimuli, with only a few exceptions. To our knowledge, the investigations by Neville and Lawson [27–29] were unique in testing the effects of focused spatial attention upon foveal as well as peripheral stimuli. Participants discriminated the apparent direction of motion in rare target stimuli at a particular location. Stimuli were small (0.5°) and brief (33–66 ms). Visual processing of both foveal and peripheral stimuli was modulated by attention at both the P1 and N1 stage. Their finding suggests that extrastriate visual processing of foveal stimuli is permeable to the effects of selective spatial attention. Mangun and Hillyard [22,23] also used stimuli centered on the vertical midline,

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but elevated above the horizontal meridian. In their tasks, participants discriminated small changes in stimulus heights, which occurred around 5° elevation. Therefore, though some stimuli were not lateralized, they were not foveal either. In the case of elevated stimuli along the vertical meridian, enhancement of visual ERP components was also observed.

Here, we used ERPs to investigate spatial attention to foveal stimuli in two experimental tasks. The study replicates and extends the investigations by Neville and Lawson [27–29]. Denser electrode sampling provides improved spatial resolution of the effects. The general nature of the effect of spatial attention upon foveal stimuli was tested by using different types of stimuli and different behavioral tasks. Stimuli were suprathreshold and stationary. Target detection required judgments either about the temporal duration (Experiment 1) or the shape (Experiment 2) of stimuli. We showed that perceptual analysis of retinally optimized foveal stimuli could be further influenced by selective spatial attention, and discovered a striking and reproducible hemispheric asymmetry in the attentional modulation of the foveal space.

2. Materials and methods

Two experiments manipulated the direction of sustained visual attention to displays with foveal and peripheral stimuli. In both the cases, participants viewed a display in which transient stimuli appeared briefly in the center of gaze or at one of two symmetrically placed peripheral locations (Fig. 1). Across attention conditions, participants either *focused* attention at one location to detect target stimuli or *divided* attention to detect target stimuli at any location. Behavioral and ERP measures were obtained during task performance. In Experiment 1, the target was defined by having a slightly shorter duration. In Experiment 2, the target was defined by a change in its shape. Except for differences in the behavioral target-detection tasks and in the subject populations, the methods in the two experiments were equivalent. The experimental protocol had ethical approval from the Department of Experimental Psychology, University of Oxford.

2.1. Participants

Seventeen healthy volunteers participated in Experiment 1. Five were disqualified from the analysis: four because of small but systematic eye movements, and one for excessive alpha frequency in the electroencephalogram (EEG). The remaining 12 participants (mean age of 23 years, six females) were right handed [mean score on the Edinburgh handedness inventory: +92] and had normal or corrected to normal visual acuity.

Fourteen healthy volunteers participated in Experiment 2 (mean age of 21 years, nine females). All were right handed [mean score on the Edinburgh handedness inventory: +90] and had normal or corrected to normal visual acuity. Behavioral data from two participants could not be analyzed because of technical problems.

2.2. Behavioral task

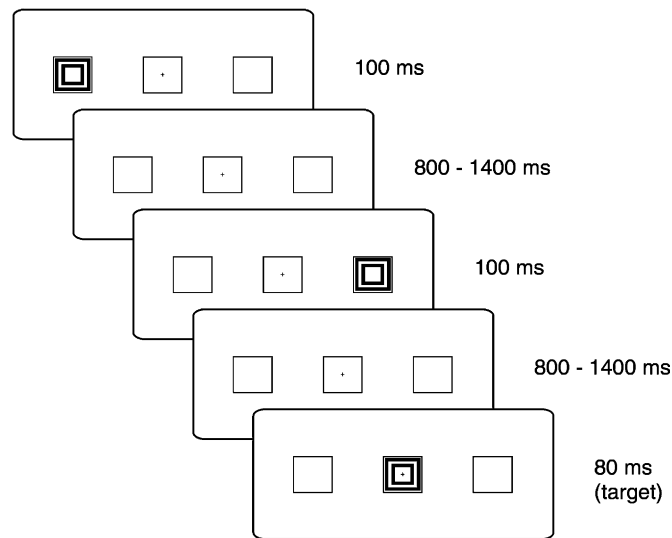
The baseline display of the tasks consisted of three square boxes (1.8° side) aligned along the horizontal meridian. Two boxes were located peripherally (midpoint at 7.5° eccentricity) and one was located centrally. Stimuli appeared briefly inside each of the boxes in random order at an unpredictable rate [800–1400 ms randomized inter-stimulus interval (ISI)]. Across task conditions, participants *focused* attention and detected targets at one location while ignoring the other locations, or *divided* attention to detect targets in all locations. They were instructed to press a key with the index finger of the right hand as quickly as possible following onset of the target. Most of the stimuli (80%) did not require a behavioral response (standards). In both the experiments, standard stimuli consisted of a pattern of two concentric squares (1.5 and 0.9° widths) presented for 100 ms. In Experiment 1, target stimuli were defined by a temporal attribute—their shorter duration (55 ms). In Experiment 2, target stimuli were defined by a visual attribute. The inner square was slightly smaller and displayed in a thinner line. The exact visual attributes for foveal versus peripheral targets were adjusted so that they were equally difficult to detect over a group of eight participants tested in a behavioral pilot experiment.

Only the details about target characteristics and distribution and the number of trials differed between the two experiments. In Experiment 1, targets appeared at the relevant location(s) only. Participants performed 16 experimental blocks, each consisting of 130 trials: 40 standard trials at each location [left visual field (LVF), central (foveal), right visual field (RVF)] and 10 target trials at the relevant location(s). No targets appeared at irrelevant locations. Participants *divided* attention between all three locations in four blocks, and *focused* attention to each stimulus location in four blocks. In Experiment 2, participants completed 12 blocks of 128–132 trials each. Participants *divided* attention between all three stimulus locations in three blocks, and *focused* attention to each stimulus location in three blocks. In both the experiments, blocks of practice trials preceded the experimental blocks until the participants were comfortable with the task.

In both the experiments, participants performed the task facing a computer monitor (100 cm distance) in a sound attenuated and electrically shielded room. The order of attention condition was randomized. At the onset of each block, a message on the monitor instructed participants about the relevant target location(s) and requested them to maintain central fixation on a cross (0.1° × 0.1°), and to avoid moving or blinking the eyes.

The effects of attentional focus (focused, divided) and stimulus location (left, foveal, right) upon behavioral performance were evaluated using repeated-measures ANOVAs on mean reaction times (RTs) and accuracy measures. The criterion and d' for target detection were also compared for Experiment 1. The effects of the direction of attention could not be evaluated between the three different *focused*

Experiment 1



Experiment 2

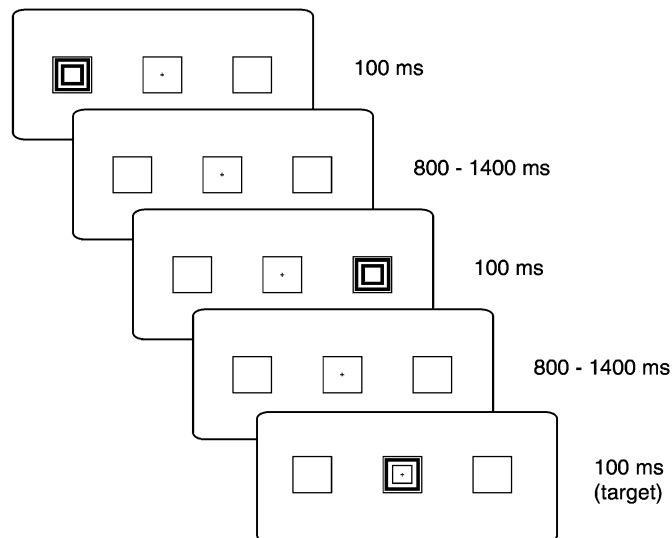


Fig. 1. Task schematics. Participants fixated a small cross ($0.1^\circ \times 0.1^\circ$) at center of the screen and monitored for the appearance of infrequent target stimuli at the instructed relevant location(s). Targets were defined by their shorter duration in Experiment 1, or by their visual shape in Experiment 2. In *divided* attention conditions, all locations were relevant. In *focused* attention conditions, participants detected targets at only one location. White stimuli were presented on a black background. Standard stimuli were concentric white squares (1.5° and 0.9° widths) that appeared at a randomized rate, 800–1400 ms inter-stimulus interval.

attention conditions, since participants did not respond to targets at the irrelevant locations.

2.3. Event-related potentials

ERPs were obtained from 56 scalp sites using standard procedures in our laboratory [26]. Recording electrodes included eight midline sites (FPZ, FZ, FCZ, CZ, CPZ, PZ, POZ, OZ) and 24 lateral pairs (FP1/2, AF3/4, AF7/8, F3/4, F5/6, F7/8, FC1/2, FC3/4, FC5/6, FT7/8, C3/4, C5/6, T7/8, CP1/2, CP3/4, CP5/6, TP7/8, P3/4, P5/6, P7/8,

PO3/4, PO7/8, O1/2, and mastoids). Data were recorded continuously (0.03–100 Hz band pass filter; 20,000 \times amplification; 250 Hz sampling rate, Neuroscan software). The right mastoid was the active reference, and the data were re-referenced off-line to the algebraic average of the two mastoids. The ground electrode was placed between FPZ and FZ. Electrooculogram (EOG) signals were recorded bipolarly. Horizontal EOG was recorded with electrodes on the outer canthus of each eye. Vertical EOG was recorded using electrodes above and below the right eye.

In addition, the direction of eye gaze was monitored using an infrared camera and video system, with $>0.1^\circ$ theoretical precision (iView, SMI). Eye gaze position was sampled at a rate of 60 Hz, using a calibration area of 544×408 pixels covering $34.3^\circ \times 25.7^\circ$ visual angle. The resulting resolution was based on the pixel size, and was therefore near 0.063° .

EEG data were segmented off-line into ERP epochs around standard stimuli (-200 to 600 ms). Trials containing incorrect behavioral responses, eye movements, or EEG artifacts (e.g. blinks or excessive drift) were rejected. Eye movements were identified by inspecting visually the EOG traces and the infrared eye gaze traces and fixations for each trial. Average EOG and infrared eye gaze traces were generated for individual participants and for the group in order to test for systematic differences in saccades or gaze. Average direction of gaze for each experimental condition was calculated between 0 and 600 ms after stimulus onset in all experimental trials analyzed.

In Experiment 1, nine types of ERP waveforms were constructed according to stimulus location (left, foveal, right) and the direction of attention (left, foveal, right) in the focused conditions. For technical reasons it was not possible to construct ERP waveforms for the *divided* attention condition. In Experiment 2, 12 types of ERP waveforms were constructed, including also the *divided* attention conditions: stimulus location (left, foveal, right) and the direction of attention (left, foveal, right, divided).

For both experiments, we compared the effects of sustained spatial attention on standard stimuli in the *focused* attention conditions. This avoided the contribution from potentials linked to response-related variables, and isolated the effects of the direction of selective spatial attention. Standard stimuli were identical in the two experiments, thus facilitating comparison of the results. In Experiment 2, we also compared the effects of focused versus *divided* attention directed toward foveal stimuli.

ERP effects were evaluated using repeated-measures ANOVAs that tested the factors of direction of attention, stimulus location, electrode site, and scalp hemisphere where appropriate. The Greenhouse–Geisser epsilon correction for non-sphericity was used where required [17]. ERP components were measured relative to the 200 ms pre-stimulus baseline. Identifiable visual components, P1 and N1, were analyzed at the three lateral occipital pairs and the latency windows where they were maximal. P1 amplitude was analyzed at PO3/4, PO7/8 and O1/2 between 80 and 120 ms. N1 was analyzed at P5/6, P7/8 and PO7/8 between 140 and 200 ms. For peripheral stimuli, only the mean amplitude values were analyzed. For foveal stimuli, both mean and peak amplitudes were analyzed, as well as the peak latency. Mid-latency (Nd2) [7,24] and long-latency (P3) [16,36] effects previously described under situations of sustained selective spatial attention to peripheral stimuli were also analyzed. Nd2 and P3 were tested over midline electrodes FZ, CZ and PZ between 200 – 280 and 250 – 550 ms, respectively.

3. Results

3.1. Experiment 1

3.1.1. Behavioral results

Accuracy of task performance was very high in all cases (95% mean value overall). Percentage correct, d' and criterion did not differentiate between attention conditions. In general, criterion levels were lower for foveal stimuli as compared to peripheral stimuli. Behavioral RT results (Fig. 2a) showed that participants were faster to detect stimuli under *focused* attention conditions than under *divided* attention conditions [$F(1, 11) = 8.95$, $P < 0.05$]. The RT advantage was also present when comparing in particular the detection of foveal targets under focused and divided conditions {post-hoc comparison of means [$F(1, 11) = 7.46$, $P < 0.05$]} and when comparing detection of left targets under focused and divided conditions {post-hoc comparison of means [$F(1, 11) = 9.64$, $P < 0.05$]}. The location of the targets also influenced performance significantly [$F(2, 22) = 4.89$, $P < 0.05$]. Directed comparisons of means using the Helmert test and the Geisser–Greenhouse correction showed that RTs were slower for LVF stimuli compared to both foveal and RVF stimuli [$F(1, 11) = 8.46$, $P < 0.05$]. RTs to foveal and RVF stimuli did not differ significantly from one another. Attention condition did not interact significantly with stimulus location. The behavioral advantage for detecting foveal targets under sustained *focused* attention implied that selective-attention mechanisms operated upon foveal stimuli, and warranted the ERP investigation of the underlying brain mechanisms.

3.1.2. Effects of spatial attention on ERPs to foveal stimuli

Analysis of ERPs was restricted to participants who were able to control their gaze at the center of the screen, and to trials that were free of behavioral or EEG artifacts. Trials were eliminated for incorrect behavioral responses (6.7%), deviation of eye gaze position (1.7%) or EEG artifacts (4.9%) (these sources of artifact could overlap in any given trial). No residual systematic biases in gaze (Fig. 2b) or eye movement (HEOG traces in Figs. 3a and 4) were present in the data.

Attentional modulation of ERPs elicited by foveal stimuli was tested as a function of the three possible directions of *focused* attention (LVF, foveal, RVF). Fig. 3a shows the ERPs elicited by foveal stimuli over relevant posterior electrode sites where visual components were analyzed, and at one representative midline site. The earlier P1 component reflecting extrastriate visual activity [3,15] appeared larger when attention was focused on the foveal space. Statistical analysis did not confirm any significant effects of *focused* attention. No significant modulation was obtained for the mean amplitude, peak amplitude or latency of the P1.

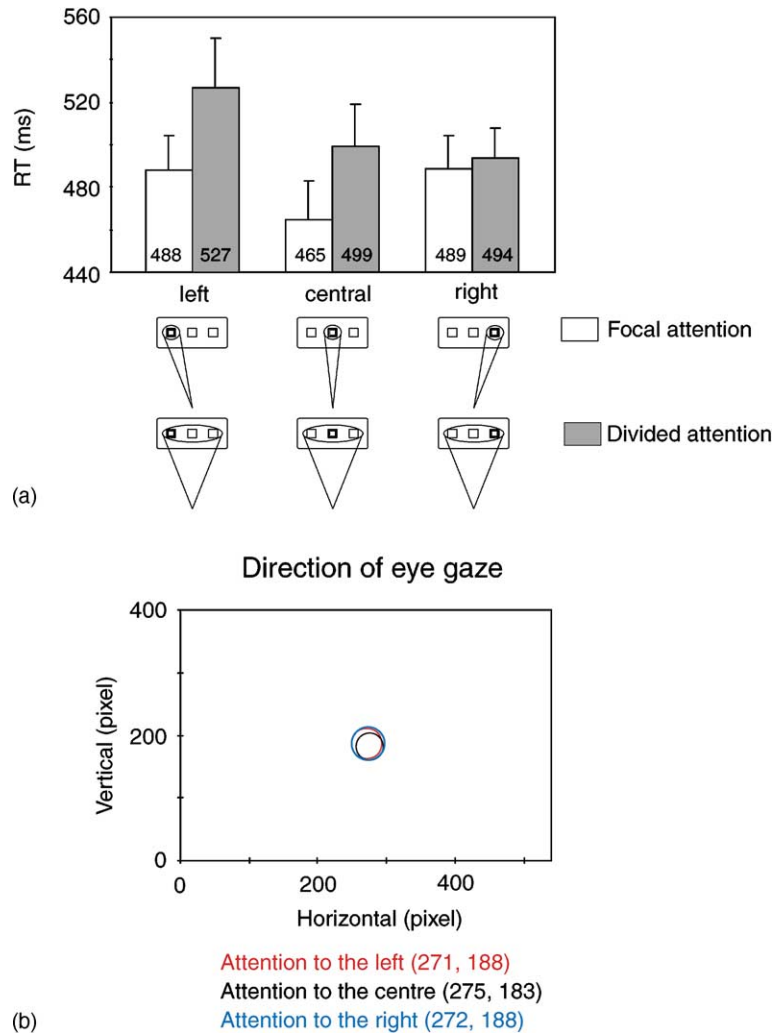


Fig. 2. (a) Behavioral results from Experiment 1. The graph shows mean RTs and standard errors to detect target stimuli in the *focused* and *divided* attentional conditions, at LVF, foveal, and RVF locations. (b) Mean direction of gaze during task performance in the three *focused* attention conditions (LVF, foveal, RVF). The center of the circle represents the mean center of gaze, and the radius represents the standard error. The fixation crosshair during the tasks was placed at pixel location (272, 188). Gaze direction was highly overlapping within and between the participants and did not show any reliable statistical variation.

In contrast, the peak and mean amplitude of the visual N1 component showed significant modulation by the direction of attention [F 's ≥ 6.7 , $P < 0.05$]. Interestingly, the attention effects showed a strong hemispheric asymmetry. When the three attention conditions were compared together (LVF, foveal, RVF), the factor of attention interacted with hemisphere [F 's ≥ 13.21 , $P < 0.05$]. Directed post-hoc comparisons between pairs of attention conditions were performed in order to identify the constituent effects. The contrast between LVF and RVF attention revealed a main effect of attention [F 's ≥ 7.04 , $P < 0.05$] and an interaction between attention and hemisphere [F 's ≥ 10.27 , $P < 0.05$]. The effects of peripheral attention upon the processing of central stimuli were larger over left hemisphere sites. The contrast between foveal and RVF attention also revealed a main effect of attention [F 's ≥ 9.30 , $P < 0.05$] and an interaction between attention and hemisphere

[F 's ≥ 12.81 , $P < 0.05$]. Attention effects occurred over both hemispheres, but were larger over the left sites. The contrast between foveal and LVF attention revealed only an attention \times hemisphere interaction when using peak amplitudes [$F(1, 11) = 10.27$, $P < 0.05$]. In this case, modulation of N1 was restricted to the right hemisphere sites.

Mid- and long-latency effects of attention modulation upon central stimuli were also observed. The Nd2 effect was obtained as an interaction between attention focus and electrode [$F(2.2, 23.9) = 10.43$, $P < 0.05$]. The largest difference occurred at CZ, where the voltage was more negative when attention was correctly allocated to the foveal location. Direction of attention to the LVF or RVF resulted in similar, more positive voltage in this scalp region. The relative polarities reversed toward more anterior electrode sites, where the voltage was more positive when attention was directed foveally compared to when attention was diverted

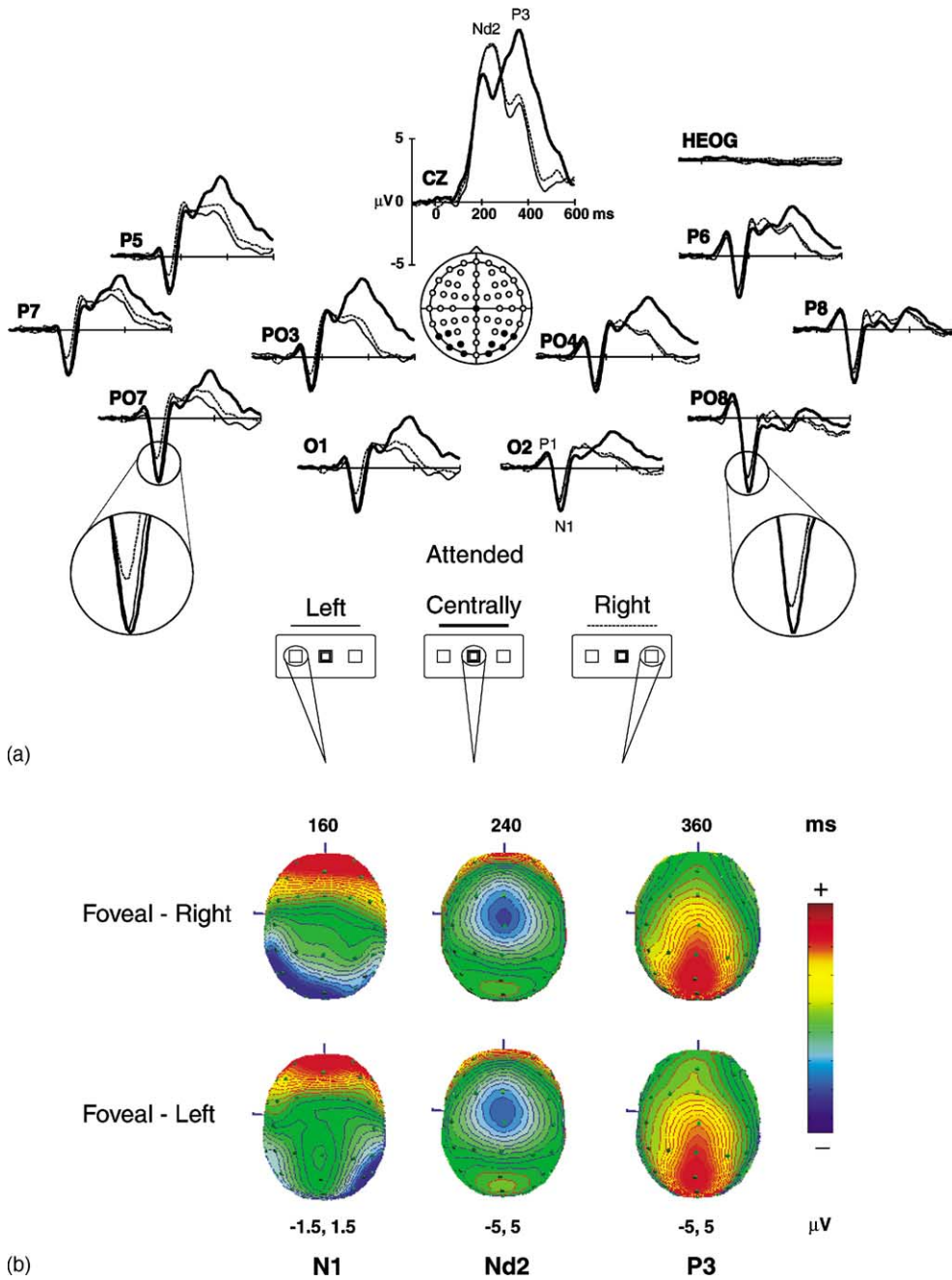


Fig. 3. Modulation of foveal stimuli by the direction of focused spatial attention in Experiment 1. (a) Grand-averaged ERPs elicited by foveal stimuli under the three directions of *focused* attention at posterior lateral sites, where the visual components (P1 and N1) were analyzed; and at a representative midline electrode (CZ), where the later components (Nd2 and P3) were analyzed. The electrode montage is shown, with the displayed sites shaded black. Voltage is plotted with positive values upward in this and all ERP figures. The first discernible visual component (P1) was not significantly modulated by selective spatial attention. In contrast, the visual N1 component showed strong and asymmetrical modulation over the left and right scalp sites according to the direction of attention. Modulation of the N1 component is magnified for electrodes PO7/8 to ease viewing. The N1 components elicited by LVF and RVF stimuli overlap completely in the magnified PO8 electrode, making it difficult to discern them. (b) Scalp topographies (ASA software, A.N.T.) of significant ERP effects. Processing of foveal stimuli is compared when attention is directed correctly to the fovea versus to the RVF (top row) or to the LVF (bottom row). The voltage amplitudes are plotted at the latency where each effect was maximal (indicated above maps), and are normalized to the greatest positive and negative voltage values in each case (indicated below maps). Positive relative voltage is plotted toward red values and negative relative voltage is plotted toward blue values of the scale. Voltage values in between electrode locations were interpolated using splines. The topographies are plotted from a bird's eye perspective. The anterior scalp is shown on the top and the right scalp is shown on the right side.

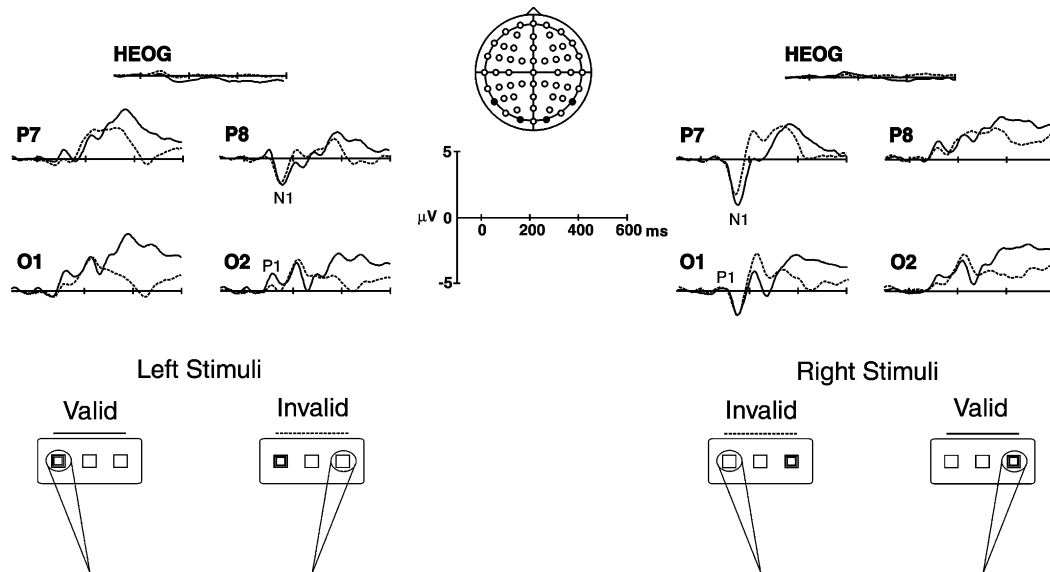


Fig. 4. Modulation of peripheral stimuli by spatial attention in Experiment 1. Grand-averaged ERPs elicited by LVF stimuli (left panel) and RVF stimuli (right panel) under focused peripheral attention conditions at posterior lateral sites where the visual components (P1 and N1) were largest. P1 and N1 visual components were enhanced when attention was focused on the relevant stimulus location. Later components (Nd2 and P3) were also enhanced (not shown).

toward peripheral locations. The late positive P3 component was greatly enhanced to the foveal stimuli that were attended [$F(1.3, 14.4) = 10.14, P < 0.05$]. The effect was maximal over the midline parietal region, as indicated by an attention \times electrode interaction [$F(1.8, 19.6) = 16.82, P < 0.05$].

Fig. 3b shows the scalp distributions of the multiple effects of selective spatial attention upon the ERPs elicited by foveal stimuli—N1, Nd2 and P3. The asymmetry of the N1 modulation by the direction of attention can be clearly observed. Compared to RVF attention, foveal attention resulted in bilateral enhancement of the N1 component that was more prominent over the left hemisphere. Compared to LVF attention, foveal attention resulted in a more focal modulation of N1, restricted to the contralateral, right hemisphere. The other effects were symmetrically located over midline regions. The Nd2 was maximal over CZ–FCZ. The P3 effect was maximal over PZ.

3.1.3. Effects of spatial attention on ERPs to peripheral stimuli

Peripheral stimuli were not of primary interest, and only restricted analyses of their ERP components were performed according to direction of peripheral attention (LVF and RVF). The results (Fig. 4) replicated well-established previous findings. The visual P1 component elicited by attended stimuli was relatively enhanced [$F(1, 11) = 5.05, P < 0.05$]. There was no main effect of stimulus location or interaction between direction of attention and stimulus location. The visual N1 component was also enhanced by selective spatial attention. The effect was sharply dis-

tributed over the lateral posterior electrodes (largest over P7/8), and appeared as an interaction between attention and electrode [$F(2, 22) = 12.68, P < 0.05$]. Mid-latency Nd2 and long-latency P3 effects were also replicated [F 's $> 15, P < 0.05$].

3.2. Experiment 2

3.2.1. Behavioral results

Target detection was accurate overall (90%) and was not influenced by whether attention was spatially focused at one location or divided between all three locations. Target location also did not affect significantly performance accuracy. Analysis of RTs (Fig. 5) showed participants were consistently faster to detect stimuli in *focused* attention conditions than in *divided* attention conditions [$F(1, 11) = 5.40, P < 0.05$]. The advantage was also significant when RTs to foveal targets in *focused* and *divided* attention conditions were tested directly {post-hoc comparison of means [$F(1, 11) = 5.40, P < 0.05$]}. The advantage approached significance also for left targets [$F(1, 11) = 4.24, P = 0.06$], but not for right targets [$F(1, 11) = 1.50, P = 0.25$]. Target location did not influence the RTs significantly and did not interact with the effect of attention condition. The lack of significant effects of target location on accuracy or RTs showed that difficulty of detecting foveal versus peripheral targets was well equated for the group of participants. As in Experiment 1, significant modulation of foveal targets by selective attention afforded the ERP investigation of the underlying brain mechanisms.

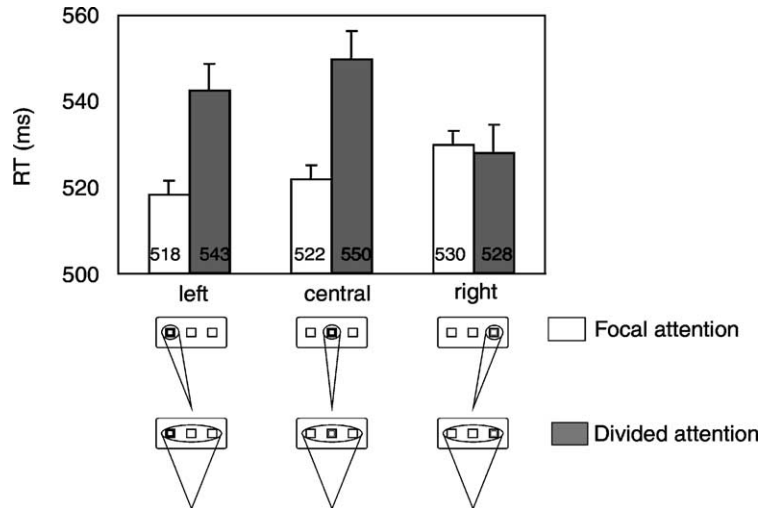


Fig. 5. Behavioral results from Experiment 2. The graph shows mean RTs and standard errors to detect target stimuli in the *focused* and *divided* attention conditions, at LVF, foveal, and RVF locations.

3.2.2. Modulation of ERPs to foveal stimuli by the direction of focused spatial attention

The effects obtained in Experiment 1 were tested with ANOVAs using mean amplitude measures of P1, N1, Nd2 and P3 components as dependent variables. Separate analyses were performed for foveal and peripheral standard stimuli. A total of 18% of EEG epochs were excluded from analysis because of behavioral errors, EEG artifacts or deviations of eye gaze.

Fig. 6 shows grand-averaged ERPs elicited by foveal stimuli at representative lateral posterior electrodes (PO7/8) where both visual potentials (P1, N1) can be seen, and at midline electrodes CZ where midline effects (Nd2, P3) can be seen. The direction of *focused* attention to detect targets defined by shape had significant effects on the processing of foveal stimuli, starting from the N1 visual component.

As in Experiment 1, the P1 visual component appeared larger bilaterally when attention was directed foveally,

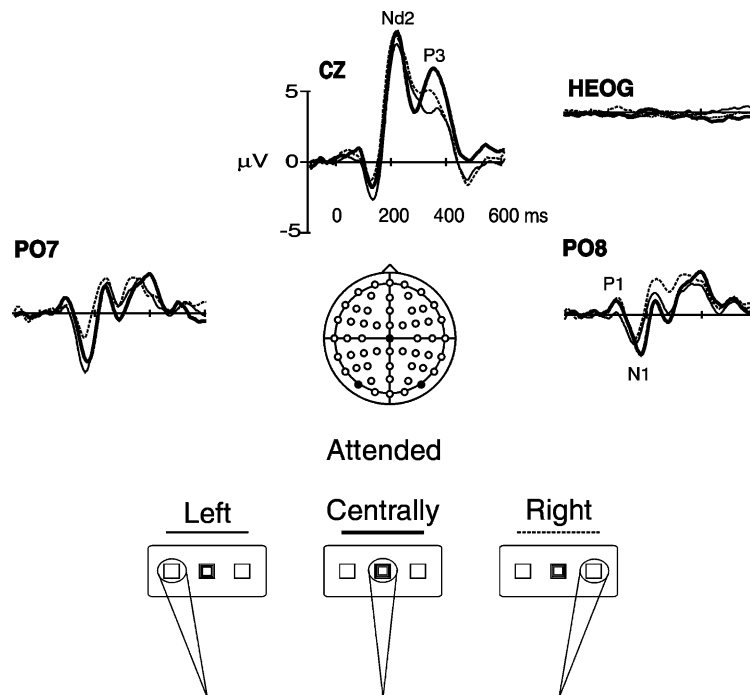


Fig. 6. Modulation of foveal stimuli by the direction of focused spatial attention in Experiment 2. Grand-averaged ERPs elicited by foveal stimuli under the three directions of *focused* attention at representative posterior lateral and midline sites. The N1 modulation showed a similar pattern of hemisphere asymmetry observed in Experiment 1. Nd2 and P3 modulations similar to those in Experiment 1 were also observed.

but the effect did not reach statistical significance [$F(1.8, 23.1) = 2.86, P = 0.08$].

N1 enhancement by attention and its hemispheric asymmetry were replicated. When all three directions of attention were tested together (LVF, foveal, RVF), the factor of attention exerted a significant effect on N1 amplitude [$F(1.7, 22.1) = 10.91, P = 0.001$]. The effect interacted significantly with hemisphere [$F(1.7, 22.6) = 9.54, P = 0.001$] and with both hemisphere and electrode site [$F(2.7, 34.5) = 5.39, P < 0.05$].

Directed post-hoc comparisons between pairs of attention conditions showed a similar pattern of results as in Experiment 1. The contrast between LVF and RVF attention revealed a main effect of attention [$F(1, 13) = 13.42, P < 0.05$] and interactions between attention and hemisphere [$F(1, 13) = 15.78, P < 0.05$] and between attention, hemisphere and electrode [$F(1.7, 22.6) = 14.03, P < 0.001$]. The effects of attention directed toward the LVF and RVF were larger in the left hemisphere. The contrast between foveal and RVF attention also revealed a main effect of attention [$F(1, 13) = 13.70, P < 0.05$], which did not interact with hemisphere or electrode site. Effects of attention occurred over both hemispheres. The contrast between foveal and LVF attention revealed only an interaction between attention and hemisphere [$F(1, 13) = 7.96, P < 0.05$]. The three-way interaction between attention, hemisphere and electrode site approached significance [$F(1.9, 24.9) = 2.86, P = 0.08$]. The modulation was restricted to right

hemisphere sites, and tended to be largest over the PO8 electrode.

The mid-latency Nd2 showed the same pattern of modulation as in Experiment 1, but it was not statistically reliable. The long-latency positive P3 component was significantly enhanced when attention was directed toward the foveal stimuli. The effect was maximal over the parietal region, as indicated by an interaction between attention and electrode [$F(1.5, 19.2) = 6.01, P < 0.05$].

3.2.3. Modulation of ERPs to foveal stimuli by focused versus divided spatial attention

Comparison of ERPs elicited by attended foveal stimuli in the *focused* attention condition versus in the *divided* attention condition also showed significant modulation of the processing of foveal stimuli starting from early perceptual analysis (Fig. 7). In this case, the earliest visual component tested, P1, showed significant enhancement by directed *focused* attention [$F(1, 13) = 9.14, P < 0.05$]. The effect was bilateral, and tended to be largest at the PO7/8 sites [interaction between attention and electrode: $F(1.8, 22.9) = 3.39, P = 0.06$]. The N1 was also larger for foveal stimuli in the *focused* attention condition, but the effect just failed to reach statistical significance [main effect of attention: $F(1, 13) = 6.07, P = 0.06$; interaction between attention and electrode: $F(1.5, 19.3) = 3.07, P = 0.08$]. There was no significant effect on the Nd2 component. Late positive activity in the P3 time range was significantly enhanced over the frontal scalp

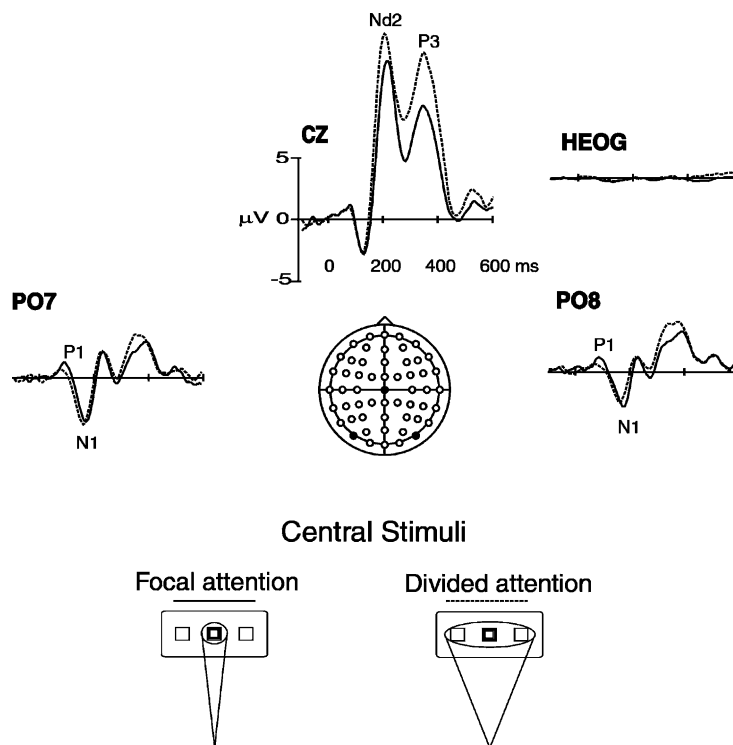


Fig. 7. Modulation of foveal stimuli by focused versus divided spatial attention in Experiment 2. Grand-averaged ERPs elicited by foveal stimuli under *focused* attention and *divided* attention at representative posterior lateral and midline sites. The P1 showed reliable and symmetrical enhancement during *focused* attention. The late P3 component was enhanced during *divided* attention, and had a frontal distribution.

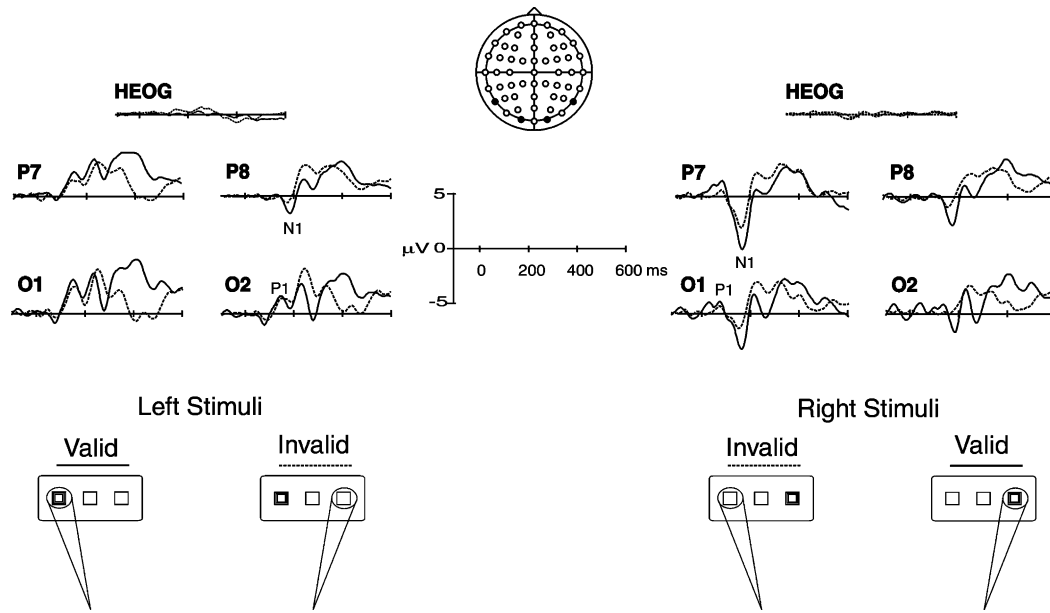


Fig. 8. Modulation of peripheral stimuli by spatial attention in Experiment 2. Grand-averaged ERPs elicited by LVF stimuli (left panel) and RVF stimuli (right panel) under focused peripheral attention conditions at posterior lateral sites where the visual components (P1 and N1) were largest. The N1 visual component was enhanced when attention was focused on the relevant stimulus location. Later components (Nd2 and P3) were also enhanced (not shown).

when attention was divided between the three locations compared to when it was focused on the fovea [interaction between attention and electrode: $F(1.1, 14.1) = 4.56$, $P < 0.05$].

3.2.4. Modulation of ERPs to peripheral stimuli by the direction of focused spatial attention

In agreement with previous studies and the results from Experiment 1, visual and later components elicited by peripheral stimuli were modulated according to the direction of peripheral attention (LVF and RVF) (Fig. 8). Visual modulation by the direction of attention started at the N1 component [$F(1, 13) = 10.26$, $P < 0.05$]. The effects of attention were larger contralaterally and over electrode sites PO7/8, as revealed by interactions between stimulus location, direction of attention and hemisphere [$F(1, 13) = 11.16$, $P < 0.05$] and between stimulus location, direction of attention, hemisphere and electrode [$F(1.5, 19.1) = 4.52$, $P < 0.05$]. Later Nd2 and P3 components both showed effects of attention that interacted with electrode site [$F > 4.75$, $P < 0.05$].

In order to examine more closely the possibility of differential lateralization of attentional effects upon the visual N1 component, the attention effects were examined for left and right stimuli separately. For RVF stimuli, there was a main effect of direction of attention [$F(1, 13) = 10.46$, $P < 0.05$] as well as an interaction between direction of attention and hemisphere [$F(1, 13) = 5.22$, $P < 0.05$]. The effect was bilateral, though larger over the left hemisphere. For LVF stimuli, there was no main effect of direction of attention, but there were significant interactions between direction of attention and hemisphere [$F(1, 13) = 10.26$,

$P < 0.05$] and direction of attention, hemisphere and electrode site [$F(2.0, 22.5) = 4.19$, $P < 0.05$]. Attentional modulation was restricted to the right hemisphere and was larger over the electrode sites P8 and PO8.

4. Discussion

The results clearly demonstrate that attention can modulate visual analysis of stimuli at the center of gaze. Over and above the inherent advantage conferred by foveation of central stimuli, their processing can be strongly influenced by focused spatial attention. In both experiments, the detection of visual targets was significantly speeded when participants focused on the center of gaze compared to when they spread their attention across central and peripheral locations. The stimuli in the tasks were clearly visible, and did not place special demands for identification. Therefore, selective attention appears to contribute to the processing of central stimuli even in the case of suprathreshold stimuli in fairly easy tasks. In the present study, measures of accuracy did not differentiate the detection of central stimuli under different attentional conditions. However, it is possible that under more visually challenging conditions, selective attention may change signal detection parameters [12]. It will be important to replicate the behavioral effects of selective attention upon central stimuli using various stimulation parameters and task requirements.

Recordings of ERPs revealed that the mechanisms for the behavioral optimization include the modulation of visual analysis. In both Experiments 1 and 2, *focused* attention to

the center of gaze was compared to attention directed toward peripheral locations. The results were consistent across experiments. The visual N1 component was strongly affected. In Experiment 2, it was also possible to compare the processing of foveal stimuli when attention was focused at the center of gaze directly versus when attention was divided between all three locations. *Focused* attention enhanced visual processing starting from the earlier stage reflected by the visual P1 potential.

Longer-latency effects of spatial attention were also observed, suggesting multiple actions of spatial attention upon the processing of foveal stimuli. Attended versus ignored foveal stimuli in *focused* attention conditions showed similar modulation to those previously reported for peripheral stimuli. Attended stimuli elicited enhanced potentials hypothesized to reflect modality non-specific selection (Nd2) [7] and decision- and response-related functions (P3) [21,36]. Attended foveal stimuli in *focused* versus *divided* attention conditions did not differ in the Nd2 component. The late positive P3 was larger in the *divided* attention condition, and had a maximal distribution over frontal electrode sites, perhaps reflecting the greater resources engaged in the *divided* attention condition.

Our results therefore replicated the findings by Neville and Lawson [27–29]. Foveal stimuli can clearly be modulated by visual spatial attention. The present results showed that the findings generalize to clearly visible and non-moving stimuli under different target-detection tasks. The ERP findings also enhance the interpretation of findings from brain imaging studies [34], showing that attentional modulations can be specific to the foveal stimuli and can occur early, probably in the bottom-up direction of visual processing.

Unexpectedly, the perceptual (N1) modulation of foveal stimuli when attention was focused at the center of gaze compared to when attention was focused at peripheral locations showed an intriguing pattern of hemispheric asymmetry, consistent across both experiments. Foveal attention enhanced the N1 bilaterally compared to when attention was focused on the RVF; whereas it enhanced the N1 on the right hemisphere only compared to when attention was focused on the LVF (Figs. 3a and b, and 6).

These findings extend the current notions of the right hemisphere dominance for the neural system of visual spatial attention [13,18,25]. In addition to a right hemisphere bias to the critical neural system that directs attention to spatial locations, which has been visualized by brain imaging studies [4,8], the present results suggest that there may also be an asymmetrical consequence upon the perceptual analysis of incoming foveal stimuli.

Artifacts from eye movements or direction of gaze do not account for this striking pattern of hemispheric asymmetry in N1 modulation. Eye movement and eye position were measured as well as possible within the limits of non-invasive ERP experiments. Direction of gaze was measured using a high-quality video infrared tracking system. The average location of gaze was analyzed for each participant and each

condition of attention. There were no systematic differences in gaze position (Fig. 2b). The EOG was examined on a trial-by-trial basis and used to discard trials with saccades or blinks. No differences in EOG across attentional conditions were obtained.

In both experiments, the behavioral effects also showed asymmetry. Effects of selective attention were larger for foveal and left stimuli than right stimuli. Detection of right stimuli was overall faster than detection of left stimuli, but showed less modulation by attention. The lateralization of the N1 effects could be directly tied to these behavioral effects.

Additional studies will be required to evaluate whether this intriguing pattern of hemispheric specialization is a general phenomenon. Especially important will be to vary the nature of the target-detection task, since any hemispheric laterality inherent in processing the relevant target attributes could affect the laterality of the attentional effects. The same pattern of asymmetrical modulation occurred in the two experiments, despite the differences in the target attributes. The target-detection tasks differed considerably in the two current experiments. In Experiment 1, participants discriminated the temporal duration of stimuli in order to identify targets. This additional background “attention” to time intervals may itself involve a left hemisphere bias in processing [5,6], which may have interacted with the spatial attention mechanisms at play. However, a similar pattern of lateralization was obtained when participants judged the visual appearance of peripheral stimuli in Experiment 2, which is not thought to involve left-lateralized brain activity.

Asymmetric attentional modulation of visual processing of foveal stimuli could be either inherent to the mechanisms of focusing attention at the center of gaze, or could be general to mechanisms of focused spatial attention. If the hemispheric bias were inherent to attending the foveal space, there would be no special predictions about the laterality of the attentional effects upon peripheral stimuli. If, however, the hemispheric bias reflected a general mechanism, it should also be observable in the attentional modulation of peripheral stimuli. However, the expected pattern of lateralization for peripheral stimuli may be difficult to predict. The attentional asymmetries are likely to be relative in nature, and to interact with the underlying lateralization of peripheral visual processing. So far, no consistent pattern of hemispheric lateralization for attention to peripheral stimuli has emerged from the literature, and nor did it occur in the present data sets. Visual modulations are typically more pronounced contralaterally [21], and this was also the case for N1 modulation in the present study.

Knowledge about the neural and functional underpinnings of the posterior N1 component would greatly facilitate the interpretation of the visual modulations observed. However, the N1 is likely to reflect the summation of concurrent activity in multiple extrastriate areas [1,2,9] that may be performing diverse sensory, sensorimotor or attentional computations. Nevertheless, functional interpre-

tations of N1 effects during tasks of selective attention have been attempted. For example, the N1 has been suggested to reflect stimulus-triggered orienting and engagement of attention at the relevant location [20]. Some support for this interpretation comes from studies of visual spatial orienting that compare ERPs to cues that build spatial expectations [11,31,37]. If true, this might suggest preferential participation and modulation of areas of the dorsal visual-processing stream [10,35]. N1 modulation in the present task would indicate that the bright brief stimuli automatically summoned attention even when they were irrelevant to task performance, and that these transient effects interacted with the sustained attention mechanisms at play. However, the relationship between N1 and automatic attentional orienting has been challenged [14]. It is likely that modulations in components like the N1, which reflect integrated activity in multiple brain areas, can arise from effects within selective participating neural generators. N1 modulation may thus reflect influences upon different neural and cognitive mechanisms, depending on the task.

Further work will be required to isolate the specific aspects of visual processing that showed modulation in the present experiment. The precise brain areas in which the modulations occur, and the cellular mechanisms of the effects should benefit from further experimentation using complementary brain imaging and single-unit methodologies.

Acknowledgements

The research was supported by a project grant provided by the Wellcome Trust to ACN. We thank Ivan Griffin for critical feedback on the manuscript and Patrizio Pasqualetti for statistical advice.

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